THE ECOLOGY AND SOCIOLOGY OF THE

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NORWAY RAT

U.S. DEPARTMENT OF HEALTH, EDUCATION, AND WELFARE • Public Health Service

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Dr. Calhoun is a member of the Laboratory of Psychology of the National Institute of Mental Health, National Institutes of Health, U.S. Public Health Service, Bethesda, Md. This report is based upon a study conducted under the auspices of the Johns Hopkins University School of Hygiene and Public Health. Analysis of the data and preparation of this report were made possible by facilities made available by the Walter Reed Army Medical Center and the National Institutes of Health. Dr. Calhoun's basic training is in ecology. Since 1949 his close association with psychologists, psychiatrists and sociologists has led him to orient his studies to provide insights relevant to concepts and problems in these disciplines. This report and these associations led to more precise experimental studies of social behavior among animals. The general conclusions of these studies, conducted at the National Institutes of Health between 1955 and 1962, are presented in reference (97) and in the February 1962 issue of Scientific American.

FOREWORD

THIS STUDY describes the way of life of the Norway rat observed over a 27 month period in a quarter-acre enclosure in which environmental conditions simulated those characterizing this species in its native haunts. Typically, this species lives in close relationship with man (*4, 5, 25, 26, 28, 29, 31, 67, 88*). The present report comprises a small segment of a broader program of investigation into the biology of this species and its relationship to man contributed to by a number of workers at the Johns Hopkins University (e.g., *3, 4, 5, 6, 8, 9, 22, 23, 25, 26, 28, 34, 35, 66, 68, 84, 88*). Among these investigators, I am particularly indebted to Drs. Curt P. Richter, John T. Emlen, Jr., David E. Davis, and Allen W. Stokes. Had it not been for the insights and techniques developed by them, the formulation and conduct of the present study would have been much less effective.

Their studies were conducted in various habitats, such as on farms, or surrounding human habitations where Norway rats normally occur. Under these circumstances rats may be trapped, marked, and recaptured, but normally great difficulty is experienced in following the history of any particular individual throughout its life. It is even more difficult to observe the behavioral relationships among known individuals in most situations where rats maintain a commensal relationship to man. In order to circumvent this difficulty I established a few rats in a quarter-acre enclosure. From a single successfully reproducing female there developed a total population of over 200 individuals spanning four generations during the 27 months of study.

Every rat was trapped and handled on many occasions. In addition every individual was marked by removing small spots of fur with a depilatory. This marking enabled observation of the behavior of the rats from a tower constructed outside the enclosure. Such observation permitted the accumulation of a large body of information regarding relationships among the members of the enclosed population. At the termination of this study I decided that its value lay in a detailed examination of all these relationships. This proved a more difficult and time consuming task than anticipated. During the next few years, following the termination of the study by June 1949, my superiors at three institutions provided me with the opportunity and facilities for making the necessary detailed analyses reported here. In this connection I am greatly indebted to the following persons and institutions:

1. Dr. J. P. Scott and the Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.
2. Dr. David McK. Rioch and the Walter Reed Army Institute of Research, Washington, D.C.
3. Dr. David Shakow and the National Institute of Mental Health, Bethesda, Md.

My objective in this report has simply been to describe the results derived from the 27 months' observation of this enclosed population. Although I have found it useful to coordinate certain data reported in the literature with my observations, no attempt has been made to evaluate all literature relevant to the ecology and sociology of the Norway rat. I have viewed this study as an opportunity to seek useful concepts, whose validation certainly requires further investigation. To this end I have frequently searched for implications beyond those definitely substantiated by the recorded observations. During the years since completion of this study I followed up some of the leads suggested by it (*16, 91, 100, 101, 102*).

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PRE-PUBLICATION STATEMENT

PREPARATION OF THE manuscript in a form suitable for publication from the original text completed in 1956 has been attended by delays causing a lapse of 6 years from completion of the manuscript to its publication. For this reason references to pertinent literature omit consideration of a number of important papers since 1955. However, in view of the fact that the main intent of this report is simply to present the results of the study, it has been considered advisable to present this report in its present form. Evaluation of this study, as well as later ones conducted by me at the National Institutes of Health, in the light of more recent studies by others has been included in other papers I have recently published, or which are in preparation.

JOHN B. CALHOUN
Sept. 12, 1962

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ORIGIN AND AIMS OF THE STUDY

1. *General Background*

Dr. Curt P. Richter (*1*) showed that rats are capable of choosing nutritive substances and avoiding harmful ones. One of his hypotheses was that there was a relationship between the taste of substances and their nutritive value. While investigating this hypothesis he (*2*) found that phenyl thiourea was lethal to rats in minute quantities. Although domesticated rats normally took sufficient food containing phenyl thiourea to be lethal, field tests on wild populations of rats were unsatisfactory in producing significant kills. Wild-caught rats transported to the laboratory demonstrated marked ability to avoid food containing phenyl thiourea, choosing, instead, un-poisoned food. There followed a search for a toxic thiourea derivative which lacked the bitter taste of phenyl thiourea. The result of this search led to the selection of Alpha-Napthyl Thio-Urea (ANTU) as a suitable rodenticide. These in-vestigations occurred at the beginning of World War II when the normal sources of several pre-viously proven rodenticides were cut off.

There developed a cooperative program of rat control and research between the city of Baltimore and the Johns Hopkins University (*3*). In the normal course of block by block treatment with ANTU, 50 to 85 percent reductions were regularly obtained. Depending upon the extent of reduc-tion of the original population, recovery to the prepoisoning level took between 15 and 44 months (*4*). This necessitated repeated applications of ANTU poison. It soon became apparent that, whereas poisons played an integral part in rat control, they were no panacea. The continued support of the International Health Division of the Rockefeller Foundation to the Johns Hopkins

School of Hygiene and Public Health enabled a broad approach to the problem. As a result, mainly through the efforts of Dr. David E. Davis, the emphasis of technical procedures in rat control turned from poisons to environmental control. The understanding of the philosophy underlying this shift in the emphasis requires an appreciation of the rat (*Rattus norvegicus*) as an organism. We must understand how they manage to live in close association with others of their kind; and how as individuals or as groups conditions of the environ-ment modify the satisfaction of those basic require-ments necessary to survival.

The study presented in this publication attempts to provide this understanding. In addition, the findings will point to the usefulness of the rat in investigating other topics which have little or no relationship to the problem of rat control. The author was given complete freedom to make such investigations as he thought would be most productive in revealing the nature of the rat's biology. At the time he joined the staff of the Rodent Ecology Project, there was one fact amply documented by Drs. John T. Emlen, Jr., and David E. Davis and Mr. Allen W. Stokes. This was that each city block where rats were poisoned would, following termination of poisoning, ulti-mately arrive at a stable population level closely approximating its original prepoisoning level. This posed the general problem of why the popula-tions leveled off, and furthermore, why two blocks of approximately the same size would have different stable levels or carrying capacities.

As an initial probing into this problem the author (*5*) introduced into a stable population a number of alien rats caught from distant blocks. The number of aliens was approximately 65 percent of that of the resident population. Following

1

this introduction considerable dislocation of the population occurred. This affected both the residents and the introduced members. Rats of both groups invaded yards where previously they had not been observed. Under these conditions of disruption of normal population equilibrium there was an increase in mortality in both groups, but the mortality rate for the aliens was approximately three times that of the residents. Emigration from the block was negligible. These observations suggested a negative correlation between the degree of stability of social relationships and the mortality rate. Under these conditions of unusual disruption of social relationships, mortality appeared to be due primarily to increased exposure to predation by man and dogs. However, the previous experience of the various workers in the Rodent Ecology Project had led to the impression that predation by dogs and cats and the sporadic attacks by the resident human population did not appreciably affect the density of the rat population. Although we had no quantitative data on this point, this conclusion was arrived at through the general observation that city blocks supporting high densities of dogs and semiferal cats frequently also supported a high population of rats. One other general observation was pertinent to the formulation of the hypothesis. This was that many blocks maintained a stable population without further increase even in the presence of a superabundance of food in open garbage containers and an excess of space, which was potentially suitable for the construction of burrows but which actually was never utilized.

These observations may be stated as premises:

1. Mortality rate increased with increases in the disruption of established social relationships.

2. Gross predation is an insignificant factor in the usual determination of the stable level of a rat population.

3. The growth of a population of rats will cease (reach the upper asymptote of the growth curve) even in the presence of a superabundance of food and an excess of potential harborage sites.

The hypothesis derived from these premises: The growth rate of a population will be inhibited in the absence of predation and in the presence of an excess of food and harborage. This inhibition arises through the social interaction among the members of the population with respect to the distribution of goals and barriers through the environment.

The genesis of this hypothesis is influenced by two sets of concepts in the field of ecology. First, it has long been recognized that social interaction through both cooperation and competition influences population density where either food or harborage or some other requisite aspect of the environment is limited. Second, the defense of territory will limit populations irrespective of the density dependent variables which may happen to be distributed through the territories. This latter situation has been somewhat overlooked, but its implication has recently been pointed out by Davis (6).

The exact methodology of executing an experimental study of a mammalian population presented quite a problem. It is obvious that one could not utilize the normal man-influenced environment in which the rat most characteristically occurs. In the first place, the physical configuration and distribution of objects through space is so highly irregular and changing as to preclude any hope of sorting out the influence of the variables. In addition, human interference in field studies of rats in the city situation often proves disconcerting. Even such a simple procedure as trapping, marking, and releasing rats meets with such obstacles as having someone kill them in the traps, release them, or move the traps about so as to defeat the original aims of the study. Investigation of the hypothesis necessitated construction of an artificial environment where at least some of the variables could be controlled. The space requirements posed problems of a magnitude not encountered by investigators in experimental population dynamics working with such insects as *Drosophila* or *Tribolium*. Also, I knew of no other experimental studies on the mammalian level where even the space requirements necessary to satisfy home range or territorial behavior were satisfied. Therefore, the structure of the experimental environment finally decided upon had to be made mostly on an empirical basis.

Although Norway rats accommodate to several types of human environments such as ships, warehouses, farms, and residential areas, it was decided to model the experimental environment after that encountered in the "row house" type of residential area (figs. 1 and 2) found through large sections of the city of Baltimore, Md. It has been within such a habitat that the majority of the Rodent Ecology Project research effort has been concentrated. Typ-

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Figure 1.—Typical backyard scene in the row-house area of Baltimore where the various members of the Rodent Ecology Project conducted many of their studies on the biology of the Norway rat.   Photograph by John T. Emlen, Jr.

ically, a "row house" block consists of a solid row of houses facing one street with the doors opening directly on the sidewalk.   Adjoining houses have a common sidewall.   The width of houses varies from about 16 to 25 feet and there are usually 14 to 20 units joined together.   Backyards are of similar width and extend from 20 to 60 feet in depth.   An alley runs through the center of the block.   Adjoining the alley on the other side are another series of backyards belonging to the row of houses facing a street on the opposite side of the block.   Occasionally there is also a small group of row houses at either end of a block.   Surrounding many of the yards there is a near-solid board fence approximately 6 feet high.   Through the fences there are occasional breaks due to broken or loose boards or where the rats have gnawed through or dug under. Fences are barriers which restrict movement through the block.   The major portion of the rats live out of doors.   Occasionally additional space becomes available to them in the basements or even in the house proper.   Protection from the weather and predators is also provided by garages, outhouses

of various types, outdoor toilets in some cases, and all sorts of miscellaneous junk.   At the time of the initial studies made by the Rodent Ecology Project ample food was available in practically every yard in open garbage containers which ranged from pasteboard boxes to 20-gallon galvanized garbage cans, which however lacked adequate covers.   In the early 1940's, at least, before the municipal program of environmental control had any effect, this description fits to varying degrees the habitat available to rats in substandard housing areas, as well as in those which were given a higher rating.

Due to the structure of the blocks each formed the limits of a single population.   There was little exchange of members between adjoining blocks. Even within a block there was considerable restriction of ranging by rats.   Studies of marking and release conducted by Emlen, Stokes, Davis, and myself have regularly shown that the population of a single block is composed of smaller aggregates or colonies.   Each has its own restricted home range, but there is some overlap in the space encompassed by the movements of members of adjoining colonies.

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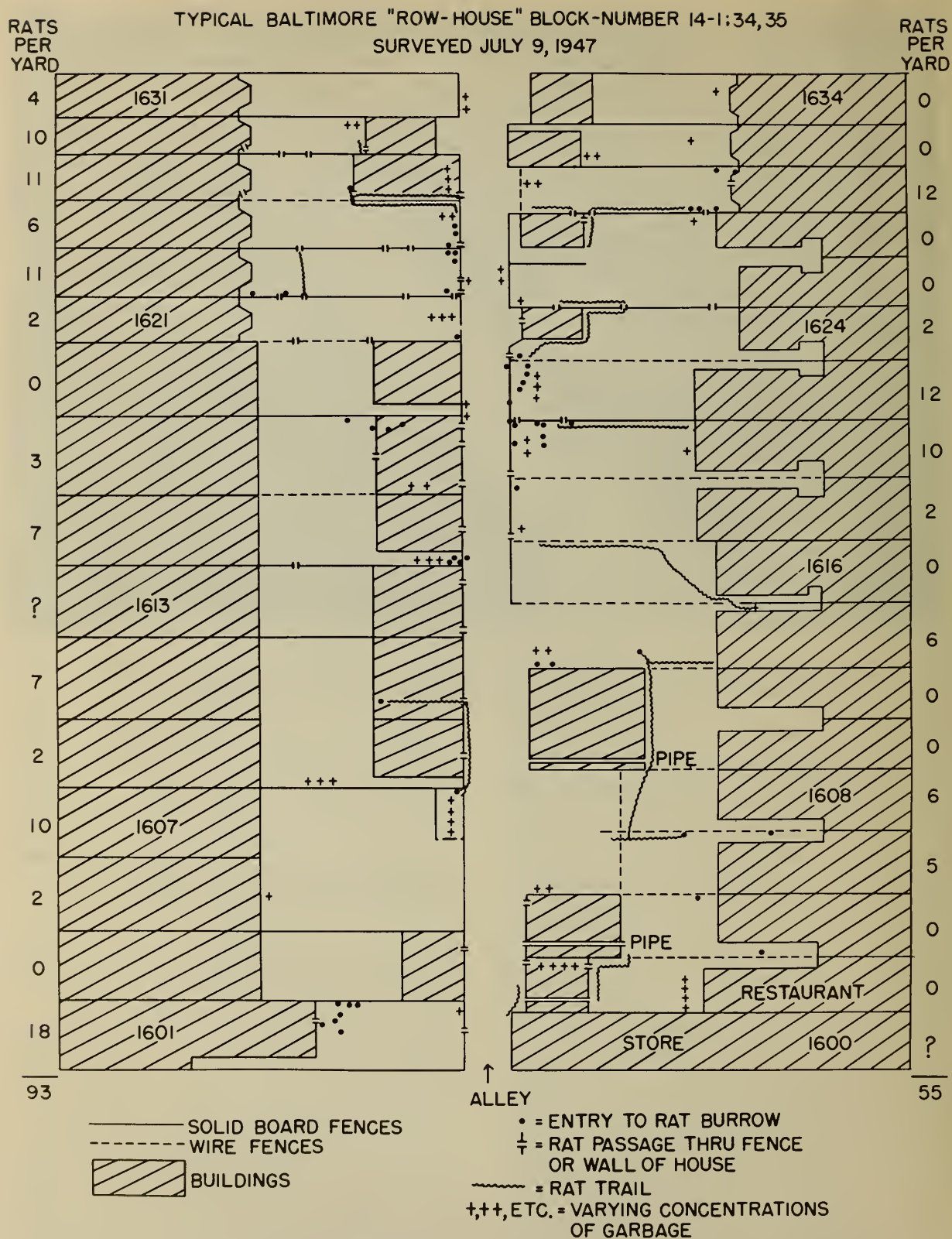
Figure 2.—The utilization of a typical Baltimore row-house block by rats.

2. *The Experimental Pen*

The following criteria were used in arriving at more exact details of the design of the pen and the establishment of the colony:

1. The pen should be large enough to accommodate several local colonies and yet at the same time be small enough that the observer from a tower could observe the rats at all points in the pen.
2. The pen should be enclosed by a barrier fence which would prevent the emigration of resident rats, or the migration into it by aliens.
3. Predation by vertebrate predators should be eliminated.
4. Food and water should be restricted to a single location accessible to rats living at all points in the pen.
5. Some artificial harborage should be provided, although the rats should have the opportunity to construct burrows at locations of their own selection.
6. Internal barriers with passages through them should be provided. This would enable the formation and delimitation of local colonies, while at the same time it would facilitate the observation of interactions among rats.
7. The rats to be introduced into the pen should be members of a wild population and yet be as nearly homozygous genetically as possible. This precaution was desirable in order to make more certain that such variability of data as might become evident would primarily be due to environmental conditions.

The manner in which these objectives were satisfied are mainly illustrated in figures 3, 4, and 5. The area enclosed by the pen was approximately one-quarter acre. In the city blocks the area available to rats ranges from ¼ to 1½ acre. However, since portions of yards are not available to rats, because of their use by man, the area in the experimental pen closely approximated the average amount available to rats in city "row house" blocks. A tower, whose floor was 20 feet above the ground, was placed on the southwest side of the pen. Although the behavior of rats on the half of the pen nearer the tower could be observed in more detail, it was still possible to identify individual rats at even the farthest points with the aid of 6-power binoculars.

The problem of preventing rats from escaping was solved by constructing a fence of hardware
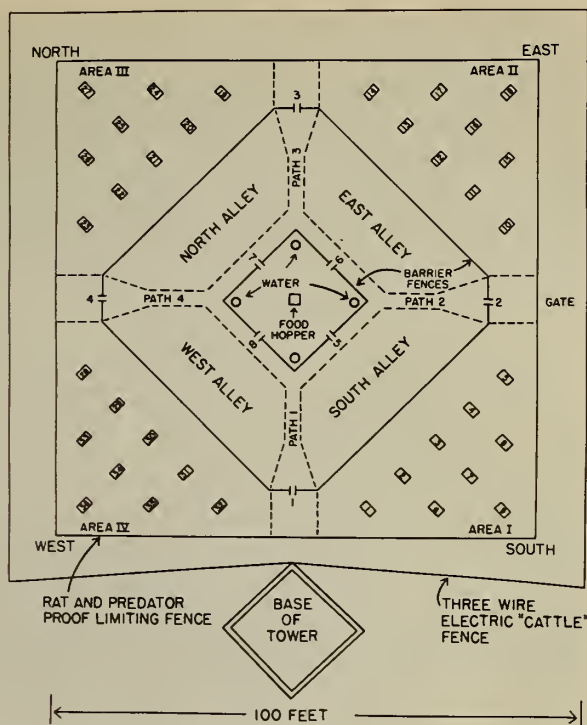
Figure 3.—Diagram of the experimental area. The numbered rectangles in each of the corner areas represent the positions of the sunken wooden harborage boxes. The dashed lines enclose paths or areas, which were maintained free of vegetation. The eight passages through the barrier fences are referred to in the text as here numbered.

cloth (fig. 6) which extended 4 feet above the ground and 2 feet underground. In addition, the underground portion of the fence had a 2-foot shelf of hardware cloth extending out into the pen at a depth of 2 feet. Thus, when the rats burrowed down, they would strike this shelf. No rats ever surmounted this underground baffle although a few dug down that far on very rare occasions. At the top of the 4 feet of fence above ground there was an 18-inch overhang sloping downward, which was sheathed with "screen glass". This is window screen with the space between the meshes filled with a clear plastic. Actually very few rats ever climbed this high since a wire carrying a high voltage, as used on cattle fences, was placed a few inches above the ground on the inside surface of the fence. Rats soon learned not to climb fences.

The problem of eliminating predators was not quite so simple but it was effectively solved. Posts supporting the limiting fence were placed at 10-foot intervals. On the top of each and at the base of each a steel trap was left permanently set. Forty-nine predators were removed during the 27 months of the study: barred owls (*3*), great-horned owls

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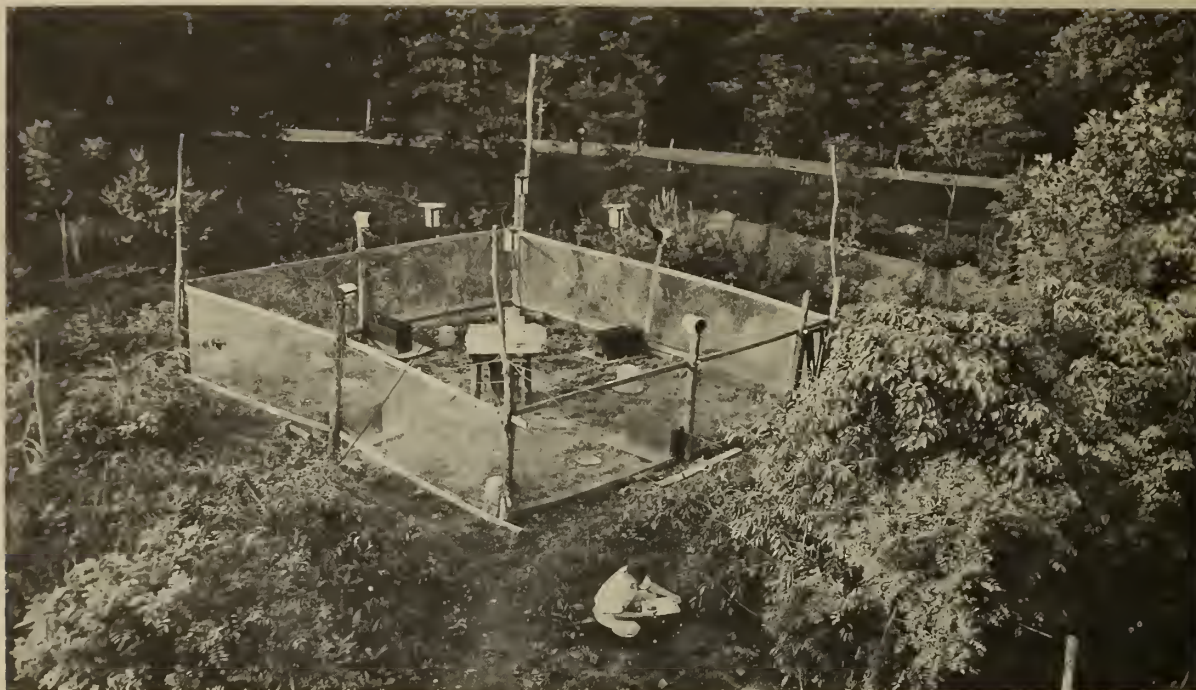
Figure 4.—View of the pen in late April 1948 looking northeast from the observation tower. The South Alley Burrow is located just to the right of where the observer is taking notes. At the four entrances to the Food Pen in the center are placed the activity recorders in the black tunnel boxes. Photograph by F. Di Gennaro.

(2), screech owls (9), sharp-shinned hawks (3), broad-winged hawk (1), skunks (13), opossums (15), weasels (3). Since the avian predators normally alight on the posts rather than fly directly in, no loss was attributed to them other than by the great-horned owls which would fly directly into the Food Pen. Probably five rats were lost to them before this problem was solved by placing traps on top of 12-foot poles surrounding the Food Pen. An opossum managed to get over in the pen during the summer of 1948 and was in for several days before being detected. It was a young animal and the evidence was that it may have destroyed one or two litters of unweaned rats. The three-strand electrified barrier fence, 10 feet peripheral to the main rat-proof fence, effectively kept dogs away. Initially cats were quite a problem although there was no evidence that any rats were killed by them. At first there was only a single strand of electrified wire on top of the fence. One day a cat was observed to make a leap from the ground over the top of the 4-foot fence, and over the electrified wire immediately on top of it, and land on the overhang from which it jumped into the pen. Following that incident three more strands of electrified wire were placed on top of

this fence. This effectively eliminated disturbance by cats (see fig. 6).

A hopper which provided a continuously available source of Purina laboratory pellets was placed directly in the center of the pen. Here 10 to 15 rats could obtain food simultaneously without crowding. The Food Pen was surrounded by a barrier fence through which there was a 3-inch diameter opening in the center of each of the four sides. This pen was 20 feet in diameter. A single water fountain was placed in each corner of the Food Pen. These were 2½ gallon chicken-watering-troughs around which it was possible for several rats to drink simultaneously. Food and water were continuously and abundantly available at this central location. Additional food in the form of garbage from the author's home or neighboring grocery stores was occasionally provided.

Nine artificial harborage boxes (figs. 7, 54, and 55) were placed in each of the four triangular corner areas of the pen. The center of each box was 10 feet from the center of adjacent ones. An 18-inch long and 3-inch diameter clay drain led from the surface of the ground down into each of of the boxes which were sunk into the ground. These 36 harborages were designated as boxes 1

Figure 5.—View of the pen from the tower in February 1949 looking toward the north corner.   Photograph by U.S. Army Signal Corps.

to 36 as shown in figure 3. Although the boxes were of 1-inch thick wood the removable tops were given further protection with a sheet of insulation board. The only place that rats were not allowed to dig burrows was in the Food Pen. These were regularly destroyed shortly after they were formed. Elsewhere in the pen burrows constructed by the rats were rarely disturbed.

The division of the pen into definite tracts which might affect the behavior of the rats was accomplished by the establishment of two internal barrier fences. The first was the fence forming the Food Pen. The second barrier fence was parallel to the first and 20 feet distant from it. As may be seen in figure 3, this latter barrier fence served to produce a band about the Food Pen 20 feet in width in which no artificial harborage was provided, while at the same time it separated off a triangular area in each corner of the main pen. A 3-inch

diameter passage was placed through this barrier fence at the points where the corner triangular areas adjoined. This system of barrier fences and passages through them provided for alternate equivalent-length routes of travel. A rat starting from the center of one of the triangular areas and going to the Food Pen could leave the triangular area through the passage at either the left or the right end of the base of the triangle formed by the barrier. At this passage the rat would find itself equidistant from two passages leading through the barrier fence into the Food Pen. The purpose of this provision for alternate choices in travel was that, in the eventuality of a passage being defended or blocked by one rat, a second rat approaching this passage would have an alternate route for attaining its goal. The goals in question at either end of the routes of travel were the source of food and the source of harborage.

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CROSS SECTION OF RAT AND PREDATOR PROOF
LIMITING FENCE
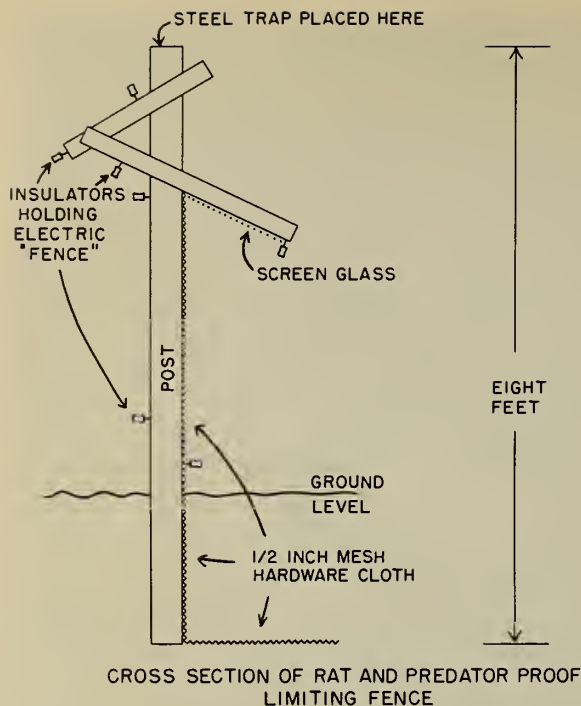
Figure 6.—Cross section of rat and predator-proof limiting fence. Both the overhanging screen glass shelf and the underground shelf of hardware cloth were directed into the pen.

In order to facilitate the systematic recording of data with reference to their place of occurrence, the following system as shown in figure 3 was devised. (1) The triangular areas were designated as Areas I to IV in a counterclockwise fashion starting with the south corner. (2) The passages through the outer of the two barrier fences were numbered from 1 to 4 in a counterclockwise fashion starting with the southwest passage between Areas I and IV. (3) The region between the Food Pen barrier fence and the second barrier fence was called the alley with the four segments of it being specifically called the South, East, North, and West Alleys. (4) The four passages through the Food Pen barrier fence were numbered from 5 to 8 in a counterclockwise fashion starting
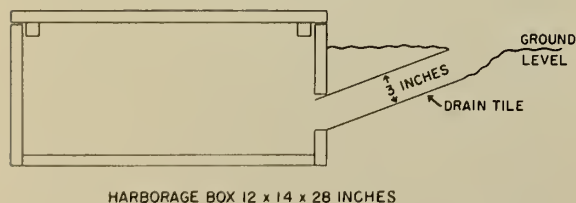
Figure 7.—Cross section diagram of the construction of the wooden harborage boxes.

with the south passage. (5) In order to facilitate observations the Food Pen was always kept clear of any plant growth. Likewise a 3-foot wide path was kept cleared around the outside of the Food Pen and from the corners of the Food Pen toward the passages through the second barrier fence. The limitations of these pathways are shown by dashed lines in figure 3. The paths were numbered from 1 to 4 in a counterclockwise fashion beginning with the southwest path.

3. *The Rats Introduced into the Pen*

The colony in the pen was begun with five pairs of rats (table 28; pp. 136–143), which were assumed to have been as genetically homozygous as it is possible to trap them in the wild state. This assumption is based on the following grounds. The rats were trapped in February 1947 on Parsons Island, a 150-acre tract in the Chesapeake Bay. A natural causeway connecting the island with the mainland was severed about 1900. Since this time the rats have been effectively isolated. The number of rats on the island has fluctuated widely both on an annual basis and on the basis of changes in agricultural practices. An experimental reduction by poison in 1923 was conducted by the Fish and Wildlife Service. A second experimental reduction was conducted in the spring of 1946 by J. T. Emlen and D. E. Davis, of the Rodent Ecology Project. Estimation of numbers: (a) prepoisoning, 670; (b) postpoisoning, 220. At the time of trapping in February 1947 surveys indicated that there were probably no more than 150 rats on the island. Under these circumstances of fluctuation in population size, it might be anticipated that considerable homozygosity would have been reached though gene drift (7). It is from this inference that variability of results in this paper are judged to arise from environmental conditions rather than from the hereditary variability among the rats.

4. *Objectives of the Investigation*

The central objective of the investigation was to determine the manner and extent to which social interactions might influence population growth. However, the nature of the experimental situation presented the opportunity for simultaneously investigating several subsidiary aspects of the biology of the rat. These include.

1. Growth and life span of the individual.
2. Reaction of the rats to the physical components of the environment.
   a. Orientation responses to those components of the environment which serve as cues.
   b. The effect of meteorological conditions and related factors which may alter intensity or periodicity of activity.
3. Investigation of population dynamics irrespective of the social factor.
4. Systematic recording of all types of behaviors and other variables with the expectation that these might lead to a better understanding of the rat as a species.

5. *Experimental Procedure and the Gathering of Data*

Once the colony was initiated, every effort was made to interfere as little as possible with the daily routine of life which the rats established. It was intended that such changes as might occur in the colony should be brought about by the activity of the rats themselves.

Observational techniques: The objective was established that, in so far as possible, all observations should pertain to known individuals and not to just rats in general. This required the permanent marking of individuals so that whenever handled each rat could be recognized, and it required the occasional marking of individuals so that they could be recognized at a distance without hampering their normal activities. The former was accomplished by inserting numbered light weight alloy fingerling fish tags in the ear lobes of the rats. It was found advisable to place a tag in each ear since occasionally the ear would become infected and the tag lost. Since two tags were rarely ever simultaneously lost, it was possible through this procedure to maintain a continuous identification of the individual. The tags utilized were obtained from the National Band and Tag Company, Newport, Ky. I have also used with success on other rodents similar tags produced by the Salt Lake Stamp Co., 43 West Broadway, Salt Lake City 1, Utah. The problem of sight identification was finally solved by using a commercial cosmetic depilatory, Nair. Spots of hair could be removed from the locations shown in figures 8 and 9. Sexes were differentiated by removing the hair from the top of the head on females. During the warmer months of the year, when the testes were descended into the scrotum,

PELAGE MARKING CODE
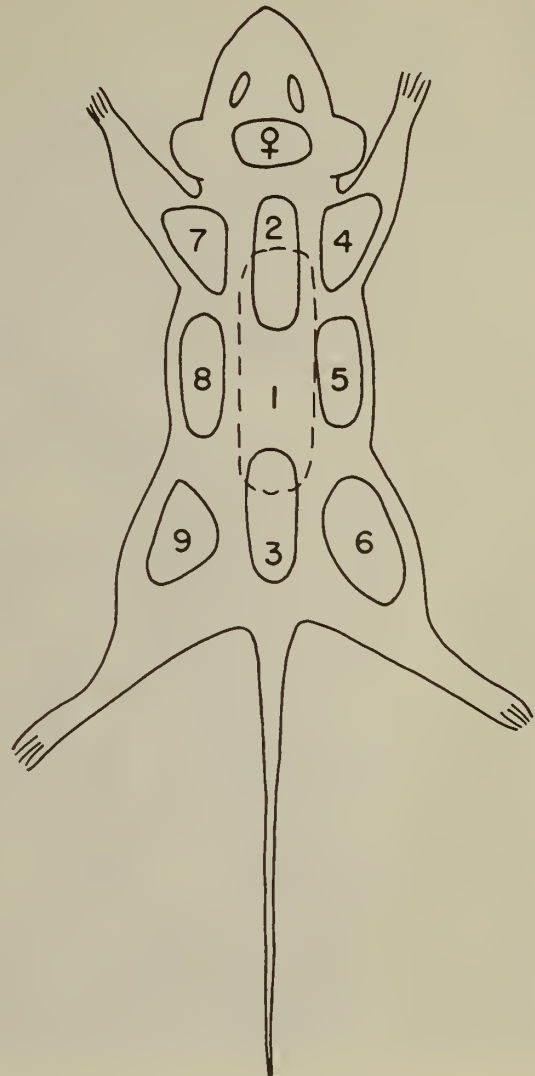
Figure 8.—Code for the pelage marking of rats. The pelage was removed from no more than two locations on a single rat. Sexes were indicated by removing a spot from the head of the female. See figure 9 as an example of marking.

males could be distinguished by this character irrespective of pelage marking. It was found advisable never to remove more than two spots on a single animal (other than on the head). This pelage marking system provided 43 combinations for each sex (table 1).

The rat is quite a nocturnal animal. This presented a problem in making adequate observations. Fortunately, there was considerable activity during at least the half-hour before sunset. Even after sunset there was sufficient light to permit

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Figure 9.—Example of pelage marking, male pelage code No. 18. This male is examining a burrow entrance through which a female in estrous has just passed. Rarely do males follow the estrous female into the burrow. Photograph by U.S. Army Signal Corps.

TABLE 1.—*The 43 pelage marking combinations possible when no more than two patches of fur are removed as shown in figure 8.*

1	14	15	16	17	18	19	
2	23	24	25	26	27	28	29
3	34	35	36	37	38	39	
4	45	46	47	48	49		
5	56	57	58	59			
6	67	68	69				
7	78	79					
8	89						
9							

observations for another half-hour or 45 minutes. A similar situation existed in relation to sunrise. Thus, it was possible to get some good observations during at least an hour and a half both in the early evening and at daybreak. Since the activity of the colony was initiated at least by 6 p.m. regardless of the time of sunset, the period available for observation was much longer during the warmer months of the year (see pp. 112–135). Observation during any time of the night was facilitated by suspending lamps in certain portions of the pen. Four 250-watt lamps were suspended over the

Food Pen, two over the burrow system which developed in the South Alley, and two which flooded Path 1 and portions of the West Alley. Practically all observations of free ranging rats were made from the tower just outside of the pen above the base of Path 1. The rats never appeared to be disturbed in the slightest by these lights. The use of a moving spot light had to be discontinued since it did disturb the rats sufficiently that they would cease their activities and enter their harborages. During April and part of May 1949, when the activities of the rats were filmed by the U.S. Army Signal Corps (8), it was possible to make rather extensive observations of rats at several places in the pen from blinds whose platforms were only 6 feet above the ground. At times there were as many as five 2,000-watt lamps flooding a rather limited area. After a short period of adjustment the rats would enter these brightly lighted areas without any hesitation and proceed with their normal activities.

Whenever any considerable noise accompanies the observation, it is necessary to drown it by broadcasting a continuous nonsense sound tract. This was found to be the effective solution of obscuring the distracting noises occurring at the time of the filming. Within a day or two after

first using this nonsense sound-tract broadcast, no further disturbance to the normal activities of the rat could be discerned.

About once every 6 weeks (see fig. 10) the attempt was made to capture every rat in the pen. The main device used in the capturing of the rats was a simple box trap (9) (fig. 31). The most effective baits used were sunflower seed, a horse-feed mixture (oats, cracked corn, and alfalfa impregnated with molasses), oranges cut in eights, garbage, and sections of sweet potato. The trapping usually was more effective when the bait was merely thrown into the back of the trap and not placed on the trigger. Rats were removed by allowing them to run into a cloth sack which was held over the opening to the trap as the door was removed. With adult rats it is best to elevate the trap by setting it on a neighboring trap. This allows the sack to hang downward, and the rats run into the sack. With juvenile rats it is frequently necessary to tilt the door end of the trap upward, while at the same time holding the attached sack also extending upward. The entering of the sack from the trap is an escape behavior which is positively geotropically oriented in adults, but negatively oriented in juveniles. During these periods of

TRAPPING PERIODS AND NUMBER OF RATS EXPOSED TO TRAPS
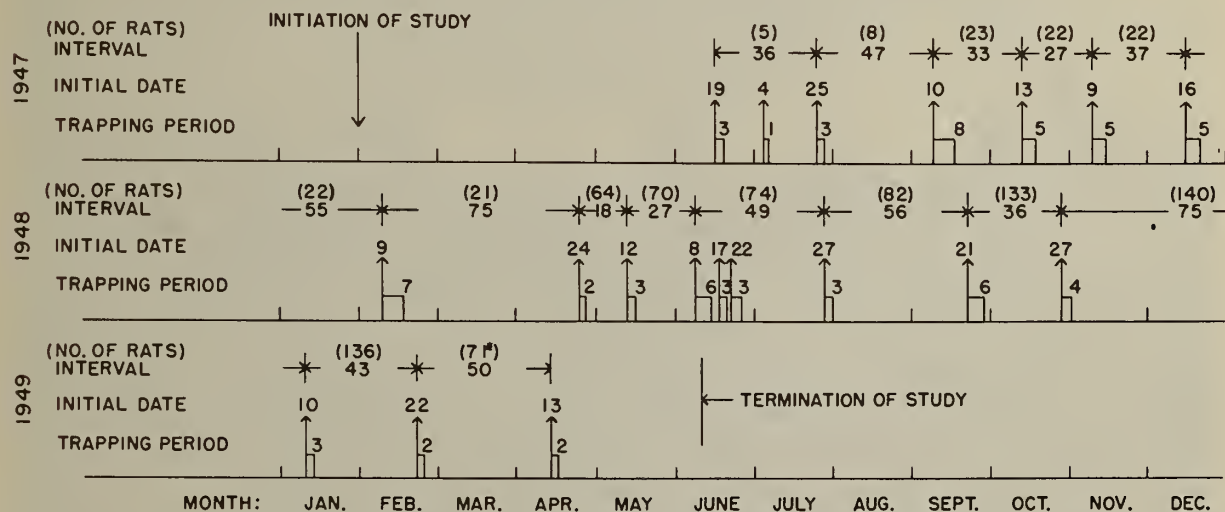
Figure 10.—Trapping periods* and number of rats exposed to traps. The number of rats exposed to traps was calculated as the number of rats 30 days or more of age at the beginning of one trapping period which lived through the following trapping period. This figure is shown in parenthesis above each trapping-period histogram. The interval in days between adjacent periods of trapping is indicated by the figures between the arrows. The duration of each trapping period in days is shown immediately to the right above the respective histograms.

*The April 1949 trapping period was the only time of trapping when all rats were not exposed to traps. At this time traps were set only in the north quadrant of the pen. It was estimated that only 60 percent of the 119 rats were exposed to these traps.

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capturing the rats, all individuals were also removed from the artificial harborages. This was done by placing a cloth sack over the end of the drain tile leading from the harborage box. Upon opening the lid of the box the rats usually ran out into the sack. The third technique utilized in capturing the rats was the excavation of burrows. A drain tile with a cloth sack attached was inserted into each exit from the burrow system (see fig. 11). Then the excavation of the burrow began at the center of the burrow system. As it was excavated, the open ends of tunnels were kept plugged with other cloth sacks. By this process the rats in a burrow system were gradually encouraged to leave. To do so necessitated their passage through the drain tiles into the attached sacks. This procedure was mainly resorted to only during the December–

January 1948–49 period and at the termination of the colony. The burrows in the alleys were only disturbed at the end of the study. While the rats were still in the sacks, each would be grasped just back of the head with the thumb and index finger of the right hand, while at the same time pressing its body down with the remainder of the hand. Then the left hand was inserted in the sack and a gradual exchange of the rat made from the right to the left hand. If one is careful, there is little danger in being bitten, even by the larger rats. When only identification of the rat was required it was immediately released, but if other observations were necessary, the rat was anesthetized before further handling.

Routine observations made usually included:

1. Weight in grams.

Figure 11.—Technique for capturing rats at the time of excavating burrows. Here the burrow emanated from the harborage box through a hole gnawed through its wall. Drain tiles with cloth sacks attached were inserted into each burrow exit. As the burrow is being excavated wads of cloth were inserted into the tunnels. Gradually the rats were forced to leave the burrow and enter the sacks as the tunnels were excavated.

2. Total length (tip of nose to tip of tail), and tail length in mm.
3. Sexual condition:
   a. For males: Whether or not the testes were descended into the scrotum.
   b. For females:
      Whether or not the vagina was perforated;
      Whether or not embryos could be palpated;
      The condition of the nipples.
4. The size and number of wounds.
5. The character of the pelage.
6. Date and location of capture.

Observations from the tower were kept chronologically. The contained data were transferred at a later date to cards (fig. 12) so that every observation pertaining to each individual rat was filed chronologically under its eartag number. The front of each card contained a list of some of the possible topics which might designate the behaviors described on the reverse side of the card. By placing checks in the appropriate places, later sorting of the data was facilitated.

At fairly regular intervals detailed surveys of the pen were made on enlarged field maps to show the locations of all changes in the environment made by the rats. In addition, the surfaces of the burrows were mapped in even greater detail. Particularly detailed maps were always prepared of trails following snowfalls, since these presented good records of orientation responses. A photographic record was made of all pertinent alterations to the environment produced by the rats.

6. *Acknowledgments*

Once the problem of investigating a free-ranging population of rats under semicontrolled conditions was conceived, it then became necessary to secure a suitable location for the establishment of the colony. During my association with the Johns Hopkins University I lived at the edge of a small suburban community north of Towson, the county seat of Baltimore County, Md. Surrounding this community there were several hundred acres of semiforest and forested land. That portion immediately adjoining my residence was owned by the late Mr. John O'Donovan of Dulaney Valley Road. He granted permission for the establishment of the experimental setup in a partial clearing

............: Ear Tag	Card number :............
............: Date (Handled)	Sex :............
............: Age in days	Date born :............
............: Weight in grams	Litter Number :............
............: Body in mm.	Mother :............
............: Tail in mm.	Birthplace :............
............: Wounds	Place today :............
............: Body/Tail	Sexual condition :............
............: Weight/Body	
............: Growth Index	Pelage condition :............

Behavior Notes Recorded On Reverse Side

............: Competitive	Food storage :............
............: Play fighting	Food acquisition :............
............: Psychol. drubbing	Water :............
............: Nose touching	Elimination :............
............: Sparring-tumbling	Sexual behavior :............
............: Chase	Rolling :............
............: Territorial	Following :............
............: Vocalization	Copulation :............
............: Manual ability	Homosexual :............
............: Orientation	Mother-young :............
............: Nest building	Among young :............
............: Burrow building	Adults-young :............
............: Aggregations	Inter-adult :............
............:	.... :............
............:	.... :............

Figure 12.—Sample of 5- by 8-inch card onto which all data was either recorded or later transferred. Details of the observation were recorded on the back of the card.

only a hundred yards from my house. I am certainly indebted to him for this consideration. Without the close proximity of the study area to my place of dwelling it would have been impossible to conduct effectively this study which required such irregular hours.

During the initial phases of the study considerable difficulty was met in constructing recorders, which would efficiently record each time a rat passed by. This was finally solved through the donation of four electronic rattraps by the L. F. C. Corporation of New York City. The circuits of these were modified to eliminate the electrocuting mechanism. Then, whenever a rat passed through the beam of light projected on the photoelectric cell, a circuit was completed which activated a pen on a tape recorder.

During April and May of 1949 the U.S. Army Signal Corps made available a photographic crew and the necessary accompanying facilities for the detailed filming of the behavior of the rat. Major W. C. Lown had supervisory control of the general operations, while Lt. Strickland directed the actual field operations. The crew consisted of six movie camera operators, one still photographer, one sound technician, two electricians and two prop men. The immediate purpose of these films was to obtain certain desired footage for its integration in a series of films on the biology, control, and epidemiology of the rat which was being jointly prepared by the U.S. Army and the U.S. Public Health Service. However, the facilities of the camera crews were made available for the recording of all obtainable details of the activities of the rats, irrespective of their use in the projected series of films. I have had the opportunity of examining this extensive footage frame by frame. This detailed examination has been a greatly facilitated proper interpretation of rat behavior. I am indebted to the Signal Corps for making available for this publication several of the included still photographs.

RESPONSES TO THE PHYSICAL
ENVIRONMENT

The social behavior of rats and the social organization of the group take place in a physical environment. Therefore, before going into the social aspects of the life of the rat it will be best to provide a background of the reactions of rats to their physical environment. In doing this it will be impossible to avoid reference to the interaction of the physical environment and the social aspects of the life of the rats. In fact a dual generalization arises from this longitudinal study of the ecology of the Norway rat. This is that the physical structure of the environment modifies the expression of social behavior, while on the other hand social experiences modify the responses to the physical environment.

1. *Burrow Systems and Harborages*

A. *The Growth of the Burrow System.* The rats frequently constructed burrow systems as places of harborage, even though there were nine sunken wooden harborages provided in each of the four triangular areas. It was possible to follow the growth of burrow systems by examining the mounds of excavated dirt and the origin of passages into the burrow. Periodically the surfaces of the two main burrow systems were mapped by the technique shown in figure 13. These two burrow systems were named the North Alley Burrow and the South Alley Burrow. In the text I shall refer frequently to these two burrows simpley as the NAB and the SAB, respectively. They were the two main burrow systems developed in the alleys. Both were begun during the first few days of April 1947. All other burrow systems in the alleys were smaller and both historically and socially were subsidiary to them. The position of these two burrows are shown in figure 14.

The changes in surface appearance of the South Alley Burrow, from April 22, 1947, to May 17, 1949, are shown in figures 15 to 20. Initially, the burrow consisted of a single entrance hole with an adjoining mound. Very shortly two changes became apparent. First, additional entrance holes appeared beyond the edge of the mound. No excavated dirt occurred about these new entrances, which resulted from the rats digging toward the surface from the terminal ends of tunnels radiating out from the initial underground tunnel. Second, trails on the surface radiated outward from the mound toward various goals. These initial alterations may be seen in figure 15B. At this time, June 14, 1947, this burrow was inhabited by a single female and the young of her litter born April 16. Major directions of travel were toward the Food Pen and up Path 1 toward Areas I and IV. This latter route of travel is the result of a centrifugal type of movement toward less intensely used portions of the environment.

Up until July 11, 1947, this South Alley Burrow was still mainly utilized by the original female and her five young, which were then nearly 3 months old. All of these six rats participated in the enlargement and use of the burrow. As will be seen from figure 16, the mound was increasing in size. Some of the newer entrance holes into the burrow began serving as foci for the excavation of dirt as tunnels continued to be extended in a radial fashion from the original site. The number of trails on the surface leading from the burrow also increased in number. By October 7, 1947, the surface area of the mound had continued to increase and in addition there were three new entrances into the burrow system beyond the mound. At this time the burrow was inhabited by some of

Figure 13.—Technique of mapping the surface of burrows. A grid of string forming squares 12 inches across was placed over the burrow.

the members of the first litter as well as the 7-week-old members of a second litter.

By May 26, 1948, there had been both a doubling of the surface area of the mound as well as changes in the number and position of entrances into the burrow. See figure 18. By this date only 13 of the 19 entrances which had been constructed were still in use. As a burrow ages some of the passages are accidently covered over as dirt is excavated from adjoining passages. In other instances, the rats intentionally plug passages (see pages 30 to 42). Two such recently plugged passages are indicated by the solid black circles in the figure. One of the interesting aspects about the growth of the burrow system was that, although it radiated from the original site, the main expansion was in a southwesterly direction. The terrain of the pen sloped gently upward from northeast to south-

west, covering a vertical rise of approximately 5 feet over a horizontal distance of 100 feet. The direction of new tunnels tended to follow in the direction of the upward slope of the terrain, while the dirt was excavated and deposited in a downhill direction.

In the last two surveys of the surface characteristics of the South Alley Burrow the position of the surface trails was omitted. However, figure 14 gives greater detail of the relationship of surface trails to burrow systems and other goals. In addition to the continued growth of the burrow system in evidence by October 6, 1948, as seen in figure 19, the main point of note is the expansion of the burrow system along the edge of the barrier fence. During the summer of 1948 there was an underground tunnel extension from SAB entrance 16 directly toward the barrier fence. At the point

16

where the tunnel contacted the underground portion of the barrier fence the rats dug upward to form SAB entrance 24. From this point the burrow system rapidly expanded along the edge of the barrier fence to extend past the tile of Passage 1 and 10 feet over into the West Alley. Sometime between October 6, 1948, and May 17, 1949, this long extension of the South Alley Burrow became separated from the older section of the burrow. Frequently in my notes this extension of the South Alley Burrow is referred to as the Passage 1 Burrow or the Tile 1 Burrow, although historically and socially the two sections were one.

By the terminal survey on May 17, 1949, figure 20, many of the isolated mounds had fused. In this figure are shown the position of 26 former entrances, which were at this date permanently sealed.

On May 17, 1949, the South Alley Burrow was excavated. The pattern of the underground burrow is shown in figure 21. It will be seen that the tunnels, passages, and cavities form a complex interconnecting system. In the northeast, older portion of the burrow the tunnels were shallow, that is, they were narrow in their vertical dimensions. In addition, the nests here were in disrepair. This portion of the burrow was inhabited by a senescent female and a younger but nonreproducing adult female. The central southwest portion of the burrow was not only the most complex in its structure, but it also housed seven females and five litters of varying ages. Here the tunnels and cavities were larger in their dimensions and the nests were in good repair. This portion of the burrow also contained one adult male, No. 49, the dominant male of the entire pen. No other adult males were present in this burrow system. The Passage 1 portion of the South Alley Burrow, while rather extensive in the total amount of tunnels present, housed only two females and their litters.

This latter is one piece of evidence, among several similar ones to be described later, that indicates a definite relationship between the physical structure of a burrow and the social structure of the group of rats which it houses. Each appears to be both cause and effect. Where the inception of a burrow near a wall causes the burrow to elongate along the wall, this separation from each other of the members of the colony appears to reduce the integrity of the group and there follows a lowering of social rank of the members of the colony. On the other hand, where other factors have caused a breakdown in the social structure of the group, the rats seem to

be unable to maintain a complex interconnecting burrow system such as is seen in the South Alley Burrow system.

Such a relationship between a poorly integrated social structure of a colony and the inability of its inhabitants to maintain a well organized burrow system is exemplified by the history of the North Alley Burrow. The pattern of the underground tunnel system is shown in figure 22. This is as it was on May 29, 1949. The surface development of this North Alley Burrow indicated that at one time the underground tunnel system was as complex as the central portion of the South Alley Burrow was on May 17, 1949. The complexity which had existed was lost through a fragmentation. This left segments of the burrow system completely isolated or only as arms with no cross connections with other arms. In other words, fragmentation of the tunnel system made it impossible for a rat to make a circular movement by following the tunnels.
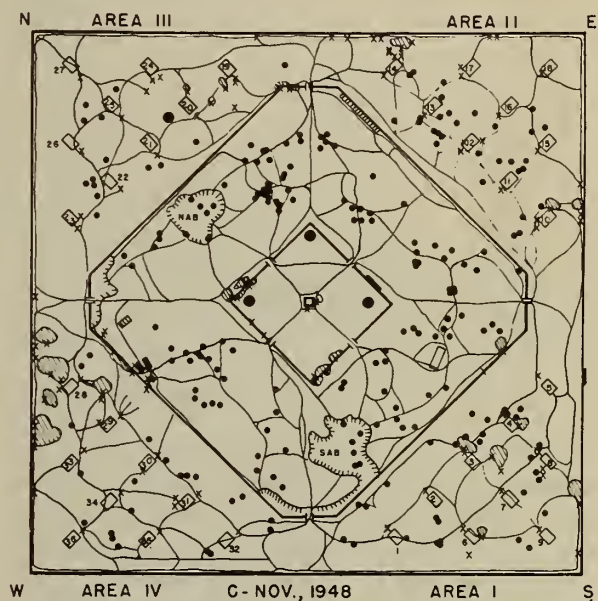
Figure 14.—Heavily worn trails November 1948. X's represent positions of drain tile entries to harborage boxes or entries through the soil to burrow systems. Cross hatched areas are mounds of burrow systems. The numerous entries to the South Alley Burrow (SAB) and the North Alley Burrow (NAB) have been omitted from the figure. The smaller dots represent the positions of trunks of trees. The larger dot between boxes 20 and 21 is the large pine tree in area III. The three large dots in the Food Pen are the locations of water fountains. The three solid rectangles in the West Alley by the median barrier fence and the one next to the Food Pen in the East Alley are rolls of wire. The row of open rectangles in the West and East Alleys are piles of traps.

Figures 15 to 20.—The development of the surface appearance of the South Alley Burrow from April 22, 1947, to May 7, 1949. The section of the burrow about passage 1 developed as an offshoot from the main burrow but later became severed from it. The entries of these two sections of the burrow are numbered independently according to the chronological order of appearance in each. The position of the initial entry is indicated by a plus mark. See figure 4 for photograph of burrow in April 1948.

A
SOUTH ALLEY
BURROW
APRIL 22, 1947

B.
MOUND AND OPENINGS
OF
SOUTH ALLEY BURROW
JUNE 14, 1947
≋ = TRAILS

o5
o3
◇1
2
4
PATH 1
FOOD PEN
5
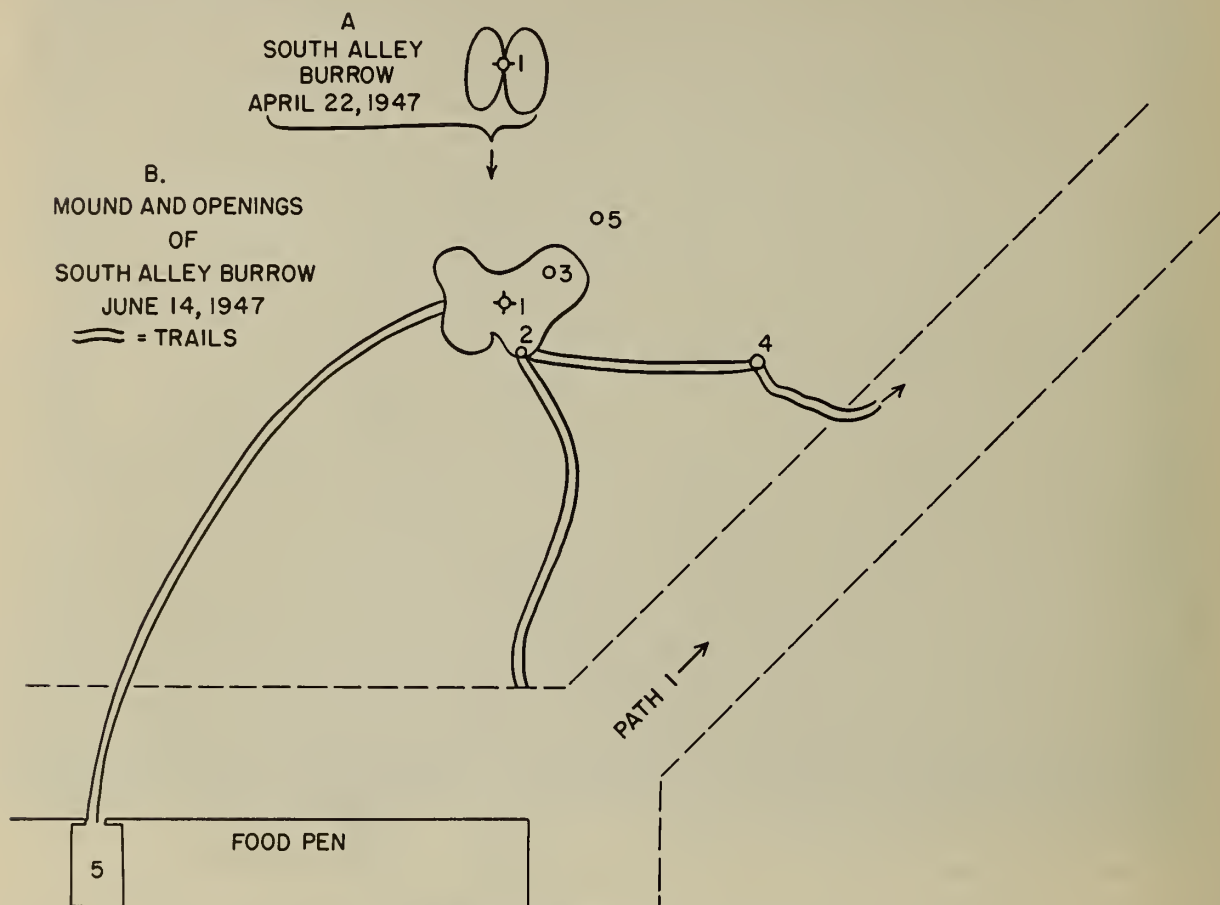
Figure 15.—South Alley Burrow, June 14, 1947.

There were two adjuncts to this decay of organization of the burrow, both of which are suspected to be causally related to this decay. The first of these was the social organization of the group inhabiting the North Alley Burrow. This organization was one characterized by an instability of interindividual relationships and low social rank of the members with reference to the colony as a whole (see pages 210 to 212). The second was the contact of an underground tunnel with the barrier fence during the summer of 1948. Once this happened there was a rapid development of the burrow along the fence with a concomitant shift of focus of activity away from the older more organized portion of the burrow.

The tunnel systems discussed above and illustrated in figures 21 and 22 represent burrows which were intensively used by many rats over a long period of time. A large number of smaller burrows was excavated both within the experimental pen and at various locations through Baltimore County. Two typical, more youthful burrows are shown in figure 23. The left-hand figure, Burrow Study 2, Site 1, illustrates the pattern which soon arises when the burrow is initiated in a plot of ground away from barriers, such as fences, or other objects toward which the rat might direct its burrow construction. This pattern is one of a single point of excavation, two entrances, several nest or food storage chambers, and a circular system of communication. The right-hand figure depicts how the development of a burrow may be soon modified by surrounding structures. This Area II Burrow 2 began along the outer barrier fence. The edge of the left hand mound is parallel with the fence as is also the

MOUND AND OPENINGS
OF
SOUTH ALLEY BURROW
JULY 11, 1947
= · TRAILS

PATH 1

FOOD PEN
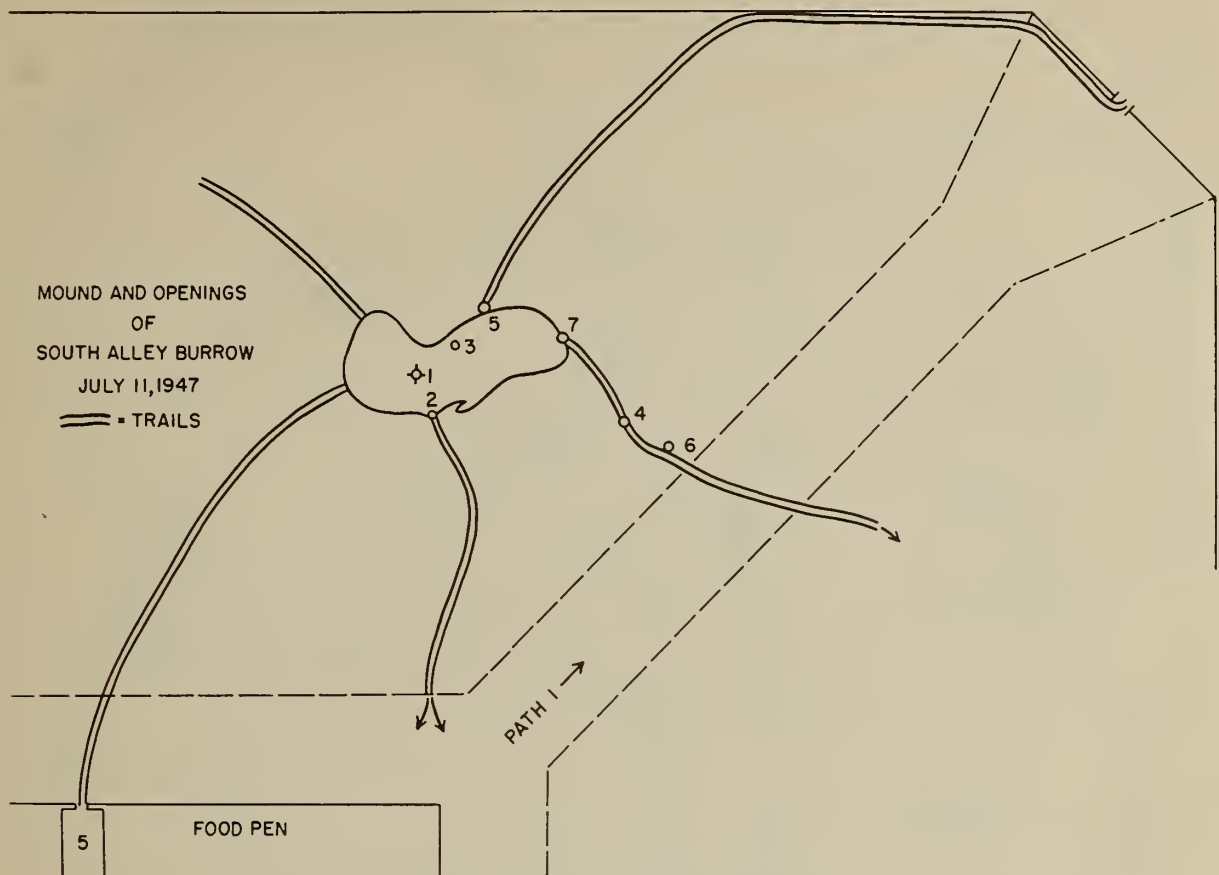
Figure 16.—South Alley Burrow, July 11, 1947. (See legend above fig. 15.)

general trend of the tunnels. The second phase of development of this burrow was the construction of a tunnel directed toward the neighboring Harborage Box No. 10. As soon as the rats contacted the edge of this box, they built an entrance to the surface and excavated dirt through it as they dug a tunnel around the edge of this sunken wooden box. Many instances were observed where burrows initiated away from a fence or a harborage box had secondary tunnel segments constructed which were apparently directed toward the object in question. From these observations it is believed that rats in many instances direct tunnel constructions toward prior points of orientation. Such a behavior will account for the development of circular routes of travel in burrow systems. Thus, where two blind tunnel segments exist, that have developed from a common point, there is a tendency for future extensions from them to bend back toward each other.

A study of the surface area covered by excavated dirt and of the number of passages or burrow entrances for the North and South Alley Burrows

provides an index of their rates of growth. For the South Alley Burrow it will be seen (fig. 24) that there was an initial rapid rate of expansion during the first 3 months when the first litter was being raised. From the time of birth of the second litter during August 1947 through the entire breeding season of 1948 a second and decreased trend in the rate of expansion is apparent. Although there is only one measurement of surface area available for 1949, it is nevertheless apparent that the rate of increase was continuing to decline. If burrows are considered as a cultural artifact, it is evident that the density of a cultural artifact follows a similar pattern of growth as does the population of rats which produced the artifact.

The trend of growth of the surface area of the North Alley Burrow roughly paralleled that of the South Alley Burrow. However, the initial expansion of the North Alley Burrow appeared more rapid until the fall of 1947. From that time on the rate of increase in surface area of the North Alley Burrow was less than that of the South Alley Burrow so that by the termination of the study

19

MOUND AND OPENINGS
OF
SOUTH ALLEY BURROW
OCTOBER 7, 1947

THROUGH WEST ALLEY
TO PASSAGE 8

PATH 1

FOOD PEN

5
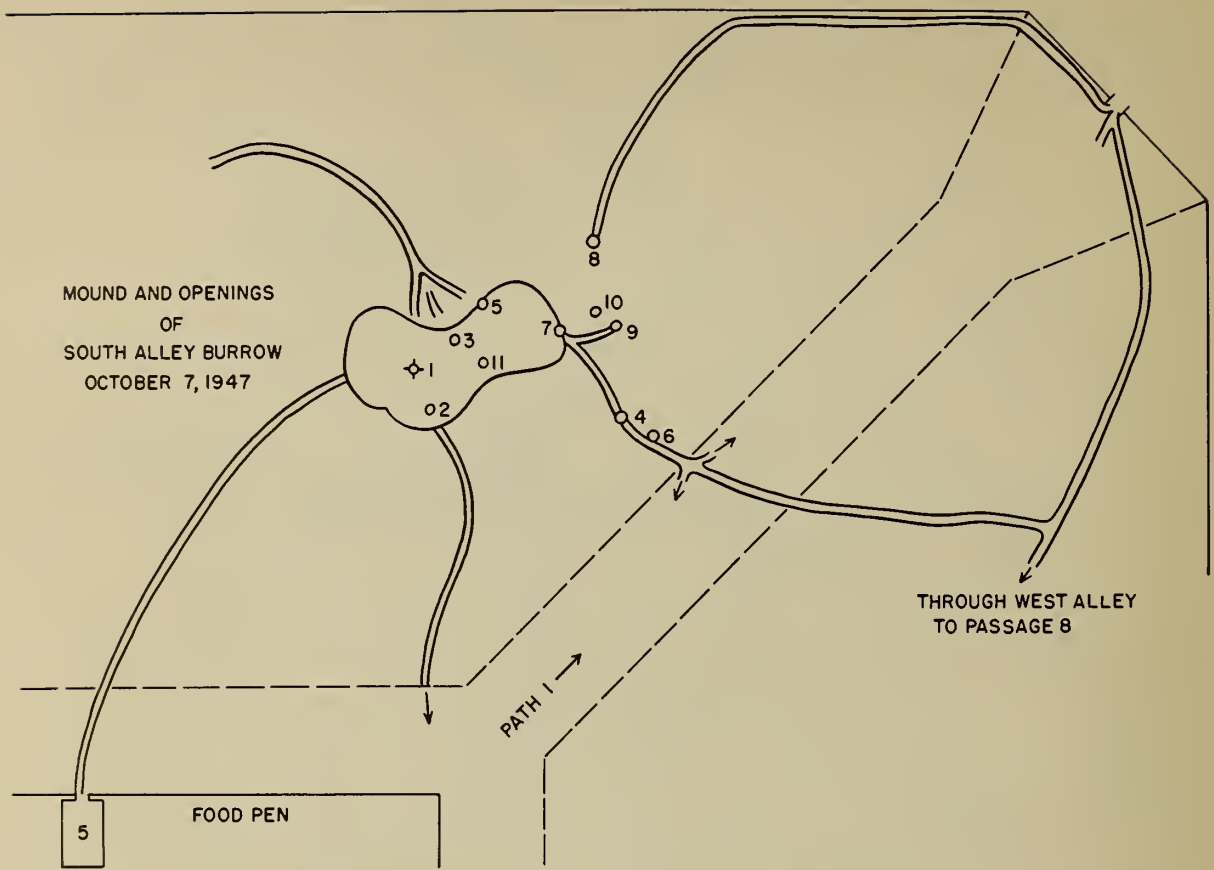
Figure 17.—South Alley Burrow, October 7, 1947. (See legend above fig. 15.)

the South Alley Burrow had an absolutely greater surface area. These differences may be considered as differences in what may be called "metabolic rate". Through the first 16-months history of these two burrows, observations were made on the time of opening of new entrances into the burrow and the time at which dirt was excavated from each of these passages. These data provide another index of the difference in character of the growth or metabolism of these two burrows (figs. 25 and 26). Two differences are apparent. First, by April 1948 26 passages had been constructed into the North Alley Burrow, whereas only 18 had been constructed into the South Alley Burrow. This is an indication of a greater underground construction by the members of the North Alley Burrow. Second, by the end of 1947 excavation from the initial 10 passages into the North Alley Burrow had ceased, whereas 6 of the initial 10 passages into the South Alley Burrow were utilized for the excavation of dirt for several more months. Where excavations cease, the adjoining tunnels deteriorate through

the accumulation of dirt falling from the roof and from rotting nesting material and stored food. Thus, early in the history of the North Alley Burrow there is evidence of the deterioration of its physical structure which was associated with the more poorly integrated social structure of the rats inhabiting it in comparison with that of the rats inhabiting the more stable physical structure of the South Alley Burrow.

Statements regarding sociology find their support on pp. 136–246, where this topic is considered in detail.

B. *A Stable Nonsenescing Burrow.* Regardless of the social structure of the group of rats inhabiting a burrow system there is usually some evidence of the deterioration or senescence of its physical structure. One burrow system was encountered in Baltimore which gave evidence of becoming stabilized in size without the accompaniment of deterioration in physical structure. It was located on the north embankment of a railway "cut" directly opposite the passenger loading platform of the Pennsylvania Railroad Station. A 35°

TO PASSAGES 2 & 6

19

O13
8

O5

9

14
18

SOUTH ALLEY BURROW

MAY 26,1948

= TRAILS

O3 ●11
O12

4
6

15

PASSAGE I

THROUGH WEST ALLEY
TO PASSAGE 8

PATH I →

FOOD PEN

5
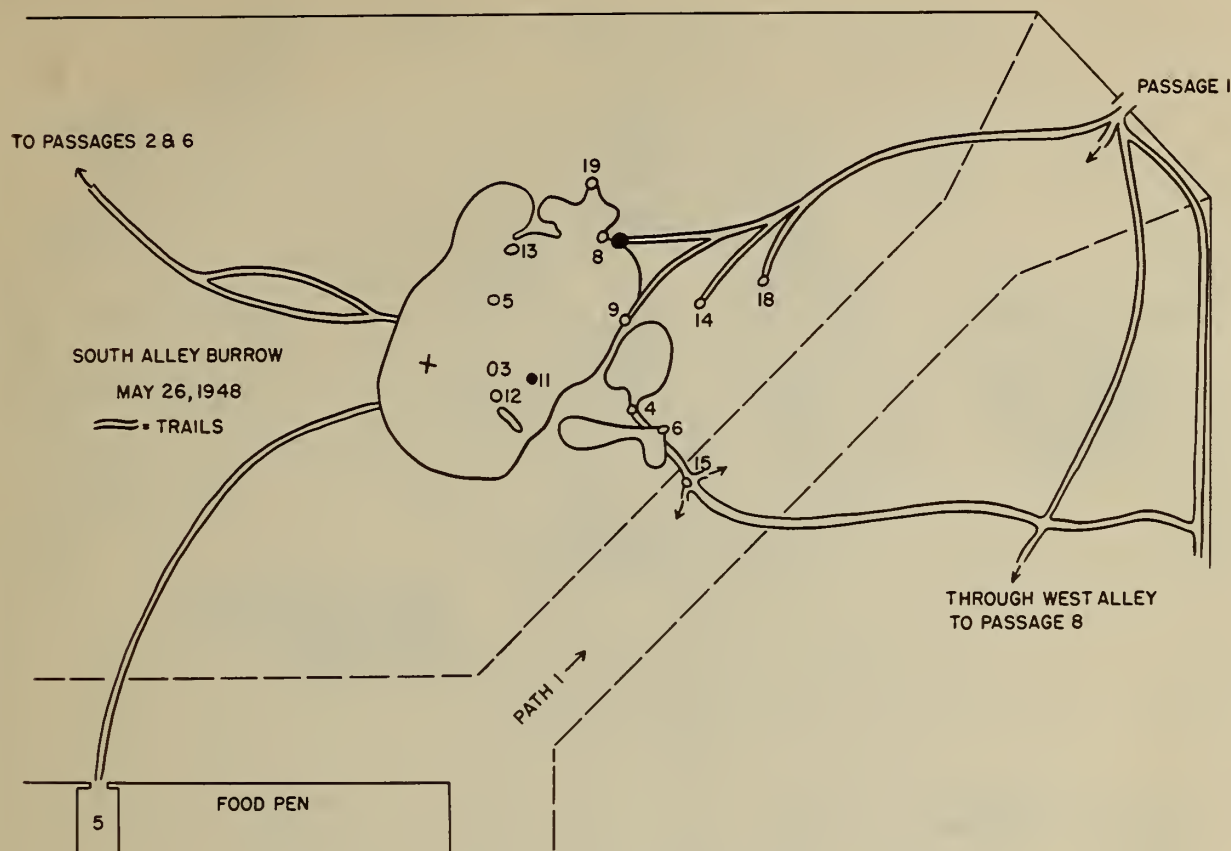
Figure 18.—South Alley Burrow, May 26, 1948.   (See legend above fig. 15.)

slope and a heavy turf of grass distinguished this situation from any others of the many I examined. At this time the burrow was inhabited by 20 rats, and I strongly suspect that it had been in active use for several years without any additional enlargement. The configuration of the tunnels of this burrow is shown in figure 27. It satisfies the basic requirement of circular movement characteristic of complex well-integrated burrow systems. Most of the initial tunnel segments led directly into the embankment so that their terminal ends, where nest cavities or other tunnel segments branched off, were covered by several times the amount of dirt (see table 4) that characterizes burrows constructed on essentially flat terrain. This greater overhead cover of earth must provide greater structural support in preventing cave-ins as well as providing a more constant temperature with respect to that of the external air. Furthermore, the fact that the entrances into the burrow were located on a sloping surface prevented as much rain water from entering as would normally funnel in on a flat terrain. In addition better drainage was facilitated by the sloping tunnels which connected one level of the burrow with

another. These factors of greater structural support, more constant internal temperature, and better drainage form what I believe are the more favorable conditions provided by a sloping terrain.

C. *The Initiation and Expansion of Burrows.* According to my experience with the rats in the pen and from studying burrows in various locations through Baltimore County, there are four categories of conditions or responses which influence the location of the site of the initial entrance passage into a burrow:

1. Thigmotropic response.
   a. Against a vertical surface.
   b. Under a horizontal surface.
2. Overhead cover.
   a. Shrubs, low trees, etc.
   b. Floors of buildings, or other such surfaces which lie above the actual contact distance by rats.
3. Slope of the terrain.
   a. An inclined terrain is preferred over a flat terrain.
4. Proximity to major goals such as sources of food and water.

21

MOUNDS AND OPENINGS
OF
SOUTH ALLEY BURROW
OCTOBER 6, 1948
(WITH ITS TILE I PASSAGE
EXTENSION)

PASSAGE I

TRAILS FROM BURROW AS ON
MAY 1948 EXCEPT ONE NEW
ROUTE BY HOLES 22,8,16,24
& 25 TO PASSAGE I.

PATH I

FOOD PEN
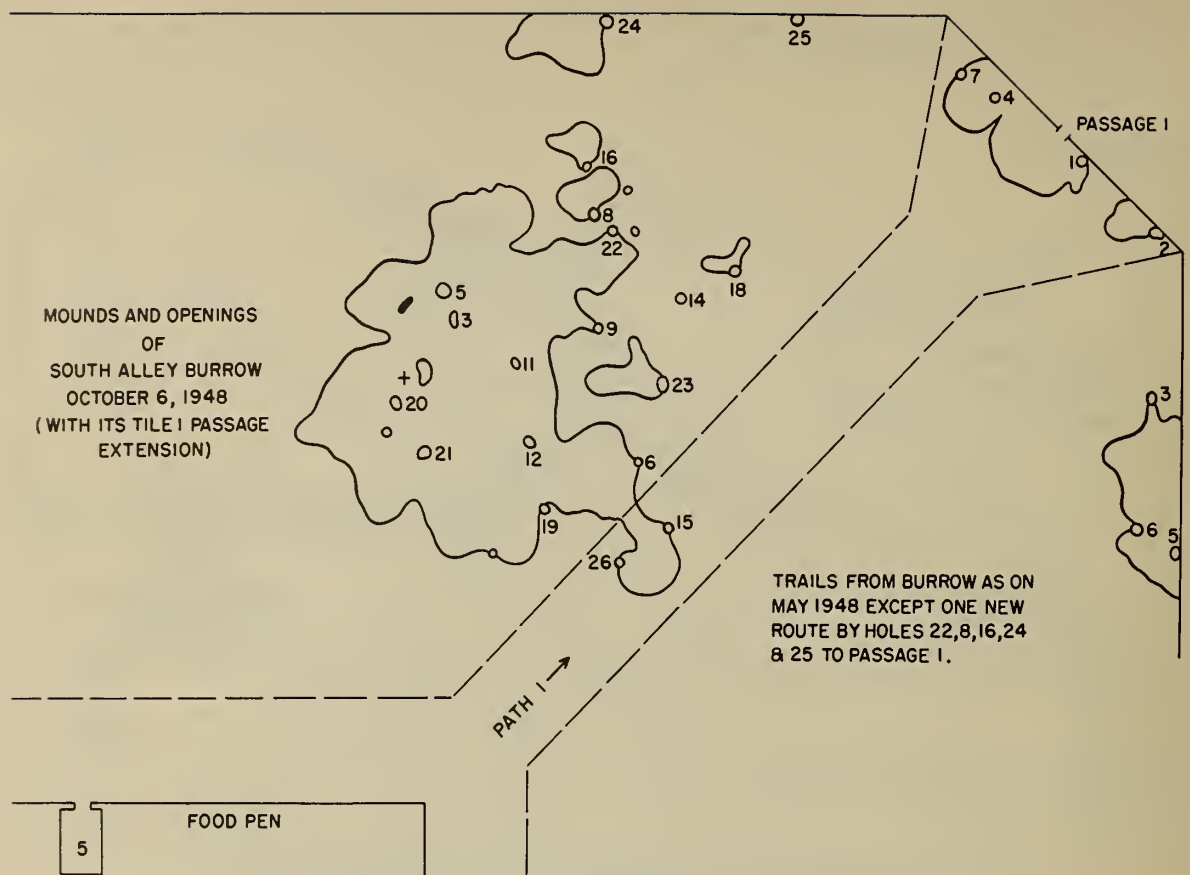
Figure 19.—South Alley Burrow, October 6, 1948. (See legend above fig. 15.)

About human habitations and within the experimental pen the most typical site of origin of a burrow was against vertical walls or fences. Such locations may be seen in figure 14. A typical example of such a location is shown in figure 28 in which a rat built its burrow directly against the outer limiting fence. Whenever any object with a flat ventral surface is laid directly on the ground, rats in the vicinity begin burrowing under it. Between periods of trapping, the wooden traps used to capture the rats were placed in small piles. Figure 29 shows such a group of traps within a few days after they were placed in a compact group. The shallow tunnel constructed under the traps is shown in figure 30 following the removal of the traps. When such a group of traps is left in place for several weeks, the initially shallow tunnels are frequently elaborated into an underground burrow. Such a situation is shown in figure 31. Here a large mound of earth may be seen in front of the traps. Since these traps were piled against the barrier fence the initiation of the

burrow at this place represents a dual thigmotropic response to both vertical and horizontal surfaces.

Where no opportunity for thigmotropic responses is available, the location is primarily influenced by the presence of overhead protective cover. Presumably this is a negative phototropic response. Within such locations there is possibly a minor thigmotropic attraction toward narrow vertical objects such as tree trunks or posts, but this reaction is not particularly pronounced. Away from man-made structures dense shrubbery satisfies this response. About human habitations the floors of porches and outhouses replace the more natural conditions; at least where these floors are elevated from the ground by several inches or a few feet.

An abrupt slope in the terrain will be utilized in preference to more flat terrain if other conditions of the environment are equivalent. This response favors the development of a burrow with greater structural support, better drainage, and a more constant temperature. Where a nearly vertical slope begins abruptly from horizontal terrain, it is impossible to separate the influence of the slope

MOUNDS AND OPENINGS
OF
SOUTH ALLEY BURROW
MAY 7, 1949
WITH ITS TILE I EXTENSION

● = PERMANENTLY SEALED
FORMER OPENINGS
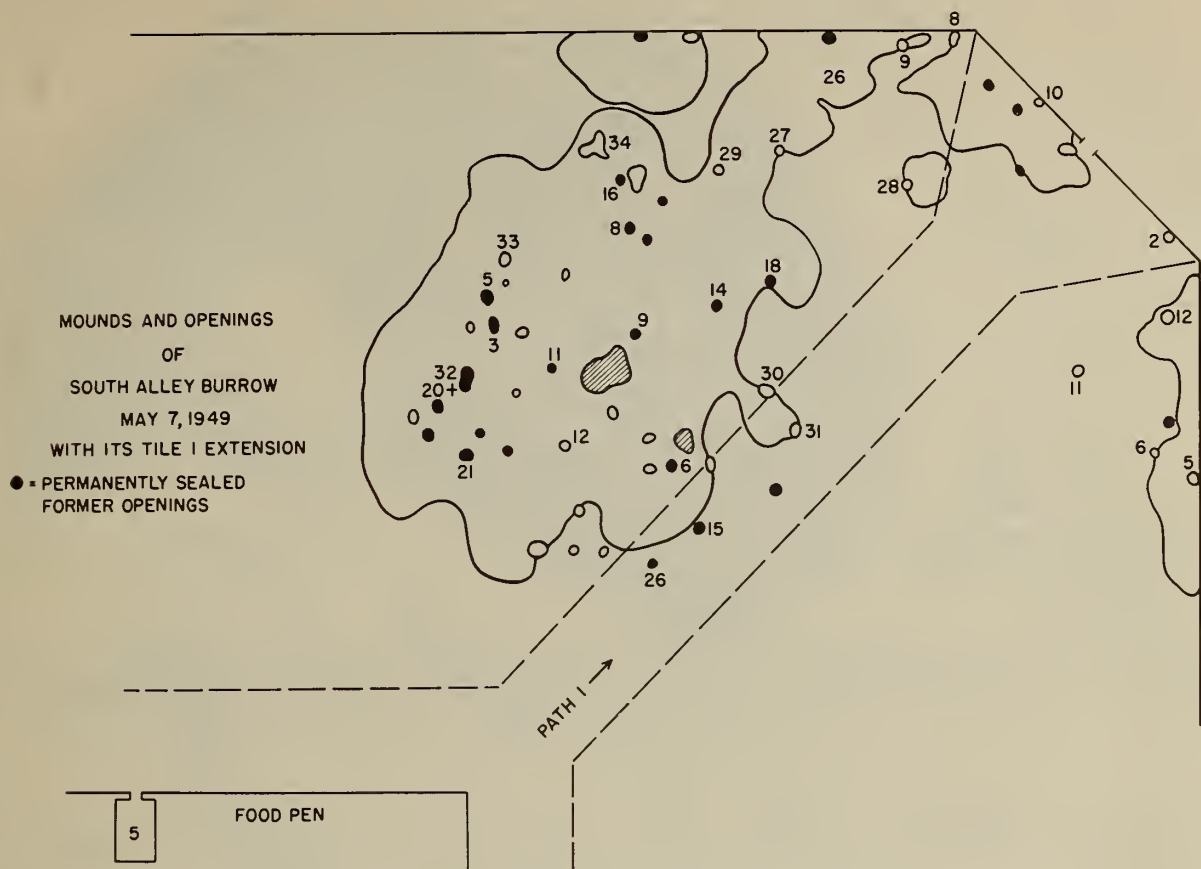
Figure 20.—South Alley Burrow, May 7, 1949. (See legend above fig. 15.)

response from that of the thigmotropic response if the burrow is initiated at the base of the slope. Such instances have been observed near the shore of Chesapeake Bay.

Whereas thigmotropic, phototropic, and geotropic (slope) responses may be considered as the primary ones determining the site of initiating a new burrow, the particular site selected will be influenced by its proximity to other goals, toward which the rats have previously oriented their movements. Of these, the proximity to food and water appear to be the principal ones. Such goals may be considered as secondary influencing factors. Social and cultural factors modify the use of space. A "no-man's-land" devoid of burrows tends to develop between the centers of areas utilized by adjoining colonies. Such processes restrict the areas in which burrows may develop. These social factors may be considered as tertiary influencing factors. They are discussed in more detail under "Home Range" (pp. 160–170) and "Local Colonies" (pp. 203–213).

A final factor which influenced the location of

the site of initiation of burrows in the pen was an artifact of the structure of the barrier fences within the experimental pen. The barrier fences forming the limit of the central Food Pen, and separating the alleys from the areas was made of ½-inch mesh wire cloth sunk into the ground to a depth that the rats did not dig under. However, the rats could easily detect the presence of other rats or the conditions of the physical environment through this barrier. During the latter part of June 1948 a burrow was started against the barrier fence in the North Alley just opposite and across the fence from Harborage Box 23. While this burrow still consisted of a single entry and a single mound, an entry and a mound were developed in exactly the same position on the opposite side of the fence in Area III. Within 2 weeks the expansion of the burrow on the North Alley side of the fence led to the formation of a second entry with its adjoining mound. This development was immediately followed by a parallel development on the opposite side of the fence. Similar instances of parallel burrow construction were observed on

23

TUNNEL SYSTEM
OF
SOUTH ALLEY BURROW
MAY 17, 1949
(WITH ITS TILE I EXTENSION)

= FOOD CACHE
= NEST

FEMALES

S.A.B.		T.I.B.
N.E.	S.W.	
39	80 L.	676 L.?
778	93 L.	689 L.
	98 L.P.	700 L.
	702	2 LITTERS
	704 L.	
	705 L.	
	767 L.	
	1075	
	5 LITTERS	

L = LACTATATING   P = PREGNANT

FOOD PEN

5
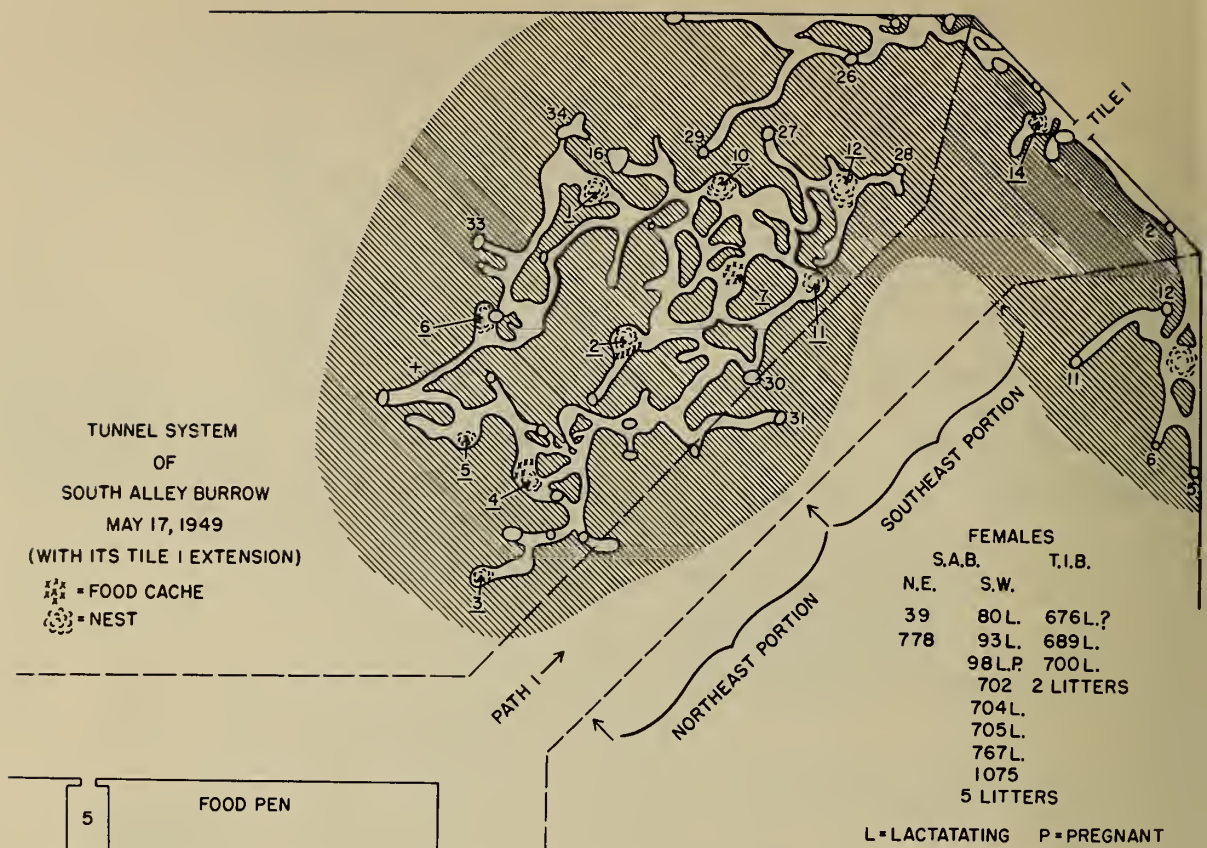
Figure 21.—The pattern of the tunnel system developed at the South Alley Burrow. The more circular outline of the older portion of the burrow with its many interconnections is typical of burrows which develop away from a limiting barrier, such as a fence or wall. The crosshatching is merely for making the tunnels more obvious.

several occasions. In a few cases the burrows on both sides of the fence were excavated and it was found that the tunnels paralleled with the wire mesh fence forming a partition between. On December 20, 1948, a survey of the pen showed that there were 30 locations where passages into burrow systems lay immediately in contact with either Food Pen fence or the median barrier fence. Of these thirty locations 18 were characterized by having openings into parallel burrows on either side of the fence.

In each of these 18 instances the initial burrow construction was adjacent to the inner surface of the fence nearer the source of food. Burrows on the opposite sides of these fences, that is away from the food source, were only initiated secondarily. Presumably this secondary burrow construction reflected the attempt of rats to enter these burrows from the outer surface of the fence. This restriction of initiation of burrows to inner surfaces of fences must be a derivative of the fact that rats frequent the inner surfaces of the fences much more often

because trails (fig. 14) occur more often adjacent to the inner surface. The presumed origin of this differential placement of trails is discussed on pages 67–70.

D. *Orientation of Mounds and Tunnels.* Dirt excavated from a burrow is dispersed about the entrance to form an arc subtended by an angle of slightly less or more than 180°. The chord across this arc normally lies at right angles to the tunnel leading into the ground. Where the terrain slopes, the initial tunnel tends to be in the general direction of the upward slope. I do not know the minimum slope necessary for this response. In the pen there was an approximately 5-foot increase in elevation from the northeast to the southwest side of the pen (a slope of circa 3.5°). The direction in which the mound was most frequently formed from the burrow entries indicates that the rats were at least able to perceive this slope. For 26 of the mounds shown in figure 14, surrounding barriers did not conflict too much with the direction of excavating dirt. Of these, 24 gave

NORTH ALLEY BURROW WITH ITS EXTENSION
TOWARD PASSAGE 4 ON JUNE 1, 1949

PASSAGE
4

FENCE

3♂♂
1♀
THEIR NESTS
WERE UNKEMPT

1♂
13♀♀
THEIR NESTS WERE
IN GOOD REPAIR

FENCE

LEGEND
NESTS   FOOD CACHES   EDGE OF MOUNDS
△ · TREES IN VICINITY OF INITIAL BURROW
18 , ETC. · SURVIVING MARKERS SHOWING POSITIONS OF
SOME OF THE FIRST FEW BURROW OPENINGS
FRESH EXCAVATIONS

+ SITE OF ORIGINAL
BURROW OPENING

8♂♂
1♀
THEIR NESTS WERE UNKEMPT

0   10   20   30

FEET
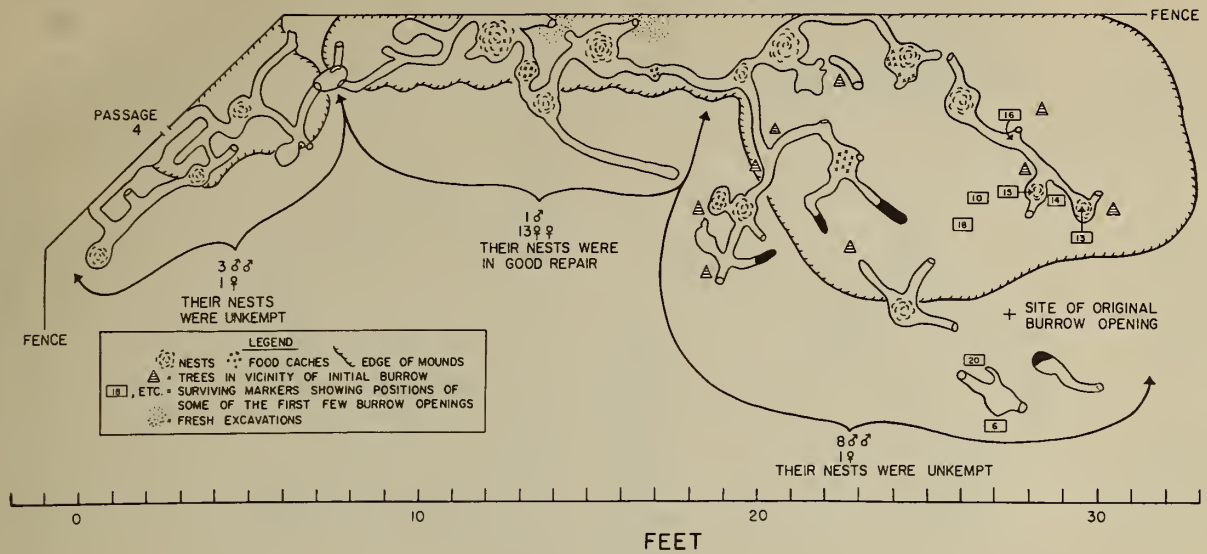
Figure 22.—The pattern of tunnel systems developed at the North Alley Burrow.   Once the tunnels contacted the fence they
followed close to it with few interconnections.   The decay of the older section of the burrow is associated with its inhabit-
ance by socially low ranking rats, which exhibit an inhibition of the behaviors involved in the development and maintenance
of tunnels and nests.

BURROW STUDY
2
SITE 1
xxx FOOD CACHES

MOUND

E

D

C

B

A

2

FOOD CACHE

MOUND

NEST

MOUND

AREA II
BURROW 2
1-6-49

0   1   2   3   4   5
SCALE   IN   FEET

0   1   2   3   4   5
SCALE IN FEET

Figure 23.—Patterns of burrow systems during the early stages of their development.   Also see figure 34.

25

676–768 O—63——3

GROWTH OF MOUNDS

SOUTH ALLEY BURROW
MOUND AREA = ⊙
BURROW OPENINGS = ⊡

NORTH ALLEY BURROW
MOUND AREA = △

Figure 24.—Growth of the surface of burrows. It will be noted that there were periods of constant growth rate, but that the later periods had slower rates. Very little additional growth should have taken place had the burrows been followed beyond the third year.

related to the distance which rats are otherwise forced to transport excavated dirt back to and out of the original opening. Such a secondary entry, or "bolt hole," presents the appearance shown in figure 32. Initially it may be surrounded by much more dense vegetation. Most of these later openings serve as foci from which dirt is excavated as further expansion of the burrow occurs.

These later elaborations of the burrow system follow the pattern of the initial expansion. However, there are three responses which influence the pattern of the developing system of tunnels:

a. *The thigmotropic response to walls and other vertical barriers which extend underground.* Whenever a burrow is initiated against such a barrier, or later comes into contact with it, the subsequent extension is in very close association with it. There is a great reduction in the frequency of tunnels extending at right angles to the barrier. Since this is so, there is little opportunity for cross connections between tunnel segments. Thus, travel within the system is limited to going up and down the burrow with the occasional opportunity for going up to the surface along the way (See fig. 22).

b. *The deflection or bifurcation response in tunnel construction.* As shall be discussed in more detail later there is a decreasing frequency of longer tunnel segments (See figs. 44 and 45). The median length of 780 measured segments was 298 millimeters. After such a distance the tunnel segment either (a) terminates in a nest cavity, (b) abruptly bends, or (c) bifurcates. By such a process tunnel segments which are initially blind will come in contact with previously existing tunnel segments. When this happens circular movements by the rats are possible within their burrow (See fig. 21). Although interconnection may develop purely by random directions taken by the bent or bifurcated tunnel segments, there remains the possibility that the rats actually direct their tunneling toward previously constructed tunnels.

c. *Directional orientation response toward prior goals.* As the wooden harborage boxes aged and became soft, the rats gnawed through them. They then dug a tunnel around the sunken box by keeping in direct contact with its outer walls. Excavated dirt was pushed into the box. In most cases radiating branches developed from these initial tunnels. During December 1948 and May 1949 all the burrows in the areas were excavated and mapped. It was noted that longer than normal tunnel segments tended to extend directly toward or actually reach

evidence of the dirt having been thrown downhill; and from most of these, observations showed that the tunnels were directed uphill. Observation of many other burrows started in the pen substantiate these generalizations.

The initial tunnel segment usually terminates in a nest cavity. A second tunnel segment is usually constructed within a few days. It begins from the opposite end of the nest cavity or from the point where the nest cavity joins the initial tunnel segment. The terminal end of the second tunnel segment, or perhaps a later one in the series, is directed upward to form a second entry into the burrow. All dirt from the burrow up to this point is carried back and excavated at the original entry. This second burrow exit has been termed a "bolt hole" (10). The interpretation given by these writers to this entry is that it serves as an escape point for the rats in the burrow when they are faced with invasion by other rats or predators. Although the availability of such additional entries may serve for escape, I suspect that their origin is

Figure 25.—The "metabolism" of burrows. Each horizontal row of dots represents the excavations from a single hole or entry into the burrow. No excavations were observed at same entries. Rate of metabolism is equated with frequency of repair (i.e. fresh excavations at an old entry), and with expansion of the burrow (i.e. opening of new entries).

the neighboring barrier fence or the nearest harborage box. In addition, there was a lesser tendency for these tunnels to approximate the route of the trails existing on the surface. There were 14 such clear-cut examples. One has already been mentioned (pp. 18–19) and is illustrated in the right-hand drawing of figure 23. Another very good example is illustrated in figure 33. This shows two adjoining harborage boxes with tunnels surrounding them and with a single very straight tunnel connecting them across a distance of 10 feet. All dirt from these burrows was excavated into the harborage boxes. The burrows about these two boxes were initiated independently during the latter part of November 1948 and it was not until in December that the connecting link between them developed. It is not known whether this tunnel developed from only one of these boxes, or whether tunnels were simultaneously constructed from each, and met half way between at a point where an entry from the surface was then built.

E. *The History of a Typical Burrow During its First Few Weeks.* The history of a particular burrow and of the female who constructed it may well be considered as typifying the conditions surrounding the origin of a new burrow system. A full understanding of some of the conditions or behaviors discussed is dependent upon more detailed accounts presented in various of the later sections.

A map of this burrow as it appeared on May 24, 1949, is shown in figure 34. It was constructed by female No. 378 who was born at the South Alley Burrow on September 4, 1948. This latter burrow was the most favorable location for birth of any in the pen. Even so, the large numbers of individuals born at this location forced many to emigrate. During the winter of 1948–49, when sexual activity was nearly nonexistent, female 378 remained at her home burrow. With the advent of spring she shifted to Area II where relatively few rats were residing at that time. Her first conception occurred about February 26, 1949. As is

27

"BURROW METABOLISM" AS SHOWN BY EXCAVATIONS AT THE NORTH ALLEY BURROW

ARROWS POINT TO TIME OF OPENING NEW HOLES

• = FRESH EXCAVATION

NO. OF EXCAVATIONS

CHRONOLOGICAL ORDER OF OPENING NEW HOLES

TIME - SPACE
SENESCENCE
OF BURROW

APR. 1947   OCT.   MAR. 1948   JULY   72
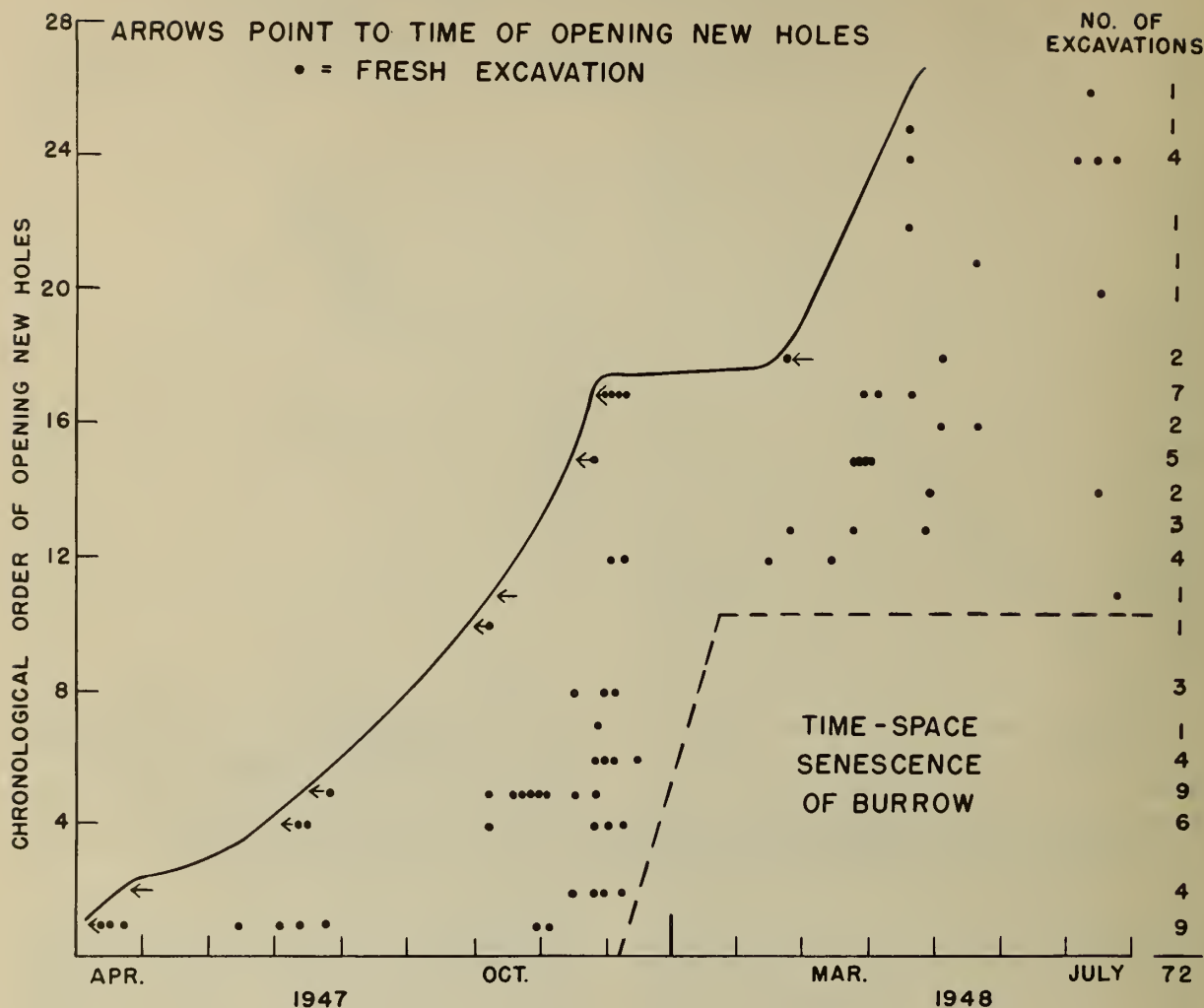
Figure 26.—See legend for fig. 25.

frequently the case with primiparous females this first litter did not survive. On the night of April 9–10 she began the burrow. At the time of the birth of the second litter on April 12, 1949, the burrow consisted of a single short tunnel terminating in a large nest cavity. The nest was made entirely of fresh green grass cut from a location only 10 feet from the burrow entry. A path was trodden into an extensive plot of grass but the material for the nest was acquired by completely denuding a patch of grass only a foot in diameter. This was an accentuation of the tendency of rats to secure nesting material close to the harborage site. Within a few days after the birth of the young, a second tunnel segment was constructed from the

terminal end of the nest cavity and extended to the surface to form a second entry. While the young were between 10 and 17 days old, the mother made an extension of the burrow. The dirt from this burrowing was excavated from the second entry. Both entries to the burrow system were kept covered with piles of grass cut by the mother and deposited over them. Most of the new burrow extension consisted of a cavity which served as a place for storing food. Shortly after this food-cache cavity was completed the secondary entry was permanently sealed with dirt by the mother rat.

There is considerable anticipatory implication to the sequence of burrow construction in such instances. Initiation of the burrow and the build-

28
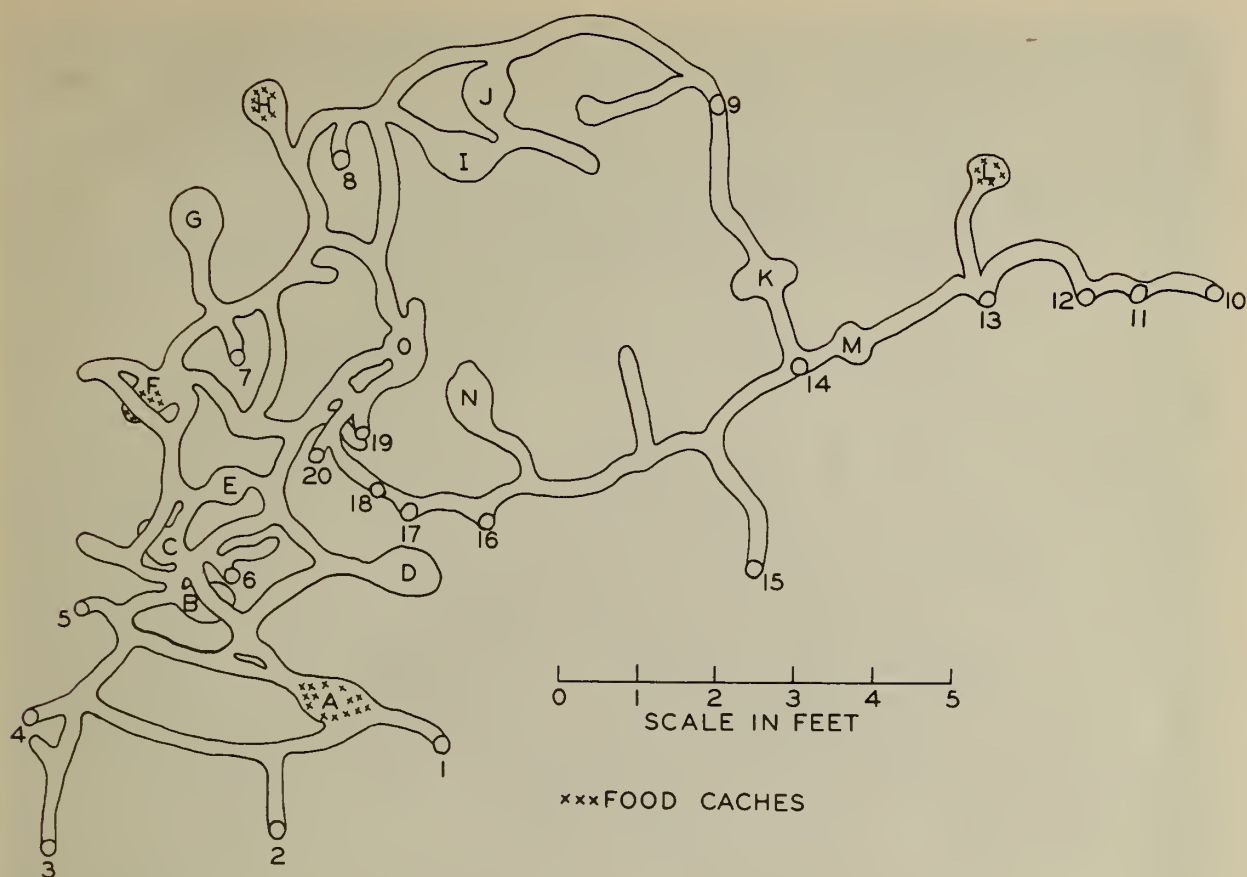
Figure 27.—A nonsenescing burrow system located in an embankment with an approximate 30° slope. Cavities are indicated by letters and entries by numerals. Entries 1 to 3 were toward the base of the embankment, while entries 8 and 9 were near the top.

ing of the nest just preceded parturition. Enlargement of the burrow and formation of the food cache just preceded the weaning of the young. This latter enables the young to avoid an excessive amount of social conditioning through the punitive action of older rats (pp. 148–151), that they might have otherwise received away from their home burrow. Although these behaviors do precede the time at which their consequences have survival value, there is no evidence that the rat is aware of their future usefulness.

The initial histories of several burrow systems constructed by females paralleled closely the course described above. Once formed, such burrows may serve as foci for the elaboration of extensive burrow systems which gradually spread from these simple beginnings. For example, see the previously described expansion of the South Alley Burrow over a period of 2 years (p. 15).

F. *The Weights of Rocks Moved by the Rats*. Rats remove rocks from their burrows either by carrying

them out with their teeth or by pushing them along with their forefeet. One hundred and forty-three rocks were collected from the top of the mounds (fig. 35). Only one rock weighed less than 20 grams. This weight was the author's estimate of the maximum sized rock carried out of the burrow in the rat's mouth. Above this point the mean was 66 grams ($\sigma = 37$ g). The heaviest 25 rocks ranged between 100 and 210 grams, with a mean of 140 grams. The physical ability of the rats, and the frequency of different sized stones mixed through the soil are factors influencing the choice of rocks moved. In assessing the ability of rats in moving such objects it must be remembered that these irregular shaped rocks were not just rolled out but rather that their flatter surfaces were subject to considerable friction against the floor and walls of the burrows. Furthermore, these objects, which frequently amounted to 15 to 30 percent of body weight, were pushed up inclines of at least 30°. When rats encountered

Figure 28.—Burrow initiated beside fence. The only burrows, of the many formed in the pen, which were not initiated along fences, under piles of traps, or from the inside of harborage boxes, were the North and South Alley Burrows. These were both started about April 1, 1947, following a period of 6 weeks when I excavated all burrows in the loose dirt beside the recently placed fence.

rocks of over 200 grams while burrowing, they merely tunneled around them. Unfortunately, measurements were not kept of the larger rocks which were moved out of the burrows. Considering that the median width of tunnels is 83 millimeters it is possible that the upper range of rocks moved out of the burrows is as much determined by the dimensions of the rock with reference to the dimensions of the tunnels as by the weight of the rocks.

G. *Alteration of Burrows.* Three behaviors, relating to usage rather than expansion of burrows, altered the appearance of the burrows. These were: (a) elevating the nest cavity, (b) excavating materials previously left in the burrow, and (c) sealing openings into the burrow.

There appears to be some optimal distance be-

tween the floor of the nest and the roof of the cavity within which the nest lies. After nesting material is deposited in the cavity the rat finds itself closer to the roof than it will tolerate. The rat then removes some of the dirt from the roof and transports it out of the burrow. As the nest becomes soiled more nesting material is brought in, which, of course, places the rat in the previous situation of being too close to the roof. Through a repetition of this process the roof of the cavity approaches so close to the surface that its thin wall collapses. Where a nest cavity lies under a mound the cavity may become so elevated that the floor of the nest may be on a level with the surface of the ground. In some instances these cavities and tunnels in mounds are made directly into the mound above those previously constructed. At

30
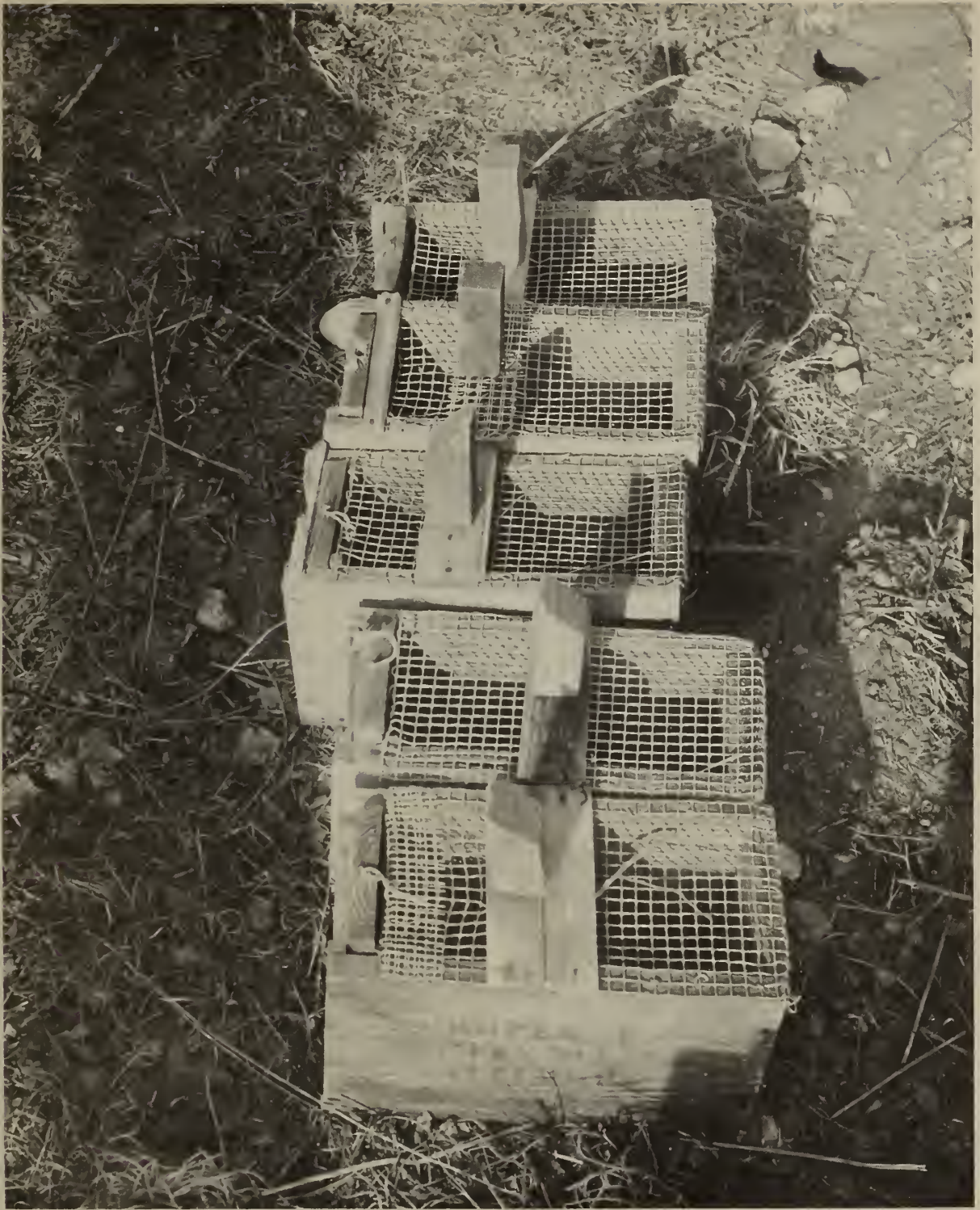
Figure 29.—The relationship of flat surfaces adjoining the surface of the soil to the initiation of burrows. This group of traps had been lined up near harborage box 6 for nearly a month prior to the taking of this picture on December 7, 1948. Note the small pile of dirt to the right of the center trap. See figure 30 for a companion scene immediately after the removal of the traps.

Figure 30.—The relationship of flat surfaces adjoining the surface of the soil to the initiation of burrows. The traps shown in figure 29 have been moved aside. Note the shallow tunnels which were under the traps. This is typical of the tendency of rats to burrow under any object laid flat on the ground. The stick passing through the center of this picture may be used for orientation with figure 29, where it protrudes from the right hand side of the center trap.

times the mounds of excavated dirt become hollow shells.

The second behavior, that of excavating materials previously left in the burrow, prevents a more rapid catabolism of the burrow system as a result of the first behavior. Both food and nesting material may be thrown out. Usually the excavation of such substances was at those times when dirt was also excavated upon enlargement of the burrow system. However, nesting material may be excavated with little accompaniment of dirt. Although both the food and nesting material which were excavated usually showed some sign of decay, very fresh material of both kinds was occasionally excavated.

The third and most complex behavior associated with the alteration of the appearance of the burrow

was that of the sealing of entrances into burrows. Directed rather than accidental sealing is referred to here. The latter occurred occasionally when the earth excavated from one entry spilled over into and eventually covered an adjoining one. However, attention is here focused on the transportation of objects by rats and their deposition in and over the entries. In these cases the primary result was the sealing of entries.

There were two general types of sealings. These two types seem to depend more upon the material selected than upon any other response associated with the sealing. The first type is a transient seal. Vegetation piled over the hole is the simplest expression of this type (see fig. 36). The specific material used at any one time depends upon what happens to be available within a few feet, certainly

Figure 31.—Mound of a burrow initiated under traps piled against the median barrier fence in the South Alley near passage 2. The rats excavated this burrow during September and October 1948. This is a typical reaction of rats to piled traps. The burrow systems in the North Alley near passage 3 and in the West Alley near passage 4 were initiated as the result of a similar response to piled traps.

not more than 10 feet away. The vegetation may also be stuffed down into the entry and perhaps have mixed through it some loose earth. In either case the seal is sufficiently light that a rat can lift it up or squeeze through it. The second type is a more permanent seal, although even these are sometimes reopened. This type takes on three general expressions: (a) loose dirt, perhaps mixed with rocks; (b) lumps of dirt; and (c) aggregates of lumps of dirt. In the latter case several small lumps that have been formed previously into moist wads are packed together to form a larger ball before being transported to the place of sealing. The loose dirt and rock seal is formed by the rat pushing the material from within the tunnel up to the opening and and gradually filling it from the inside. Dirt and rocks are pushed into place with the forefeet and

nose or actually put in place with the teeth (see figs 37 to 41). Where either small or composite wads of dirt are used, the sealing may be done from the inside, otherwise the rats carry or push the wads or balls of dirt out of one entry and over to the neighboring one which is being sealed.

There are three conditions which appear to influence the expression of this behavior. They are: (a) a draft of air into a nest cavity; (b) the state of lactation; and (c) low social rank.

With regard to the influence of a draft of air the description of specific instances will adequately present the relationship. During the latter part of 1948 a burrow made contact with Harborage Box 10 in Area II (see pp. 18–19). The tunnel followed around the outside surface of the box and a nest cavity was formed at about midway down one side.

33

Figure 32.—Secondary entry or bolt hole. Note that there is no dirt deposited about the hole. At the time of its formation such a hole forms the termination of a previously blind tunnel segment. All of the dirt excavated up to the time of the formation of such a bolt hole is removed from some other entry.
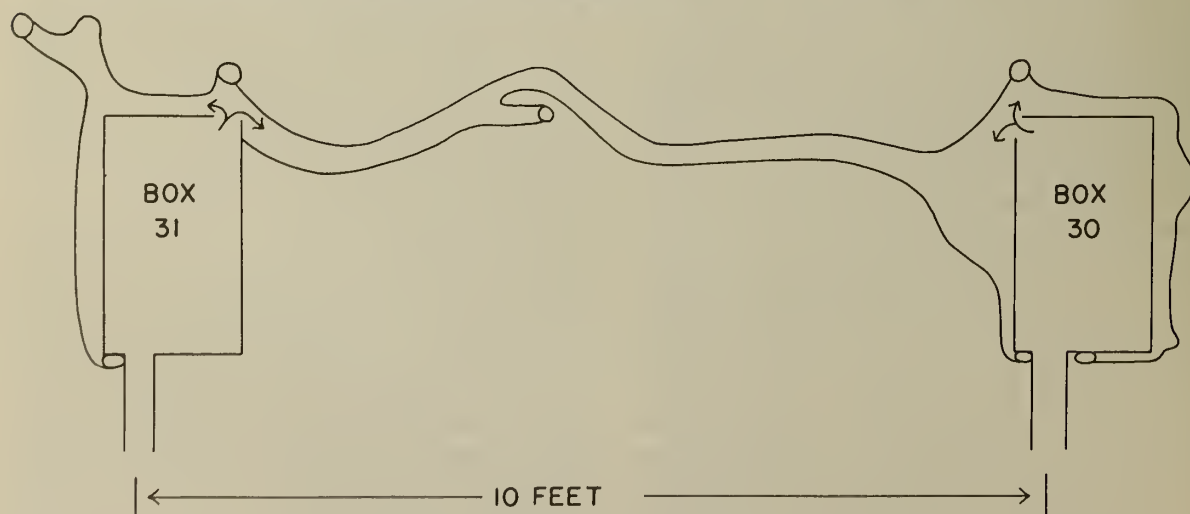
Figure 33.—Orientation in burrow construction. The tunnel between these two boxes parallels the trail connecting their drain tile entries (see fig. 14). Prior to the union of these two boxes by this tunnel, they were inhabited by rats of the same local colony which interchanged members. This is the connection existing between boxes 30 and 31 on December 21, 1948 (fig. 58), before they were excavated on the 22d and 23d.

SEALED ENTRANCE

FENCE

MOUND

NEST OF
GRASS
9 42-DAY OLD YOUNG

MOUND

FOOD CACHE

TRAIL

5 FEET

SITE OF SECURING
ALL NESTING MATERIAL

BURROW OF ♀378 MAY 24,1949
E.S.E. OF PASSAGE 2
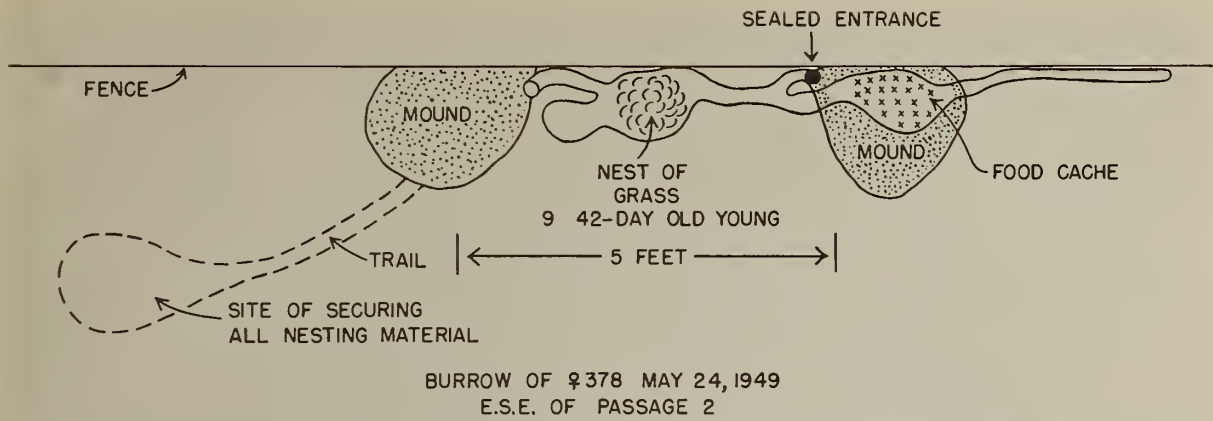
Figure 34.—A typical burrow system during its early stages of development. As discussed in the text, the history of this burrow reveals many of the behaviors which are associated with the initiation, construction, and utilization of a burrow.

Figure 35.—Mound between harborage boxes 2 and 3. This depicts the initial appearance of a mound. When rocks are present in the soil they are deposited in an arc near the periphery of the mound.

Figure 36.—Sealing of an opening into a burrow with vegetation. On the night of November 24, 1948, the roof of a nest cavity in the mound of the North Alley Burrow caved in. The rats climbed the neighboring small pine trees where they cut fascicles of needles and with them covered the opening. Presumably this behavior has the result of reducing air drafts into the burrow or in preventing the entry of other rats.

Figure 37.—South Alley Burrow hole 18. This shows the excavations made during April 1949 at the time a female had a litter here. Except for once in early October 1948 (fig. 19), no other excavations took place here. Shortly after this photograph was taken this female began sealing the opening (figs. 38 to 41). The position of hole 18 with reference to the tunnel system may be seen by examining figures 20 and 21. Photograph by U.S. Army Signal Corps.

Twenty-four inches from the center of the nest an accessory exit or bolt hole had been formed. During a snowfall in mid-December 1948 this bolt hole was sealed. The entry was initially plugged with grass. Following this the rats made small balls of mud inside the burrow and brought them out of another entry (as shown in the right hand illustration of fig. 23), crossed over the snow making a muddy trail, and deposited them on top of the grass plug. This sealing is shown in figure 42. On January 6, 1949, four rats born in Area II and one born in Area III were in the nest.

During the heavy rain of the night of May 16–17, 1948, the roof of a nest cavity at the North Alley Burrow partially caved in. It had not collapsed sufficiently for a rat to enter the burrow at this point. For this reason the resultant response of the

rats was assumed to be unrelated to the exclusion of other rats from direct entry into the nest cavity. Rather, this sealing was more likely related to the exclusion of light or air from direct access to the nest. The rats attempted to close this hole by dragging nine goldenrod stalks over it. Each stalk contained several leaves. This is shown in figure 43. A similar response is shown in figure 36 where pine fasicles were used to seal the hole.

With regard to the effect of lactation on this sealing behavior, it may be stated that 16 of the 80 observed sealings occurred at burrows where rats were known to have young less than 2 weeks old. In most of the cases the evidence indicated that the sealing occurred very shortly after parturition. Certainly the association of this behavior with the time at which the young lacked fur and

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Figure 38.—The female is pushing balls of mud into place with her nose so that they block the entry.   These balls are formed farther down within the burrow.   Photograph by U.S. Army Signal Corps.

had poorly developed temperature regulatory mechanisms should be of survival value. The type of sealing characteristic of lactating females is the pile of vegetation over the burrow entry. This behavior is very similar to another one frequently exhibited by mothers of new born young, which is to cover the young with a layer of vegetation such as forms the nest.

Low social rank tends to increase the frequency of this sealing behavior. A specific series of observations relates to the three females (17, 20, and 25) of litter 3, who were frequently found in association with each other. See pages 186 to 196 for further documentation of conditions indicating the low rank of these females. On eight occasions between November 1947 and September 1948 these three rats were involved in the sealing of the drain tiles going down into harborage boxes. Only one of

these was associated with a parturition, and this litter was not raised. In fact only one of the 12 litters conceived by these females was believed to be raised to weaning. All the others must have died within a day or two after birth. Of course the state of potential lactation may have influenced the occurrence of observed tile plugging with vegetation by these females.

The distribution of the location of burrow sealings also gives some support to the belief that this behavior has a higher incidence among socially low ranking individuals (see table 2).

As will be documented later in this paper, there were two regions in the pen whose members were differentiated both on the basis of genetic lineage and social history. These two regions were (A) the South Alley and Area I and (B) the North Alley and Area III. Between these two regions

Figure 39.—Details of the balls of mud that have been formed and pushed into place at the South Alley Burrow hole 18. Photograph by U.S. Army Signal Corps.

there lay a comparable amount of space (the East and West Alleys and Areas II and IV) in which few animals were born and in which the residents were from both of the two breeding areas. From table 2 it may be seen that there were only 15 burrow sealings in the south quadrant of the pen with its more favorable social structure while there were 46 in the north quadrant with its more unfavorable social structure. One might assume that the difference in frequency was purely a result of the difference in the total usage of the two regions. However, I am of the opinion that the total usage of these two regions was essentially identical. Although there is no way of conclusively proving this, figures 106 to 116

record a representative sample of captures within each of these regions: 422 in the south quadrant and 415 in the north quadrant. With this near identity in usage of the two regions (Chi square= 0.0583) which might be anticipated to occur 8 times out of 10 on a pure chance basis there is no evidence for a differential usage of these two sides of the pen.

Differences in frequency of lactation in the two regions is also not likely a factor in explaining the difference in the frequency of the burrow sealing behavior in the two regions. In fact one might expect an opposite difference in the frequence of the burrow sealing behavior had lactation largely influenced it (see table 3) since more young were reared in the south quadrant.

Figure 40.—Completion of the sealing of hole 18 of the South Alley Burrow. This picture was taken about 2 weeks after figures 37 to 39. The dark, slight depression in left center is the sealed hole. Rain followed by sunshine had completed the sealing. Photograph by the U.S. Army Signal Corps.

TABLE 2.—*The sealing of burrows as a function of social rank*

Relative social rank of inhabitants	Location of burrow sealings	Number of sealings		
		At tile entrances to harborage boxes	At burrows	Total
High	South Alley Burrow................	....	12	12
	Area I............................	3	0	3
	Area II...........................	1	7	8
Subtotal—high...............	....	4	19	23
Low	North Alley Burrow................	....	31	31
	Area III.........................	12	3	15
	Area IV..........................	5	6	11
Subtotal—low.................	....	17	40	57

Figure 41.—*Surface of the South Alley Burrow during April 1949. The sealed hole 18 is in the center of the circular area of bare dirt in the extreme right center. Path 1 crosses the foreground. Hole 31 is in the center of path 1. See figures 20 and 21 for other features. Also compare the appearance of this burrow with its state a year previously as seen in figure 4. Photograph by U.S. Army Signal Corps.*

TABLE 3.—*Number of burrow sealings related to number of young weaned*

	South Alley and Area I	North Alley and Area III
Number of burrow sealings...	15	46
Number of young weaned during 1947 and 1948......	107	62

Considering this evidence I think that it is fair to assume that the incidence of this burrow sealing behavior is in some way dependent upon the character of the social structure of the group. It is more likely to occur in groups with an unstable composition of members and in which the members are rather low ranking with regard to the hierarchial structure of the whole society. The exact dependency relationship between this behavior and social rank is rather problematical. There are at least two possible causes: (1) The presence of a burrow seal may make it less likely that a more dominant rat will enter the harborage of a socially low ranking rat. (2) The burrows of rats having lower social rank exhibit a higher "catabolism", with which is associated more breaks in the burrow system which allow light or air leaks. Thus, the increased incidence of the burrow sealings may only relate to the greater frequency of breaks in the structure of the burrow system. See the previous discussion of the histories of the North and South Alley Burrows (pp. 15–20).

There are two behaviors closely associated with this burrow sealing. Each was observed only twice. One of the ways in which rats seal openings into their burrows is with wads of mud which they

41

Figure 42.—Sealing of a burrow entrance with balls of mud. Previously this entry had been plugged with grass. After the snowfall the rats formed small balls of mud inside the burrow, came out of another entry, crossed the snow, and deposited them on top of the grass plug.

form down in the burrow and bring out and deposit in the opening. The Purina food checkers were about the size of these wads of mud and were observed to be similarly used: February 11, 1949. A nest cavity at the burrow by Passage 3 in the North Alley caved in. The rats had plugged it with grass, pine needles, and Purina checkers.

The other behavior was that of sealing the warped lids of the harborage boxes by lactating rats. Usually the lids of the harborage boxes fitted quite tightly, but occasionally they became warped so that a crack developed along a portion of the lid. In addition to the crack at the lid two other conditions characterized each of the observations: (A) There were young in the box; in one case they were 17 days old, and in the other instance 10 days old. (B) Moist dirt was present

on the floor of the box. It had been excavated from a tunnel leading from a hole gnawed through the box. In one instance the crack was sealed for a distance of 10 inches and in the other instance of 28 inches. The mud seal extended for an inch away from the crack both over the inner surface of the lid and against the side wall. In such cases the female rat had to stand on her hind legs in order to place the mud in position. Three hundred and seven-day-old female 43 at Box 19, and 257-day-old female 734 at Box 9 were the two individuals involved. This behavior is probably an elaboration of that of sealing burrow entries with mud.

H. *Some Quantitative Aspects of Burrow Systems.* During the excavation of 44 burrow systems on level ground 82 measurements were made of the

Figure 43.—Sealing of an opening into the North Alley Burrow with vegetation. During the night of May 16, 1948, the roof of a nest cavity partially collapsed. The hole was not large enough to permit the passage of a rat. During the night the rats cut and placed the goldenrod leaves shown just above marker No. 11. The pine needles shown above and to the right contain those shown in figure 36.

height, width, and depth of tunnels. A few additional measurements were available for a single large burrow on a 30° to 40° slope (see table 4).

TABLE 4.—*Typical internal dimensions of burrows*

Characteristic	Dimensions in millimeters		
	"Minimum" [1]	Median	"Maximum" [1]
Tunnel:			
Depth of floor from surface...............	140	194	291
Height.................	52	75	99
Width.................	64	83	110
Depth of roof from surface..	88	119	192
Chamber:			
Depth of floor from surface...............	170	251	320
Height.................	90	145	195
Width.................	146	184	248
Length.................	155	221	298
Chamber on 30° to 40° slope:			
Depth of floor from surface...............	300	520	650

[1] The "minimum" and "maximum" measurements represent an attempt to designate the more typical extremes. Actual extremes were quite atypical. Therefore, the "minimum" measurement was that for which 10 percent of the items were smaller. Similarly, 10 percent of the items were larger than the "maximum" measurement.

1. An adult rat has a standing height of approximately 67 mm. at the shoulders. Here its width is 59 mm., or circa 70 mm. if the layer of loose fur is included. It is thus quite apparent that most tunnels will only accommodate the passage of a single rat.

The greatest depth to which rats were observed to dig a burrow was 460 mm. This burrow was located in the loose soil in the pen adjoining the peripheral barrier fence shortly after the soil had been excavated in order to lay the wire mesh apron underground. Once this soil had become compacted only shallow tunnels were constructed here. The inference is that the depth to which a rat will burrow is in some way dependent upon an interaction between the soil structure and the effort required by the rat in making the excavation. In other words, the greater the effort required to dig a given distance of tunnel, the sooner will the positive geotropic response diminish to the point that the rat will burrow along on a horizontal plane.

44

2. Mensuration data representing 35 chambers is shown in table 4. From them inferences may be made concerning the maximum size of groups which might inhabit individual chambers.

Sixty by one hundred mm. approximates the minimum floorspace to which an adult rat may accommodate itself in the nest cavity. Thus, the number of rats per nest cavity are approximately: Minimum sized cavity, 3 rats; median, 7 rats; maximum, 11 rats. This range is interesting, because it suggests that rats construct nest cavities no larger than is sufficient to accommodate a group of adults approximating the litter size. The greatest number of adult rats taken from a single chamber was 11. One may use this observation as an inferential basis for supporting the belief that the number of individuals (mainly sibs) with which a rat makes its first associations determines the size of those groupings of adults in which each individual has its more intimate associations.

I. *Pattern of Work as Reflected in Burrow Construction.* Forty-four of the excavated burrows were drawn to scale on cross-section paper at the time of excavation. From these drawings it was possible to make close approximations of the length of each tunnel segment. The frequency distribution for 780 such measurements is shown in figure 44. With the exception of the first class—interval, 1 to 100 mm.—these reflect the frequency with which rats engage in tunneling operations of increasing magnitude of effort. An inspection of this frequency distribution indicates an exponential curve of the type $F = \frac{1}{C} e^{-x}$, where C is a constant.

The data was replotted as a three-point moving average on semilog paper (figure 45) in order to obtain a more precise understanding of the nature of the distribution. A straight line of the equation $f = \frac{-64d}{1,040} + 1$, where d is the length of the tunnel segment, makes a close approximation to this distribution. Having derived this equation to fit the data, the question is: Can we derive any insight into the behavior of the rat which might produce this distribution.

In this discussion the frequency (f) of tunnel segments shall be considered to be inversely proportional to the work (W) or effort involved in constructing the tunnels. That is $f = \frac{1}{W}$. The proportional amount of W required increases with

80%

20

15

PERCENTAGE

MEDIAN
298 mm

10

5

455 mm

0

FREQUENCY DISTRIBUTION OF LENGTHS OF 780 TUNNEL SEGMENTS FROM 44 BURROW SYSTEMS.

150 350 550 750 950 1150 1350 1550

LENGTH OF TUNNEL SEGMENTS IN mm
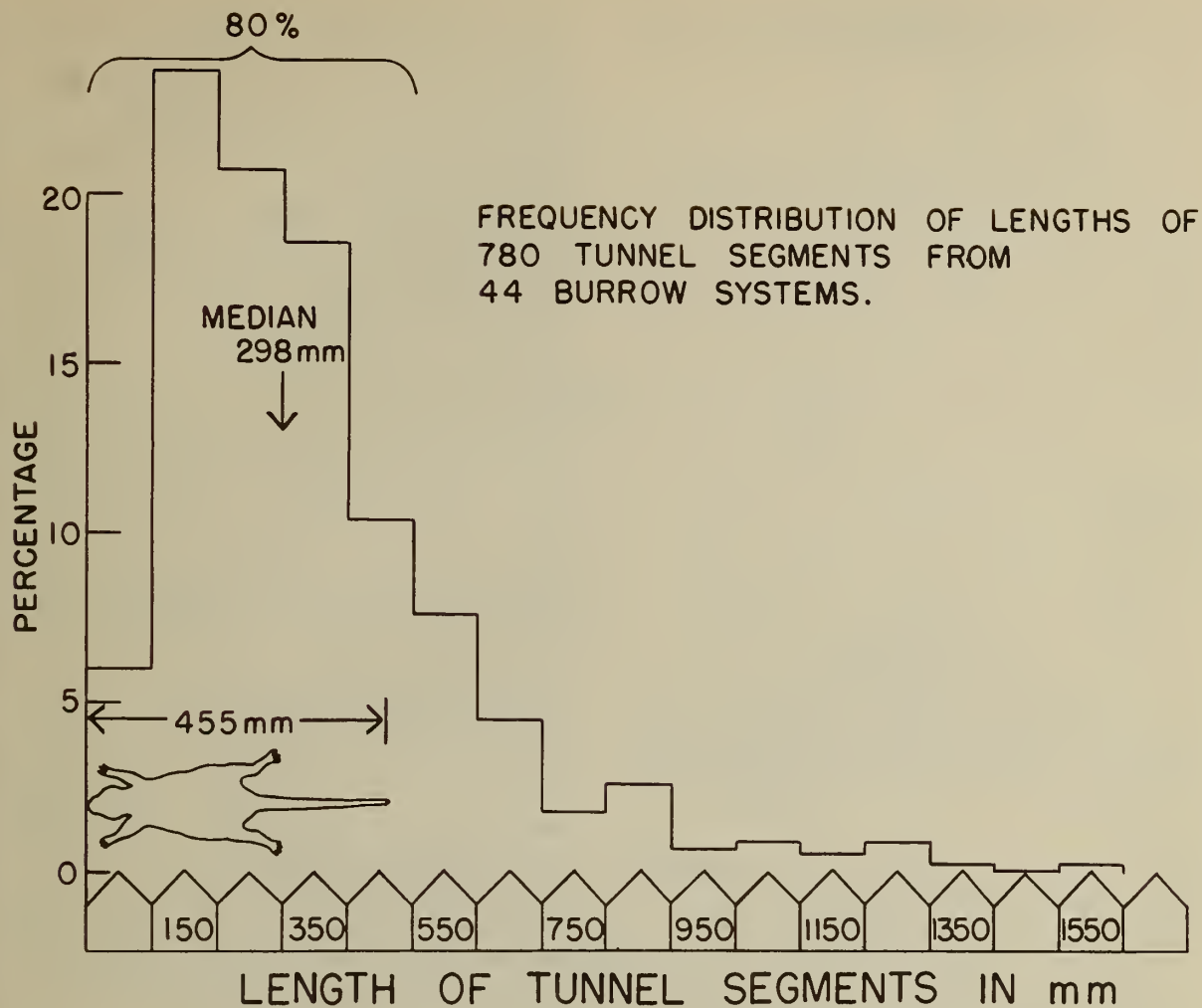
Figure 44.—Lengths of tunnel segments. Note that the great majority of the tunnel segments are no longer than the total length of an adult rat.

distance. If it did not, f would approach $\dfrac{K}{d}$, the second curve shown in figure 45, which does not fit the data. Our problem then resolves itself into the consideration of the contribution to the variability in W.

$$W = Ce^z \equiv C\left[1 + x + \frac{x^2}{2} + \frac{x^3}{2 \cdot 3} \cdots \frac{x^n}{n!}\right]$$

where $n! = 1 \cdot 2 \cdot 3 \ldots n$

Each of the succeeding factors in this equation represents the effort required by behaviors which are brought into play as the tunnel becomes longer·

C may be designated as the work involved in the decision to begin excavating a tunnel.

CX may be designated as the work involved in excavating the dirt from the surface at the end of the tunnel, irrespective of its transportation. CX will be directly proportional to the length of the tunnel.

$C\dfrac{x^2}{2}$, the primary transportation factor, may not be designated quite so simply. However, the following logic will show the nature of this factor: Let us suppose that rats A and B each dig a tunnel of the same length ($d/2$). After finishing this tunnel each again constructs another tunnel of similar length. Rat A makes this second tunnel a continuation of the first. This means that any dirt excavated from the second tunnel must be carried back through the first tunnel to be deposited on the ground. However, Rat B initiates his second period of work at the surface of the earth and so has a much shorter distance to transport the dirt (see fig. 46). In other words, the longer a

45

FREQUENCY x LENGTH (i.e. EFFORT) = CONSTANT

$f = k\dfrac{1}{d}$

$f = (64)^{\frac{-d}{1070}} + 1$

RELATIVE FREQUENCY (f)

LENGTH OF TUNNEL SEGMENT IN
MILLIMETERS (d)
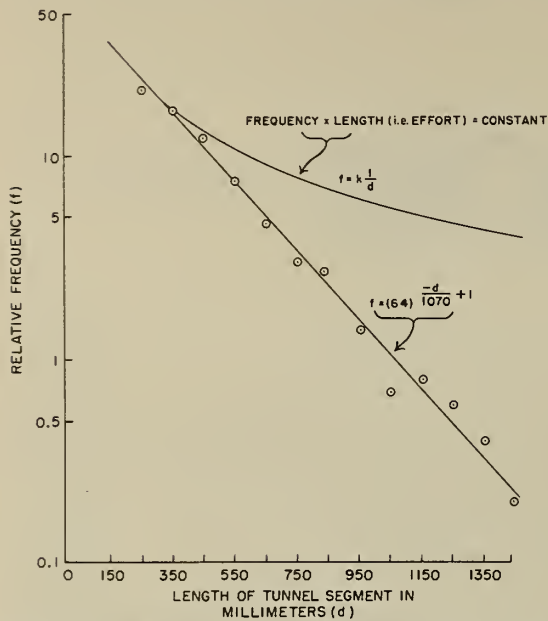
Figure 45.—Lengths of tunnel segments—3-point moving average. Note that the frequency of tunnel segments declines more rapidly than does an inverse proportionality to distance.

tunnel segment, the proportionately greater will be the work involved.   In summary:

Type of work

1st term: C = decision
2d term: CX = digging from end of tunnel
3d term: $\dfrac{CX^2}{2}$ = transportation

Later terms, to $C\dfrac{x^n}{n!}$, will presumably involve other behaviors such as the likelihood of the dirt carried in the mouth crumbling, stopping to defecate, et cetera.   The farther the tunnel is extended from the point of decision, the more behaviors come into play.   The relative influence of each of these behaviors (i.e., sequential terms in the equation) may be seen diagrammatically in figure 47.

At any d, the effort equals the sum of the values of the curves for the factors C to $C\dfrac{X^n}{n!}$.

That is to say, at the shorter distances the effort is mainly determined by the decision (C) and digging (CX) terms.   For the longer length tunnels the later behaviors $\left(\text{terms}, C\dfrac{X^2}{2.3}\ldots C\dfrac{X^n}{n!}\right)$

make a relatively greater contribution to the total work involved.   I am indebted to Mr. James U. Casby (formerly of the Army Medical Service Graduate School) for the concepts presented in this section on the "Pattern of work as reflected in burrow construction."

J. *The Location of Chambers.*   At the end of some tunnels rats make enlargements which may be used for either nests or storing food.   Distances from the center of chambers to the outside were taken for 178 chambers from the 44 burrows (fig. 48).   The half of the records involved in the shorter distances appear to be approaching an asymptote.   Some factor existing outside the burrow must be sufficiently ameliorated by the time a distance of 550 mm. is attained that the internal environment of the burrow is at an optimum.   Beyont this point the character of the distribution abruptly changes to one of an exponential equation governing the lengths of individual tunnel segments.   This section of the curve is probably a direct reflection of the fact that where one tunnel segment branches off from another the laws governing the frequency of the sum of the lengths of two or more tunnel segments follows closely those governing the frequency of single tunnel segments.   The reason for believing this is that slightly more than 50 percent of the chambers occur at the termination of two or more tunnel segments from the outside.   An analysis of four of the larger burrows gave the following:

Number of tunnel segments between
chamber and nearest exit to the outside. . 1   2 3 4
Number of chambers. 28 30 6 4

K. *The Balance Between Types of Tunnel Segments, and its Relationship to Social Organization.*   Three types of tunnel segments may be discerned: (a) Blind.   These include all those whose terminal end is without bifurcation or enlargement into chambers.   (b) Exit.   These include   all   those which connect on one end with an opening to the surface.   (c) Internuncial.   These include all those which do not connect with an opening to the surface but which have either a chamber or another tunnel segment at either end.

The proportion of the total formed by each of these three types of tunnels changes as the size of the burrow increases (see fig. 49).   While the burrow is in its initial stage of expansion, up to 10 tunnel segments, there is an increase in the blind tunnels until a stable level of approximately 15 percent is reached.   The exit tunnels gradually

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RAT A · RAT B

EFFORT PER UNIT OF LENGTH

LENGTH OF TUNNEL · LENGTH OF TUNNELS

$$\text{AREA } \triangle: \quad \frac{d^2 M}{2} \qquad \frac{d^2 M}{4}$$

IS PROPORTIONAL TO EFFORT
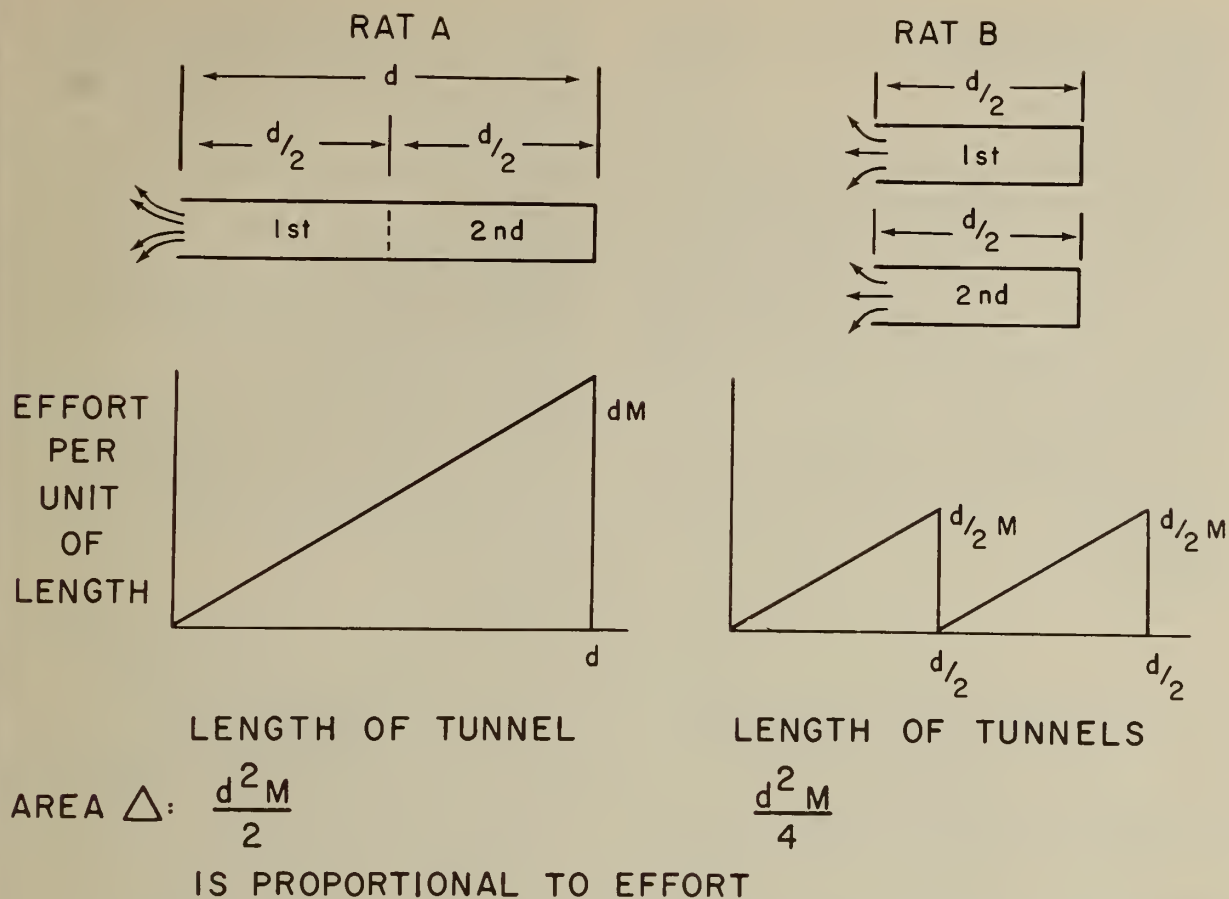
Figure 46.—Diagrammatic explanation of the transportation factor. Effort involved in transporting excavated dirt increases proportionately more rapidly than does the corresponding distance over which transport takes place. M=rate of using effort. Arrows indicate removal of dirt at entrance to tunnel. See text.

decrease until they form one-third of the total tunnels. In this structural balance internuncial tunnels cannot appear until there are at least three segments. As the size of the burrow increases internuncials increase in frequency until on the average they form approximately one-half of all tunnels. The development of this structural balance reflects certain behavioral characteristics of the rat: (a) The blind tunnels reflect the tendency to dig. (b) The frequency of exit tunnels is bound to the previously discussed response (see fig. 48) of locating the chambers not too far removed from the outside. (c) The origin of internuncials probably reflects several components of behavior including: (1) The cessation of a particular pattern of work as a function of the increasing magnitude of effort required for its continuance. (2) The inhibition of one behavior in favor of its replacement by another (i.e. nest cavity construction versus tunnel digging). (3)

Redirection of digging toward a parallel tunnel. (4) Maintenance of contact with both ends of a tunnel segment.

In the light of these considerations we can make an approximation of the optimum size of a burrow. Certainly optimum conditions cannot be said to be complete until the proportion of blind tunnels has become constant. This beginning has been arbitrarily assigned as 16 tunnel segments. The upper limit of the optimum range has been assigned at 40 segments, the burrow size where internuncial and exit tunnels approach an asymptotic level. Even under the most favorable conditions, the crowding of rats about burrows consisting of more than 40 segments begins to produce marked strains on the social stability of the groups.

From the curve of number of rats per exit, shown in figure 50, the number of adult rats inhabiting burrows within this optimum range may be calibrated.

47

Number of tunnel segments.................. 16 to 40
Number of exits........................... 8 to 15
Number of adult rats...................... 7 to 12
Number of chambers........................ 4 to 11

These estimates are interesting in their indication that the presumed optimum range of size of burrows accommodates a number of adult rats over the range of normal litter size. This is only one line of evidence which suggests that the group size which adults tolerate is determined by the number of associations made prior to weaning among sibs.

From figures 49 and 50, and from table 5, one can derive something of the characteristics of an optimum burrow (table 6). We shall take 40 tunnel segments which is at the upper limit of the optimum range.

When these considerations are coupled with the tendency of rats to develop circular burrow systems, which have a higher frequency of internuncial tunnels toward the central, older section of the burrow (see fig. 21 for the South Alley Burrow), it is possible to arrive at a hypothetically ideal burrow structure. This is shown in figure 51. From this figure it is possible to visualize the altered structure of a burrow system when it develops for a similar period, but with an orientation along a fence or similar elongate vertical structure. If the outer circle is severed at "A" and the inner circle of the burrow system severed at the three points designated "B" and stretched out into an essentially straight line the two burrow systems then have the differences in structures shown in table 7.

$$\frac{cx^4}{2\cdot3\cdot4} \qquad \frac{cx^3}{2\cdot3} \qquad \frac{cx^2}{2}$$

cx

CONTRIBUTION TO TOTAL EFFORT (W)

c

d

LENGTH OF TUNNEL
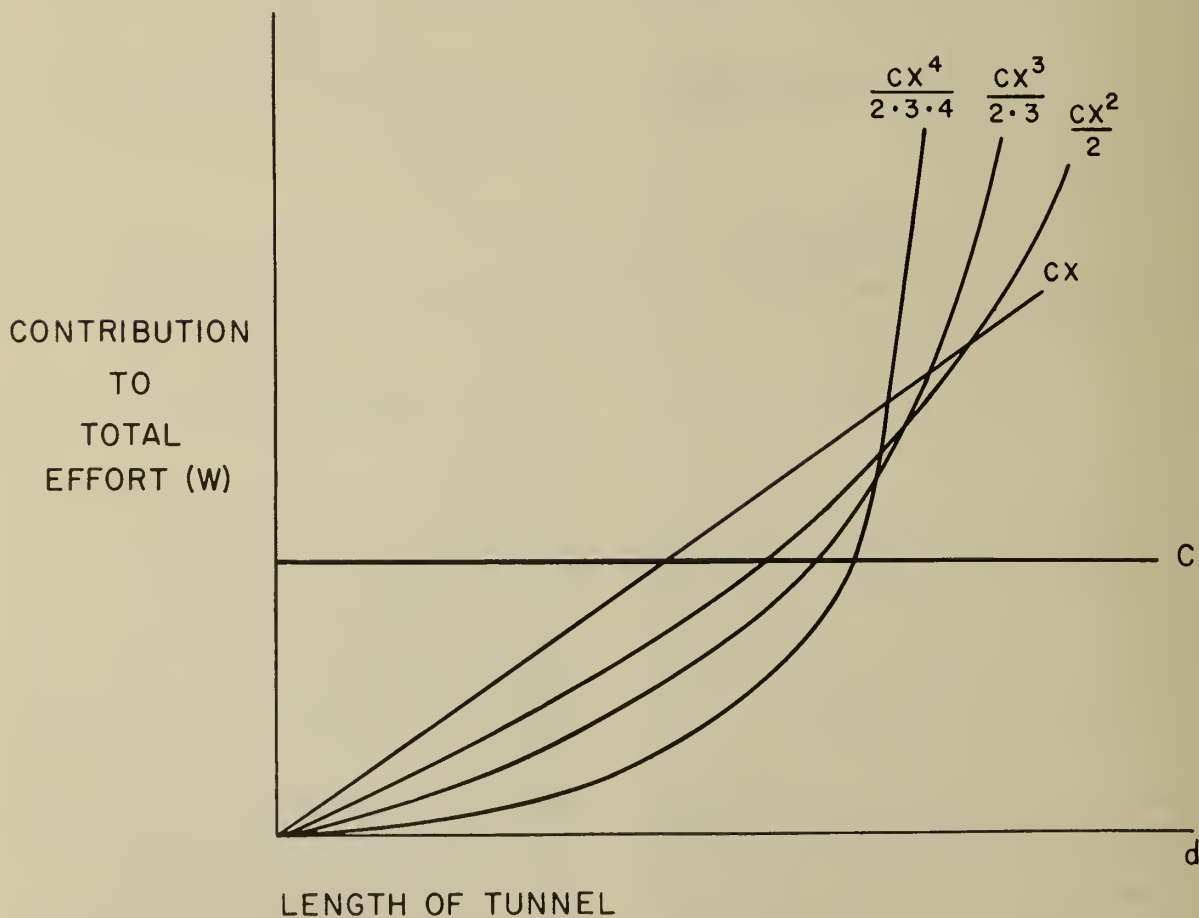
Figure 47.—Relative contribution by successive behaviors to the total effort involved in constructing a tunnel. According to this notion the effort in constructing a tunnel of a given length is equivalent to the sum of the values for each curve where a vertical line drawn from the abscissa intersects them.

TABLE 5.—*Summary of characteristics of 44 burrow systems*

Item	Total number	Mean
1. Exits......................	300	6. 8
2. Chambers:		
a. Terminal................	38	. 9
b. Tunnel at either end......	160	3. 6
c. Total...................	198	4. 5
3. Tunnel segments:		
a. To exits................	316	7. 2
b. Blind..................	111	2. 5
c. Internuncial............	287	6. 5
d. Total..................	714	16. 2
4. Number of weaned rats.........	243	5. 5
a. Rats per exit............		. 8
b. Rats per chamber........		1. 2
c. Rats per tunnel segment...		. 34

TABLE 6.—*Characteristics of a presumed optimum burrow housing 11 adult rats and having 17 exits* [1]

Tunnel segments		Chambers	
Kind	Number	Kind	Number
To exits..........	13	Terminal.......	2
Internuncial.......	20	Tunnel at either	
Blind............	7	end.........	8
Total........	40	Total.....	10

[1] See figure 50.

TABLE 7.—*Structural differences between circular and elongate burrows*

Structure	Circular burrow	Elongate burrow
1. Maximum distance across bur-row.	7.5 to 8.0 ft.	18 to 20 ft.
2. Balance between "internuncial" and "to-exit" tunnels:		
a. Internuncial...........	27 (67.5%)	20 (44.4%)
b. To exits..............	13 (32.5%)	25 (55.6%)

3-POINT MOVING AVERAGE OF THE PERCENTAGE FREQUENCY DISTRIBUTION

$$f = (63)^{\frac{-d}{1490} + 1}$$
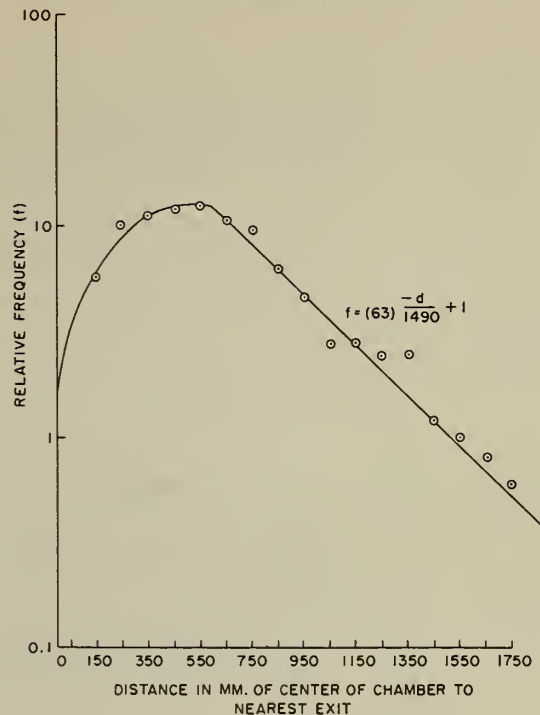
Figure 48.—The distance of burrow chambers from the nearest exit.

These are the two fundamental differences between the structure of the two types of burrows. These differences must ultimately have profound effects upon the lives of the rats inhabiting them. Within the circular burrow and on the surface above it each inhabitant will be brought into frequent and nearly equivalent contact with every other inhabitant. On the other hand, each inhabitant of the elongate burrow will have relatively fewer contacts with its associates and these contacts will be such that the farther apart in the burrow two individuals live the fewer will be their contacts. These conclusions are derived from the known differences in burrow structure, and upon the observation that each rat tends to concentrate its activity within and over a restricted portion of the burrow.

The comments in the above paragraph refer particularly to the frequency of social contacts that each individual has with its associates. However, the differences between the two types of burrows may also produce profound effects upon the ability of the individual to conceptualize and integrate the complexities of its physical environment. In the circular burrow, even though an

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Figure 49.—Relative frequency of types of tunnel segments in relation to the size of a burrow. The number of tunnel segments per burrow is listed on the abscissa. This figure is based on the classification of 712 tunnel segments from 44 burrows.

individual inhabits only a portion of the burrow it is possible for it to experience, and presumably conceptualize, the situation of alternate or multiple routes of travel between goals. Rats living within the elongate burrow have relatively fewer opportunities for experiencing alternate routes of travel to goals and thus may develop a more sterotyped, less complex conceptualization of possible modes of action. It is suspected that such differences in conceptualization of the complexities of the physical environment have reverberations on the ability of the individual to develop complex social interrelationships.

In fact the hypothesis is forwarded that there are mutual cause and effect interrelationships between social integration and burrow integration. The effect of social integration upon the mainte-

nance of burrow integration is reflected in the histories of the South Alley Burrow (fig. 21) and the North Alley Burrow (fig. 22). As will be documented later (p. 204) the greater social integration of the inhabitants of the South Alley Burrow is reflected in (a) a higher reproductive rate, (b) fewer males per female, (c) higher rank in the social hierarchy by its members, and (d) more rapid growth rate of the individual members. These two burrows—and their contained colonies— have histories of identical duration in time. When the study was terminated in May 1949, the rats in the South Alley Burrow had maintained the older section of the burrow system in fair repair and in direct connection with most of the newer sections. By this time the rats of the North Alley Burrow had allowed the older sections to become
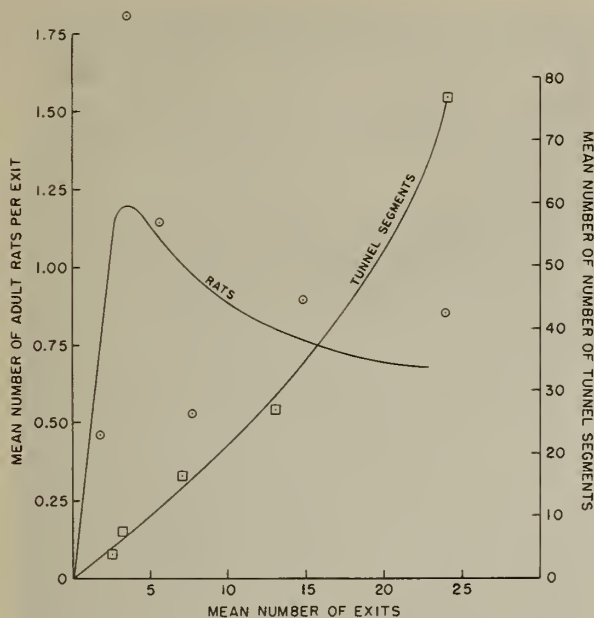
Figure 50.—Relationship between number of exits, the size of the burrow, and the number of rats inhabiting the burrow. In the estimation of densities of rats from sign surveys, a rough rule of thumb is that there is slightly less than one rat for each active burrow exit. There is no regularity of the relationship between chambers per exit and number of exits. Therefore the mean of 0.66 chambers per exit must be used for any further computations.

quite disintegrated. In fact, it remained as five completely isolated segments and two separate arms which connected with the newer portion of the burrow system.

The relationship between elongate burrows developed along fences and the ability of rats to maintain them through time is reflected by two burrows which arose about the same time in November 1948 (see fig. 14). One began in the South Alley near Passage 2. The second began in the North Alley near Passage 3. On the basis of the four criteria mentioned above each of these colonies was less well integrated socially than the neighboring older colony.

This instability of the social structure was no doubt partially responsible for the rapid disintegration of these two burrows following their initial expansion to a size approximating that of the hypothetical elongate burrow system discussed above. By May 1949 the North Alley Passage 3 Burrow had so completely disintegrated that no rats were then living in it. At this time the South Alley Passage 2 Burrow had fragmented into three separate units, despite the fact that it was inhabited by one adult male, four adult females, and five

juveniles. It is believed that the elongation of these burrow systems was a factor contributing to the disintegration of both the social structure of the group and the physical structure of the burrow. The later discussion of colonies c and k (tables 46 and 55, pp. 206 and 214) as they existed in the spring of 1949 pertain to the rats inhabiting these burrows.

L. *Harborage Boxes and Nests*. The wooden harborage boxes placed in each triangular area of the pen permitted observations that were not possible in the burrows. At this point comments will be confined to nests. Other activities relating to the usage of harborage boxes will be noted under other topics.

Periodically the observer removed nests and other material deposited by the rats in the harborage boxes. This was done to prevent the boxes from becoming too fouled with rotting organic matter. Rats rarely cleaned out such material from the harborage boxes as they did regularly from burrows. In fact removal of old nesting material from harborage boxes was noted on only three occasions.

Descriptions were prepared of a few of the nests observed. The number of times each of the five major materials were observed was as follows: pine fasicles (32), honeysuckle vine (38), leafy stems of

HYPOTHETICALLY IDEAL BURROW STRUCTURE
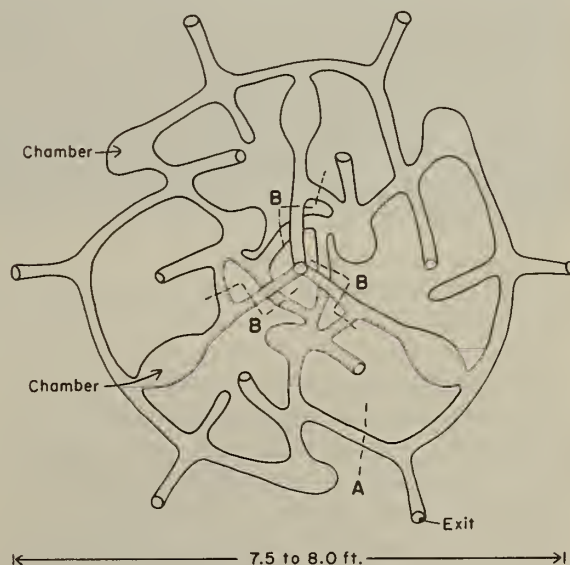
Figure 51.—The hypothetically ideal burrow structure for the Norway rat. As discussed in the text, this pattern was derived from several separate approaches as to what constituted an ideal burrow system.

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goldenrod (33), grass (34), and leaves as lining (35). No pine fasicles or honeysuckle vine were ever used in nests in Area I. This corresponds with the fact that no pine trees or honeysuckle vine grew in this area. Similarly 0.33 of the material in nests in Areas I and II consisted of grass whereas this formed only 0.12 of the nesting material used in Areas III and IV. Again this corresponds to the fact that Areas I and II were more open and grassy than Areas III and IV. These observations are in harmony with other similar ones which support a general conclusion that rats utilize for nests only such material as is found within the immediate vicinity of the nest site.

A common characteristic of all nests is an unorganized base. The materials used in construction of the base appear to have been brought in and just dumped in one spot. Usually the base is composed of coarse stems greater than $\frac{1}{16}$ inch in diameter. The simplest type of nest, designated as the *pad*, has only a few flat objects, such as oak leaves or bits of paper, laid over the base. Such nests were usually just large enough to elevate one rat above the floor. Fighty-six (0.473 of the total) recorded nests were of this simple type.

When the initial basal structure is larger, the nest gradually assumes a greater degree of organization. Frequently, the grass or stems used become finer in texture, and are tightly interwoven to form a cup-type nest. Leaves or paper is again used as a lining. This floor of the nest is elevated 2 to 6 inches above the floor of the box. Three to five rats can sit comfortably in the cavity of one of these larger nests. On two occasions seven adults were observed in a well-kept nest. Eighty-four (.462 of the total) recorded nests were of this more complex type.

Occasionally, the process of weaving is continued until it forms a globular *hooded* nest with a single entrance on one side just large enough to provide access for one rat. Hooded nests are normally associated with the birth of young rats. However, by no means do all parturient females achieve this most complex level of nest construction. I never observed more than three medium-sized adult rats in a hooded nest at the same time. Twelve (0.066 of total) recorded nests were hooded.

Organized nests rarely survived simultaneous usage by more than five adult rats. Both cup- and hooded-type nests become flattened with such intensive usage. In contrast to cup- and hooded-type nests, which were usually quite clean, the flattened nests were fouled with feces. The fact that the harborage boxes were so much larger than the nest chambers built by the rats in their burrows seemed to serve as an additional inducement toward the formation of harborage aggregates of more than seven individuals. These aggregates occasionally attained the size of 18 to 20 individuals. One of these harborage aggregations, which had 14 individuals, is shown in figure 57. With these larger aggregations, which are usually composed of the socially lower ranking individuals, the harborage box soon becomes so filled with nesting material that the rats when curled up asleep have their backs nearly or actually touching the lid. This nesting material becomes a soggy flat mass saturated with urine and covered with a thin mat of trodden feces until no semblance of a nest remains. One possible factor associated with the formation of these larger harborage aggregates among socially low ranking rats is their smaller size. The more rapid heat loss presumably experienced by these smaller individuals should be ameliorated by their grouping together. In figure 53 the snow may be seen to have melted off the lids of two harborage boxes which contained such large aggregations.

Examples of the several types of nests may be seen in figures 52 to 56.

Beginning shortly after the rats were introduced it was always possible to encounter nests in boxes where no rats were at the time harboring. Some would be in good repair. Those not in good repair were frequently found to have been repaired by a later date. Usually it was only necessary for the rats to add a little lining material to the nest. This represents a means by which the rats conditioned their environment to make it more favorable. When a rat was disturbed by the observer, even though this involved only a momentary opening of the lid of the box, it would normally shift its place of residence. At such times the rat could find another nest in a neighboring harborage box, which at most needed only slight repair.

Pad nests inhabited by a single individual were occasionally encountered in the patches of honeysuckle. Similar nests were encountered at times where the traps were piled for storage. An even more unusual location for a nest was encountered on the campus of the Ohio State University. A Norway rat had relined an old robin's nest some 12 feet above the ground in a mulberry tree. It is the occasional use of such out of the way retreats by

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Figure 52.—Nest made entirely of broom sedge in harborage box 32 on May 10, 1948, by socially low-ranking male No. 8. Note that there are fresh feces (dark and shiny) and moldy feces (white) on the bottom of the box but none in the nest.

solitary rats that makes it nearly impossible to say with surety that a region suspected of harboring no rats, actually does not.

Rats of both sexes and ranging in age from 25 to over 400 days of age have been observed to transport materials into the harborages. Nest building by females is frequently accentuated at about the time of parturition. In most cases the newborn young were merely observed in a large well built nest on the morning following their birth. At such times other large new nests were frequently found in neighboring harborage boxes, and the inference has been made that these were also built by the female who gave birth to the observed litter. Such bursts of nest building occurred only in association with the birth of a litter. In four instances large nests were constructed the night prior to that on which parturition occurred. When the mother with her newborn young were disturbed only to the extent of quickly opening and then closing the

Figure 53.—Nest made entirely of leafless sections of honeysuckle vine. The lining is of oak leaves. Nests are frequently lined with leaves, although paper may be similarly used when it is available.

lid of the harborage box, she would frequently build a nest at another location and transport her young there. The young often disappeared following this minimum disturbance, so it is assumed that the mother destroyed them. On two occasions the young of primiparous females were found on old pad nests. The infrequency with which primiparous females reared their young is perhaps associated with the poor development of the nest-building behavior and allied maternal behaviors.

There are two other closely related behaviors exhibited by females with young. The first of these is the covering of the young with nesting material. On two occasions females were observed nursing young in cup-shaped nests lacking hoods. Upon reexamination of the nest within 2 hours the mother was absent and the surface of the nest was flat with the young not visible. In each case the young were found in the nest depression

when this covering material was removed. The second behavior was that of sealing the lid with mud (p. 42).

2. Trails, Orientation, and the Utilization of Space

A. *The Growth of Trails in the Experimental Pen.* Rats usually confine their movements to the same routes through the same localities day after day. Resultant trails may even be detected over bare ground. More frequently the trails lead through vegetation. This vegetation is kept cleared from the floor of the trail, although it may form an arch overhead.

Even before the initial colonizers had the opportunity of increasing their numbers through reproduction a few trails began to appear (see fig. 59A for May 1947). At this early stage the

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Figure 54.—Nest (in upper left) in box 36. Although the next cavity is in one corner and elevated, the base covers the entire box. It is composed of honeysuckle vine and the terminal fascicles of pine leaves. Despite the peripheral location of this harborage box, more rats defecated here than in any other box. As the lining became soiled the rats brought in more nesting material, thus producing a gradual elevation to the structure. Most of the feces are moldy and whitish. Photograph taken May 10, 1948.

Figure 55.—Harborage box 1, May 10, 1948. Pad nest is at right center. Note the pile of goldenrod stalks to the left. These were cut and dragged into the box by rats. This behavior was particularly characteristic of the rats which inhabited area I during the entire history of the colony. The wooden triggers to the traps were similarly taken into the harborage boxes. One such trigger shows in the photograph. No suitable explanation for this behavior was apparent.

Figure 56.—Hooded nest in box 31, May 1948. It is made nearly entirely of freshly cut goldenrod stalks. Similar hooded nests were made of either grass or honeysuckle vine. Such hooded nests were much less frequently constructed than were the open nests such as shown in figures 52 and 53.

676–768 O—63——5

Figure 57.—Aggregation of rats in box 30 on December 22, 1948. In addition to the 14 seen here there were 9 others in this aggregate which were crowded into a burrow nest cavity (see fig. 33) immediately adjoining the box at the lower right. The unbalanced sex ratio of 17 males to 6 females was one indication of the low social rank of this large aggregate.

basic pattern of the trailway system was apparent. This pattern was one of trails connecting basic goals. One harborage is connected with an adjacent one; harborages are connected with sources of food; and had there been alternate sources of food, as is usually the case with natural populations, trails would have connected them.

The trails are normally just wide enough for a single adult individual to travel. Frequently, two individuals pass without showing antagonism. In such cases each appears to step slightly aside. The frequency of this event is probably not great enough to cause much widening of the trail. Unfortunately, a series of measurements of the

Figure 58.—Heat production by large aggregates of rats. The bare tops of boxes 30 and 31 may be seen in the upper right of the photograph. See also figure 33. At least 33 rats were housed in and moved between these 2 harborage boxes. The heat produced by these aggregates was sufficient to pass through the 1½ inches of wood and insulation board and melt a several inch covering of snow. Approximately 60 rats were using the mudstained trail to the right on this date, December 21, 1948. As was the case prior to the snowfall, the trails connect passages into burrow systems, into harborage boxes, or through barrier fences. Such passages into harborages were primary goals in spatial orientation.

59
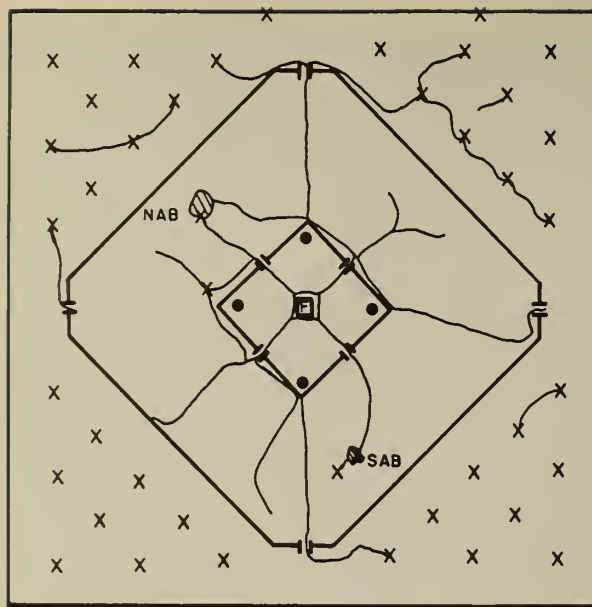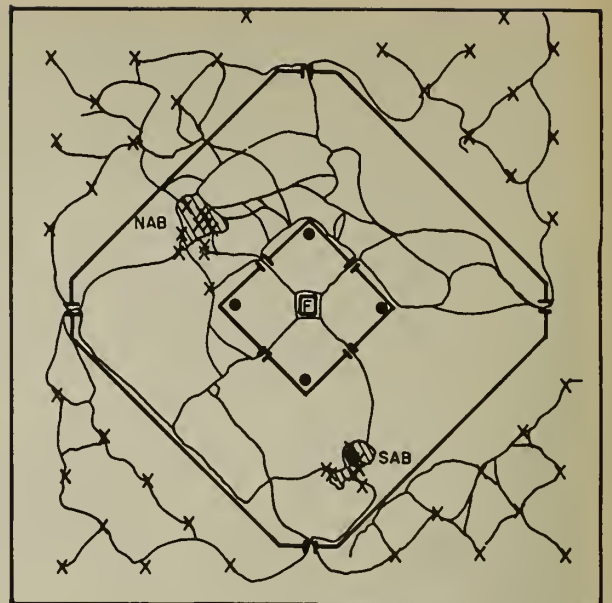
A - MAY, 1947   B - NOV., 1947

Figure 59.—Clearly discernable trails. X's represent tile entries to harborage boxes or entries through the soil into burrows. Crosshatched areas are mounds to burrows.

width of trails was not obtained. When an adult meets a juvenile along a trail going in the opposite direction, they may both maintain their direction of travel with the adult walking over the juvenile.

By November 1947 (fig. 59B) there had been a considerable increase in total amount of trails as well as an increase in the number of pairs of points between which alternate routes had developed. For example, from Passage 1 through the median barrier fence to Passage 6 into the Food Pen the number of well defined routes of travel had increased from one to three. Similar increases in alternate routes were apparent elsewhere. Also by this date most of the harborage boxes were connected to each of the immediately adjoining ones. This occurred even though many of the boxes were not used as daytime retreats. A rat in traveling from one harborage box to some more distant point would frequently enter and remain for a few seconds in each harborage box it passed. This momentary stopping at any place offering overhead cover was a characteristic behavior of rats.

By a year later in November 1948 (fig. 14) the pen had developed into a veritable mesh of trails. In addition to new trails leading from new burrows, and additional alternate trails connecting most goals, the one major new location of trails

was adjacent to the inner surfaces of both median and limiting barrier fences.

Surveys, other than the three illustrated examples, were made from time to time. From these it was possible to determine the total footage of trails for successive dates (See curve A in fig. 60).

These measurements define the degree to which rats biologically condition their environment. If this increase in trails is considered in an analogous fashion to that of the growth of an individual or the growth of a population, it may be described in terms of a "growth potential" and "environmental resistance."

During the first 3 months the growth potential of trails was slightly greater than 100 feet per month, but by the end of 9 months it had attained an apparently stable and lower rate of 45 feet of additional trails per month. However, just as an understanding of changes in growth rates of individual animals or of populations demands that growth be phrased in terms of the number of the biological units contributing to the increment, so we must consider trails in terms of the rats which produced them.

In terms of rats over 60 days of age each rat produced over 10 feet of trails per month during the first 3 months but by March 1949 the rate had fallen to approximately 0.35 feet per month per
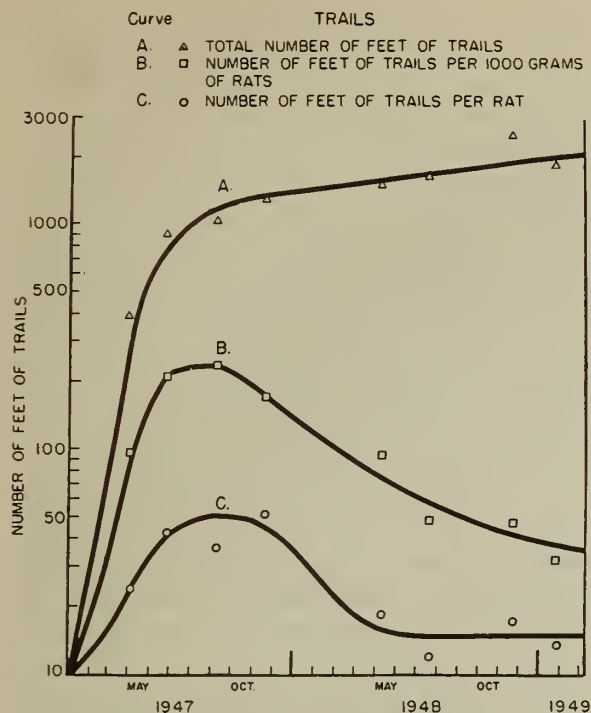
Figure 60.—The growth of trailway systems. All curves are empirically drawn to approximate the observed points. A. Increase in total feet of trails. The apparent continuous increase in the total feet of trails results from the fact that peripheral expansion was still possible. From figure 61 it is probable that the trails would have become stabilized at about 2,100 feet. B. This curve probably would have stabilized at approximately 34.3 feet (see remarks under C.) per 1,000 grams of rats on each following March 1, on and following March 1, 1950. March 1 marks the approximate initiation of the breeding season. C. Number of feet of trails per rat. Note that this curve becomes essentially stable at 15 feet per rat. On March 1, 1949, there were 127 rats with an average weight of 437 grams or 2.288 rats per 1,000 grams. If the same sex-weight-age relationship continued to exist at the initiation of future breeding seasons, we can calculate the expected level at which the number of feet per 1,000 grams of rats becomes constant. Fifteen feet per rat × 2.288 rats per 1,000 grams = 34.3 feet per 1,000 grams of rats.

rat. This naturally raised the question: "What contributed to this decline in rate?" For one thing it is quite apparent that as neighboring goals become connected with trails there is less need for the construction of new trails. New rats born into the population could then utilize and maintain preexisting trails. But this leads to greater contacts along trails. The rats' solution of this situation was the construction of alternate routes.

If one examines those sections of the pen in which systems of alternate routes of travel had already

been developed by November 1947 (fig. 59B), it may be noted that during the succeeding year (fig. 14) essentially no increase in amount of trails had occurred in these regions, although there had been slight alterations of position. Reflection upon this point suggested that failure to develop more trails in a given region is related to intolerances of rats to close proximity with other rats. The network of trails formed irregular-shaped polygonal cells whose centers were devoid of trails. Now let us assume that the distance across these cells is limited by a certain distance that one rat will tolerate the approach of another. Transects taken in a random direction across these cells will approximate the distribution of distances between rats on opposite sides of cells. Since the long axes of cells appear to have no regular compass orientation transects taken in fixed directions should closely approximate random directions. Therefore transects were taken for the survey of November 1948 (fig. 14) at 5-foot intervals in both NE to SW, and SE to NW directions. For the 554 measurements thus taken the mean was 5.90 ft. ($\sigma=4.05$ ft.). In a crude way this may represent an "approach tolerance distance." It is this inferred approach tolerance distance that constitutes the environmental resistance to the continued growth of trails.

An attempt was also made to approximate the average diameter of cells for this November 1948 survey. Two measurements were made of each cell: (a) the greatest distance across it, and (b) the greatest distance across the cell at right angles to this first measurement. The mean of these 245 measurements was 7.95 ft. ($\sigma=5.61$ ft.). There still existed a few areas of the pen where the typical pattern of cell development of trails had not yet been completed. Even were these to develop trails in a similar fashion, and even if some of the larger cells were to be divided by intervening trails it is unlikely that the approach tolerance distance characteristic of rats would have permitted more than 3,000 feet of trails to develop in the pen even if the colony had been maintained after 1949. Curve C in figure 60 suggests that as the population began to grow rapidly (see also fig. 146) at least 15 feet of trails are required per rat. Thus this method of viewing the data suggests that the colony would never have exceeded 200 rats.

There was actually a decline in the number of feet of trails between November 1948 and the beginning of the breeding season in March 1949.

This accompanied the drop in population to 127 rats (fig. 146) due to mortality and an increase in average weight to 437 grams. At this latter date the number of feet of trails per 1,000 grams of rats was near an asymptotic level of 34.3 grams (fig. 60B). Consideration of this number of feet as a fair approximation of the asymptotic level leads to another estimation concerning density of rats. The number of feet of trails per 1,000 grams of rats as a function of total feet of trails is shown in figure 61. This curve presumably results from an interaction between (a) the ability of available rats to construct trails (growth potential), and (b) the tolerance of rats to too close approach by other rats on neighboring trails (environmental resistance). Beyond the last trail survey in March 1949 one might extrapolate the curve. Such extrapolation indicates a marked diminution in the amount of trails per unit weight of rats. However, we have already seen from figure 60B that one could not expect the number of feet of trails to drop much below 34.3 per 1,000 grams of rats. Thus an upper

limit of approximately 2,200 feet of trails results beyond which trailway expansion cannot exceed. This amount of trails is that which should have existed by the beginning of the breeding season in March 1950 with 146 adults.

By two lines of reasoning the usage and development of trails by the rats led to estimates of an upper level of density characteristic of the initiation of future breeding seasons. Despite the several crude approximations inherent in this reasoning, a later self-restriction of the population to 146 to 200 individuals is quite in harmony with other lines of evidence regarding population growth.

It has long been recognized that competition for food is a potent factor in contributing to the force of environmental resistance in limiting population size. More recently Davis (6) has pointed out that territoriality is also an important phenomenon contributing to environmental resistance. Similarly the manner in which rats construct and use trails modifies the intensity
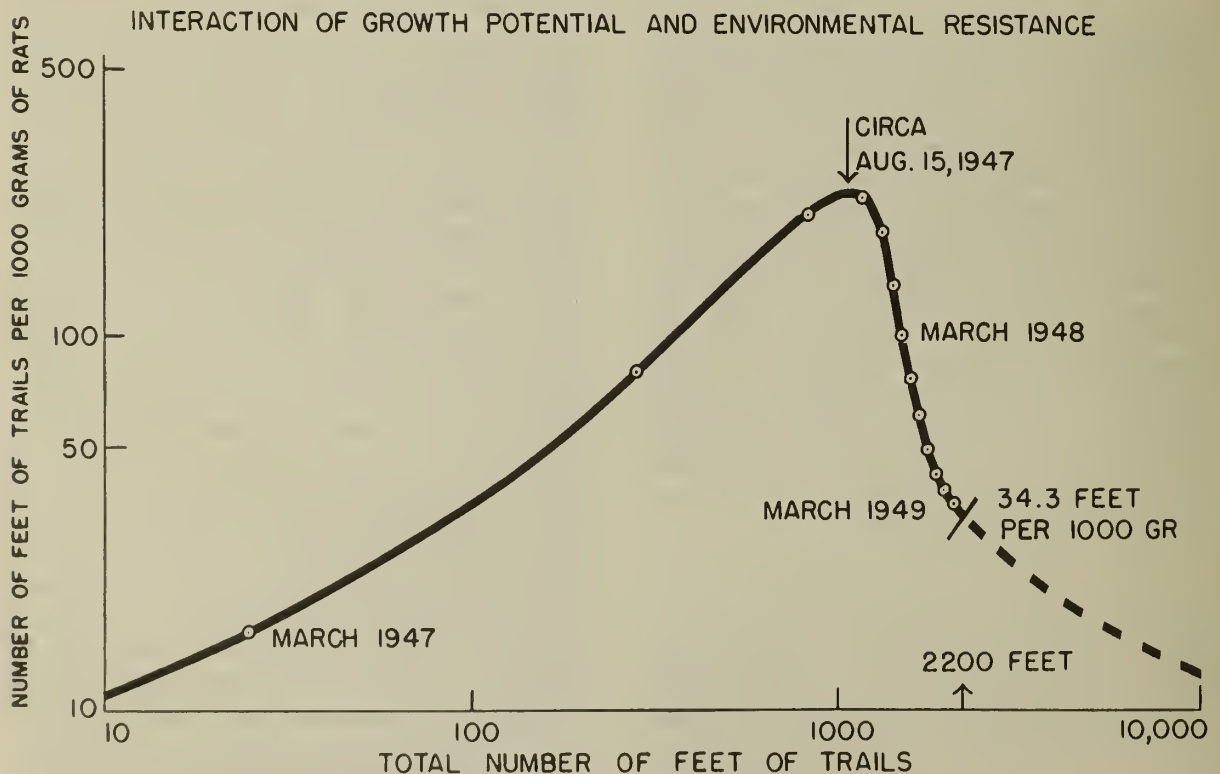
Figure 61.—Trailway systems as indicating the interaction between growth potential and environmental resistance. Growth potential is here considered in the light of the ability of rats to construct trails; whereas environmental resistance is considered as all those factors which tend to inhibit the expression of this behavior. Environmental resistance was probably near maximum at 2,200 feet of trails, since according to figure 60 the minimum number of feet per 1,000 grams of rats was 34.3. Thus one might anticipate little increase in density of either rats or their trails beyond the termination of the study in June 1949.

with which a particular area can be utilized. Therefore, such limitations to how space is used must contribute to the action of environmental resistance in retarding population growth, despite an excess availability of food and harborage in satisfying more basic needs. It is apparent from figures 14 and 59 that the distribution and density of goals affects such orientation responses. Furthermore, the character of the physical structure of the environment may affect the frequency with which an individual moves about particular portions of its environment when all other aspects of the environment are identical (*11*). These considerations point to the fact that the distribution, type, and density of goals are variables which influence population ecology and social behavior. Extremely little experimental research has been done in this area, although the leads which exist indicate that if they are followed up systematically they will produce many valuable concepts.

B. *The Position of Trails with Reference to Physical Objects*. Although there is a considerable tendency for trails to be developed along the shortest or least impeded route between a point of orientation and a goal, it is, nevertheless, apparent that objects along the route will produce deviations. Where no impediment existed along a route and no physical objects occurred within 18 inches to either side of the shortest route between two points, an essentially straight trail usually developed. This was the typical situation between the corners of the Food Pen and the passages through the median barrier fence (see fig. 62). If, however, an object such as a box trap was placed within 18 inches of the straight trail, the rats deviated from the preexisting trail toward and along the object. Such an example is shown in figure 63, in which the trail is first deflected to the right toward one group of traps, while a few feet farther along it is deflected to the left toward another group of traps. Where minor impediments to free travel exist, such as grass, herbs, vines, and similar vegetation, the rats gnaw and remove them. This frequently results in a partially or completely arched-over trail (see fig. 64). Where an unsurmountable barrier exists the rats may initially start out in the direction of the shortest distance between the point of orientation , and the goal. When the barrier is encountered, the rat follows along it until a passage through or around the barrier is encountered. Continued

experience with the barrier rapidly modified this initial behavior to one in which the route of travel was directly from the point of orientation to the passage through the barrier, whereupon the movement was again more directly goal oriented provided no other barriers intervened. It was such a sequence of events which prevented the development of trails adjacent to the outer surface of the median barrier fence as rats traveled from their places of harborage in the areas toward the Food Pen.

The most characteristic pattern of trails within the pen was their orientation toward vertical signs, such as tree trunks. Some of the movement of rats toward trees is undoubtedly associated with the attraction toward them as a source of over-head cover. The orientation of trails with respect to poles or trees without leaves was sufficiently frequent to indicate that the vertical object itself is the prime factor. An examination of the position of the trails with reference to trees in November 1948 (fig. 14) provides many examples of this relationship. A specific example may be more instructive. The trail between the North Alley Burrow and Passage 3 through the median barrier fence will serve as the example.

A number of surveys are available for this trail. The more pertinent ones are shown in figure 65. On May 15, 1947, (A) there was no trail through this portion of the North Alley. The position of the 17 trees are indicated and numbered. By November 22, 1947, (B) the basic route of travel by these trees had been established, although the goals being connected were the North Alley Burrow and the Food Pen via the East Alley. At this time there was insufficient travel between Areas II and III and the North Alley Burrow to produce a trail from Tree 13 toward Passage 3. Judging by the trail produced on January 14, 1948, communication between these two regions had begun. During the morning of January 13, 1 inch of snow fell. During the afternoon a little more snow and considerable sleet fell forming an icy coat over the ground which completely obscured prior trails. Despite this event the rats reproduced a trail (fig. 65C) with essentially the same orientations to trees as had existed previously. Since prior cues of the trail itself, whether they are visual, tactile, or olfactory, must have been essentially absent, it is concluded that the present orientation with respect to the trees is an indication that the prior

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Figure 62.—Rat trail down path 3 from the north corner of the Food Pen to tile passage 3 through the median barrier fence, November 23, 1948. Note how the rats have worn a narrow trail down the middle of the 3-foot wide cleared path. The lightness of the path is due to a profuse growth of microscopic plants, cultured on the urine-and-feces-enriched soil. This illustrates the fact that even when rats cross bare, open spaces, they adhere to a restricted zone of travel.

trail through the vegetation also resulted from similar orientations toward vertical objects.

On January 24, 1948, 5 inches of snow fell between 8 a.m. and 6 p.m. The majority of the snow fell before the rats became active. It obliterated the trails existing over previously fallen snow. Even so, the rats again developed a trail (see fig. 65D) with essentially the same orientations to the

tree trunks. Such a trail is shown in figures 66 and 67.

The subnivean trail shown in figure 65E is discussed in more detail elsewhere (pp. 74 to 78). Although the point-to-point orientation is apparent in this figure, the visual orientation to vertical cues was no longer possible. Once the rats make contact with one vertical cue they must have

Figure 63.—Snow Trails approaching passage 1 through the median barrier fence and continuing down path 1 to the Food Pen. These trails were made during the preceding night of December 19–20, 1948, immediately following the termination of snowfall. Note the deflection to the right toward the first group of snow-covered traps and then a similar deflection to the left farther down the trail. This swerving of the trail was induced during the previous 2 weeks following the placing of the traps on either side of path 1.

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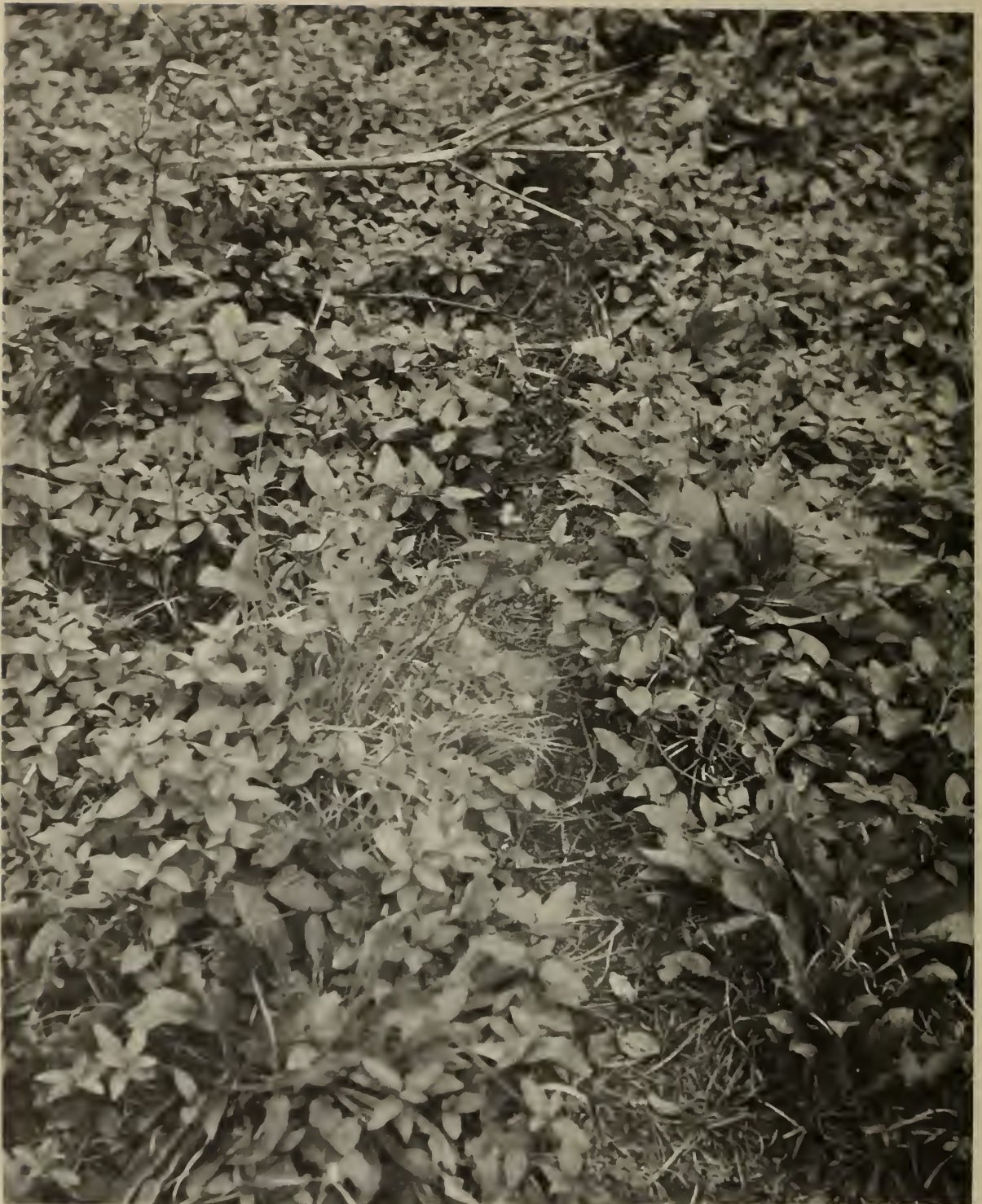
Figure 64.—Rat trail through honeysuckle and herbs in West Alley on October 6, 1948. Such trails were kept cut and cleared of all vegetation for a width just sufficiently wide to allow two rats to squeeze by each other.
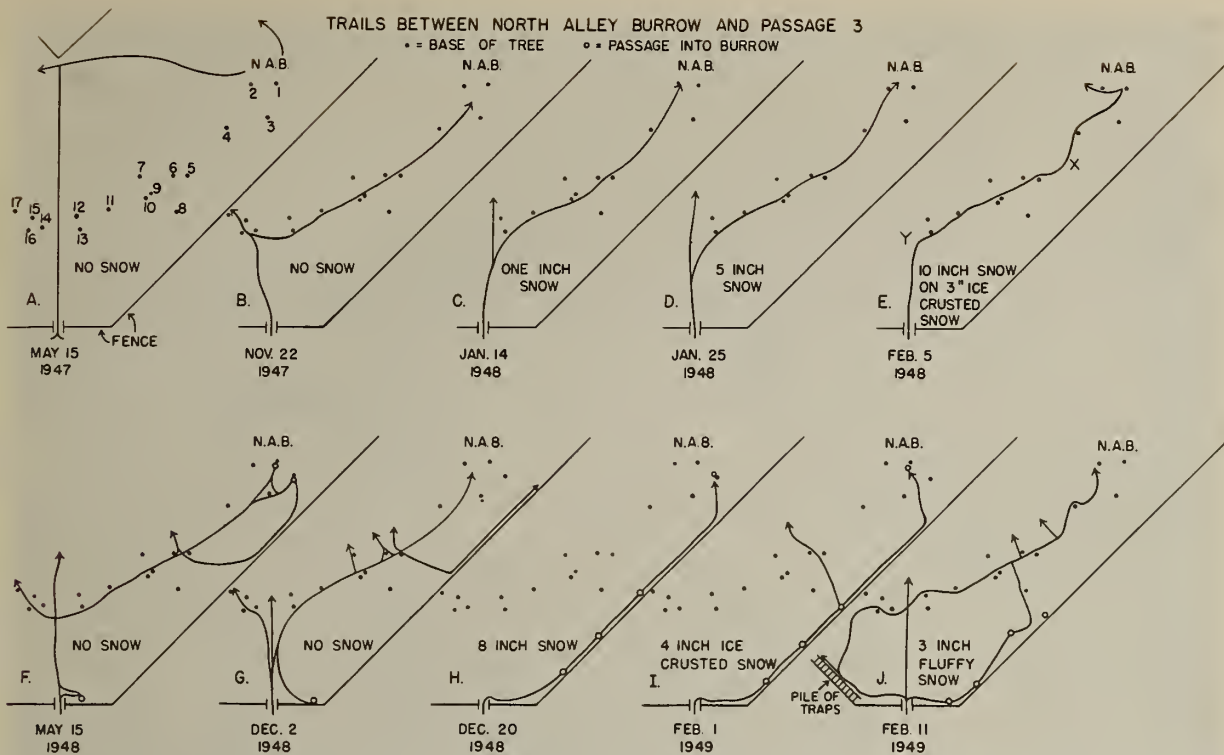
Figure 65.—The position of trails in relation to vertical objects. Dots represent tree trunks, solid lines represent trails, open circles represent entrances into burrows.

oriented to the next one kinesthetically. The deviation of the trail at X toward Area III and at Y toward the route of travel through the East Alley to the Food Pen indicates a conflict exerted between alternate goals upon the kinesthetic orientation of the rat.

Later trails as on May 15, and December 2, 1948 (fig. 65 F and G) indicate similar orientations to previous ones when there was no snow cover. However, as a burrow had developed in the North Alley along the median barrier fence from Passage 3, the attraction of the rats between this burrow and the North Alley Burrow was sufficiently great to inhibit occasionally the development of trails through the trees in the North Alley. Such situations are shown in figures 65 H and I, although the basic pattern of orientation toward tree trunks became apparent again following a slight snow on February 11, 1949 (fig. 65J).

Despite the fact that the trees in the above situation were all conifers there was no evidence from the trails through the snows that during such weather the rats were attracted to the trees as a place of retreat with respect to the overhead cover. When such an attraction to trees occurs there are invariably traces of urine and feces. Apparently only extremely momentary hesitations occurred along the trails through the snow. Similar close duplication of trails over the snow to those previously existing over the ground regularly occurred in such places as the West Alley where only deciduous trees were located. It was through the accumulation of a great many such records that I have become convinced that the visual orientation toward vertical objects plays an important role in the life of the Norway rat. Tactile, olfactory, and kinesthetic perception may enhance the point to point orientation under some circumstances, but where vision is possible, these other means of perception are certainly not requisite.

C. *The Wall Response*. The attraction of rats toward the surface of traps or similar objects placed near their trails has already been mentioned. This may be considered as a special case of the response to vertical cues. Vertical cues are frequently encountered about human habitations in the form of board fences or the walls of buildings. Examples of this may be seen in any mapping of a residential area inhabited by rats (see fig. 2).

Although the wall response is undoubtedly a real one, all trails adjacent to continuous vertical objects, such as fences or walls, should not be

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Figure 66.—The snow trail as an example of the operation of point to point orientation to vertical objects such as tree trunks. Despite a 4½-inch snow, the rats duplicated the pattern of the trail (fig. 14) previously existing over the ground. The black squares in the background under the small pine trees are tags marking passages into the North Alley Burrow. The view is that of looking toward the North Alley Burrow from the direction of passage 3. Note how the snow trail passes just to left of the tree (No. 5 in fig. 65A) in the left foreground and just to the right of the two trees (Nos. 4 and 2 in fig. 65A) in the right background. The snow trail shown here was made on the night of December 24, 1948. However, its route is nearly identical with that of January 14, 1948, shown in figure 65C. See figure 67 for companion scene of another section of this snow trail.

Figure 67.—Continuation of snow trail shown in figure 66. The trail in the upper right hand corner of this photograph joins the snow trail in lower left corner of figure 66. The tree in the center foreground is No. 11 of figure 65A.

interpreted as resulting from an attraction to the vertical surface. That an additional phenomenon is involved may be seen from an examination of the position of trails with reference to barrier fences in figure 14. It will be recalled that these fences were constructed of ½-inch mesh screen, a condition which may actually preclude the wall reaction

itself. Nevertheless, in certain places trails did run adjacent to these fences. The critical place to note is the median barrier fence. It will be seen that trails existed all along the Food Pen side of the median barrier fence. A much smaller amount of trails existed along the area side of this fence and these trails were in general much farther from the

fence. The lack of trails on the area side of the median barrier fence was not a result of the rats in the areas failing to build trails adjacent to fences. This is revealed by the fact that trails were located nearly entirely around the pen adjacent to the inner surface of the limiting barrier fence.

A general hypothesis will now be presented to account for these differences in the location of trails adjacent to barrier fences. This hypothesis is actually a formulation of the factors influencing the movement of the rat through space. The placement of trails along the barrier fence is merely a special case where the movement through space is modified by the intervention of a barrier. This latter response will be designated the "barrier wall response" in contrast to the "vertical surface wall response".

D. *The Movement-Through-Space Hypothesis.* Movements through space fall into two major categories:

1. Goal directed movements. Such movements are restricted to those directed toward those places of harborage and sources of food which are sufficiently permanent for learned responses to have developed. Movements toward such goals tend to be along the shortest route or the route requiring the least expenditure of energy.

2. Investigatory movements. A rat which is at some point of orientation and which has temporarily satisfied those basic needs, that may be fulfilled by responding to localized goals, will tend to make movements in a random direction away from the point of orientation. In the absence of any objects in the environment along the outward route of travel, locomotion will nevertheless be interrupted from time to time. This interruption presumably arises from the need of the animal to defecate, urinate, or rest. Once having stopped the animal tends to redirect its movement toward (a) the prior point of orientation, (b) some localized goal, or the point of stopping will itself become a point of orientation from which outward travels will radiate in a random direction. Such outward movements from a point of orientation will be of decreasing frequency of increasing length. This is discussed in more detail on page 82 under the section titled, Utilization of Space by Rats. Where cues, goals, or minor obstructions are abundantly dispersed through the environment the rate of decrease in the occurrence of ever longer movements will become accentuated. In other words, there will be even still fewer of the longer movements. This arises from the fact that these cues, goals, and minor obstructions will more rapidly bring about an inhibition of movement away from the point of orientation. Once having been inhibited the movement will more likely be redirected toward a prior goal or point of orientation.

These formulations on orientation will permit a more exact insight into what is meant by "home range" in mammals, than a mere statement that it is the area inhabited by the individual. Those few localized places of harborage and sources of food toward which the individual has developed learned orientation responses will form an approximate "center" of the home range. Outward movements from this center will be in accordance with the interaction of (a) the need for resatiation of a basic need at one of the localized goals, and (b) the density of more widely dispersed goals, cues, and minor obstructions. The boundary of the home range may be considered merely as some arbitrary statistical probability of encountering the individual at a given distance from the center.

When a physical barrier occurs not too far from the center of an animal's home range there will be a piling-up or concentration of activity at the barrier which is presumably equivalent to the amount of activity that would have occurred beyond the barrier had it not been present. This is the explanation forwarded for the presence of trails adjacent to the Food Pen side of the median barrier fence. It is also the explanation for the close proximity of the trail along the inner surface of the limiting barrier fence.

However, this leaves unexplained the fact that the trails along the outer surface of both the Food Pen fence and the median barrier fence do not nearly so closely approach the fence. In general, these trails approached no closer than eighteen inches of the fence, whereas, the trails on the inner surface of both the limiting and median barrier fences were usually less than 6 inches from the fence.

The orientation dependent upon the investigatory travel stipulates that there should be a moderately used trail immediately adjacent to the outer surface of the median fence. On the other hand, the more goal directed locomotion between the sources of food and harborage stipulates that there should be trails leading directly between the harborage boxes and the passages through the median barrier fence. Apparently what happens is that these two forces affecting the position of a trail are combined to produce a trail about half-

way between the two positions that these forces acting independently would have produced a trail. Another factor contributing to the fusion of these two trail positions into a single trail is the tendency of rats not to construct parallel trails too close to each other (see pp. 61–63).

E. *Orientation in Space*. The usage of trails constructed by the rats and the observed movements of rats with reference to goals and the physical configuration of the environment provide considerable information relating to the orientation of rats in space. Much of the insight into the means by which rats orientate their movements was provided by the reaction of rats to the obliteration of pre-existing trails by a cover of snow. Following snowfalls rats reproduced the hidden former trails with remarkable exactitude except for a few striking errors. Prior to observing these trails developing over snow, I had considered the use of trails as a very simple type of behavior resulting from direct perception of the trail itself. Once there dawned the realization that orientation might not be such a simple phenomenon, I sat down and tried to conceive of all the means of perception of the trail itself. These are as follows:

1. *Tactile perception*. When no snow exists one may assume that tactile perception is at least partially responsible for the orientation of rats along trails since the trails are kept clear of vegetation for a width just slightly larger than the bodies of the larger rats. However, the depth of the snowfall, particularly when accompanied by an icy crust on top, precluded any possible functioning of this type of perception.

2. *Visual perception*. At times the snowfall was as deep as to preclude the use of low-lying vegetation as visual cues. However, the barrier fences, the food hopper, the activity recorders at the Food Pen passages, as well as the trunks of the smaller trees, extend above the snow so that these might serve as possible cues for spatial orientation.

3. *Kinesthetic perception coupled with a "cognitive map" of the environment*. It is possible that in the total absence of reliably detectable cues that the rats can nevertheless duplicate previously established routes of travel. This requires a time-distance cognition in which the direction of movement and the angle of change of direction of movement is determined by kinesthetic stimuli which must have been responded to in a particular pattern or sequence before the rat moves from one known position toward another. If the rat can

detect distance through speed-time relationship it will be possible for it to arrive at a second position of orientation even though the normal cues for orientation are impossible to perceive. Once at this second point in space, another portion of the pattern of kinesthetic stimuli may come into play and be sufficient to induce an altered course of travel. Through an orderly sequence of such orientations a rat might be able to duplicate a fairly complex route of travel despite the absence of any obvious cues to facilitate orientation. It is realized that I am here postulating a rather elaborate mechanism for the rat. The reason for believing that such a mechanism is within the range of possibility of achievement by the rat is that many orientations have been repeated thousands of times. Each major section of a route of travel was covered between 20 and 50 times each night. This is a rather conservative estimate, but even so it gives a repetition frequency of 1,000 times per month and all the rats living in the pen during the latter part of January 1948 had at least 5 months of experience.

4. *Olfactory perception*. Although no conclusive proof can be presented to show that olfaction was not utilized in the detection of the previous trails, the following reasons will be offered as supporting the belief that olfaction was not operative in the observed orientations over snow:

a. The trails lay under 5 inches of snow, the uppermost portions of which formed a hard crust on certain occasions.

b. Even when a high wind was blowing rats were observed to duplicate exactly the trails existing under the unmarred snow.

c. Temperatures were below freezing.

d. The rate of movement of the rats over the snow was rapid. Although it was not the fastest run the rats were capable of, it might be characterized as a rapid lope.

Considering these four conditions it is difficult to conceive of olfaction playing a significant role in the orientation of trails over snow.

The next six sections (pp. 72 to 82) will cite specific examples of orientation from which interpretations of possible mechanisms involved are derived. Although focus of attention upon orientation began with snow trails a number of other observations relating to this topic will be included from other seasons of the year.

a. *Orientation over snow*. The conditions of snowfall during the day of January 24, 1948, were such

as to produce an unusual situation for the study of the manner in which rats orient in the absence of the perception of previously developed trails.

Between 8 a.m. and 6 p.m., 5 inches of snow fell. This was sufficiently deep to cover over the the grass and other vegetation, as well as the depressions in the vegetation mat, where the trails occurred through it. For more than an hour before the first rat was observed to be active at 6:10 p.m. a high wind was sweeping the pen and the snow had changed from soft flakes to a hard sleet-like condition producing a crust over the surface of the snow. This condition of wind and snowfall continued through the sequence of first activities of the rats which are recorded below. By 10 p.m. the snowfall had ceased.

We shall now examine the movements of the first three rats which dug through the snow and made excursions across the pen. In order to follow this discussion it will be necessary to refer to figure 14. In addition to trails existing at a later date in the history of the colony, this figure shows the positions of all the tree trunks, fences, etc.

First movement: 6:10 p.m. A rat left Hole 15 of the North Alley Burrow and proceeded eastward through the North Alley and through Passage 3 across to the outer limiting fence where it entered the nearest hole, by digging through the snow, of the burrow system which extends along this fence opposite Box 14. The interesting thing about this route of travel was that the rat passed directly by the trunks of seven small trees in an identical fashion to the trail existing through the vegetation under the snow. By the next morning there was a heavily traveled muddy trail over the snow along this same route (see fig. 65D)

Second movement: 6:22 p.m. A rat emerged from hole 1 of the South Alley Burrow and proceeded by the southwest corner of the Food Pen, a distance of approximately 10 feet, and thence along the west side of the Food Pen to Passage 8, through which it entered the Food Pen. It then went directly to the food hopper but without pausing turned left at 90° and went to and through Passage 7 and directly to and by Hole 15 of the North Alley Burrow. There were several small pine trees about the North Alley Burrow, one of which was very close to Hole 15. The rat then proceeded eastward along the trail of the first rat but stopped in a burrow by Passage 3. This was a route of travel exhibited previously by South Alley Burrow rats.

Third movement: 6:25 p.m. A rat left Box 9, crossed over the top of Box 7, circled around Box 3, dug through the snow to its entry, entered it, but soon left and proceeded to Box 2 where it behaved likewise. From Box 2 it went by Box 1 and to Passage 1 and directly across to the position of Hole 9 of the South Alley Burrow which was covered with snow. Here it paused momentarily before going to Hole 1 (the one left by the second rat), which it entered momentarily. It then went directly to Passage 5 of the Food Pen and thence across to the hopper where it ate.

Conclusion: From these three observations it seems apparent that rats can make rapid orientations which duplicate previously existing routes of travel in such a manner as to strongly indicate that orientation is a point to point orientation between such visible cues as fences, passages through fences, and the trunks of trees. Whereas, I do not believe that olfaction is utilized in these orientations, it may well be that the precise ability to dig through the snow into a burrow entry is facilitated by olfaction. When several rats live in a burrow, there must be some passage of warmer scented air through the snow. Thus, when a rat arrives at the approximate location of a burrow entry a slight pause and sniffing about may reveal the exact location. There is no evidence in these observations to indicate to what extent, if any, kinesthetic perception may play a role in such orientations. For further comments on this point refer to the discussion (pp. 74 to 78) of the subnivian trails developed on February 4 to 5, 1948.

Although these three movements were the only ones observed on the evening of January 24, 1948, in which rats traveled over the otherwise unmarred snow, the trails existing over the snow on the morning of January 25 further reveal the nature of this orientation.

Example No. 1: A path produced by the travel of a single rat from Passage 1 through the West Alley to Passage 8 of the Food Pen. In figure 14 it will be noted that the trunks of eight small trees protrude through the snow in the West Alley between these two passages. The distance between these two points is somewhat less than 35 feet, and I believe that a rat at Passage 1 can actually see Passage 8. At least I have seen rats turn to avoid another rat which was motionless and approximately 25 feet away. If a goal 35 feet away can be seen by a rat one might suspect that it would go directly across the snow between

these points. This however, was not the case. Instead the route of travel was roughly sigmoid in nature and made in such a way that it approached six of these tree trunks about as close as it was possible for the rat to travel. If these trees are numbered from 1 to 8 from Passage 1, the travel was: Directly to the left of trees 1 and 2, 2 feet to the right of tree 3, directly to the right of tree 4, 6 feet to the left of tree 5, directly to the left of trees 6, 7 and 8, and thence to Passage 8. One might suggest that the orientation toward the trees is for the purpose of their protective cover. However, I suspect this is not likely the case since three of the trees were bare deciduous ones. The orientation between trees 6, 7, and 8 is particularly instructive. Trees 6 and 8 were small pines whereas tree 7 was a dogwood. Had the rat been traveling between points of protective cover alone it would not have bent back to tree 7 which took it away from the most direct route of travel. Other similar instances could be cited but this one is typical.

On two later occasions (January 30 and February 1, 1949) the first rat in the evening to travel over new fallen snow between Passages 1 and 8 was observed. By these dates a post had been placed in the ground in the West Alley about half way between Passage 1 and tree 1. On each of these occasions the rat left Passage 1 and ran just to the right of the post and just to the right of trees 5 and 7 and to the left of tree 8 and thence to Passage 8. This route of travel formed essentially a straight line between the two passages. In each case the other rats who traveled between these two points followed identical routes so that by the next morning the surface of the snow was covered with a narrow muddy ribbon.

Example No. 2: Path between Box 1 in Area I and Passage 1. Prior and following the various snowfalls there was a single arched trail of travel between these two points. From Box 1 the trail led for a distance of about 5 feet through a group of bare stalks of the goldenrod plant. Each stalk was about one-quarter inch in diameter. Two feet beyond this clump of stalks the trail passed just to the right of one small tree and then 18 inches farther on it passed just to the left of the trunk of another small tree. From the latter the trail kept along a very slightly bent arch for a little over 6 feet, to Passage 1. This is shown in figure 68. The point of interest here is the reaction of the rats to the system of physical cues existing
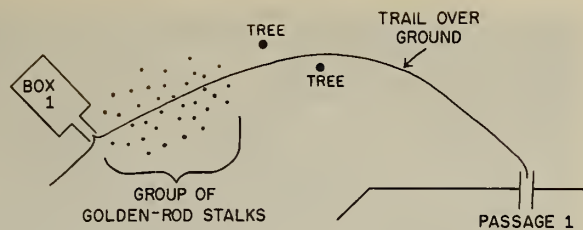
Figure 68.—Trail over ground during fall of 1947 and during the following winter. The same pattern developed after a 1-inch snow on January 14, 1948. However, after a 5-inch snow on January 25, 1948, the rats were unable to duplicate that section of the trail which passed through the group of vertical goldenrod stalks. See figure 69.

along this trail on the night of January 24–25 when the trail itself and the low-lying vegetation was obscured by the snow. There was a single trail over the approximately 12 inches from the exit from Box 1 to the beginning of the clump of goldenrod stalks. At the edge of the clump of stalks the trail diverged into several trails which reconverged 5 feet farther along at the opposite edge of the clump. From that point on the trail was essentially the same as had existed previously. The conclusion drawn from this is that rats are unable to utilize a large number of cues for orienting their path of travel over a short distance. When the snow was not on the ground it must have been that the rats utilized visual, tactile, and olfactory cues to the trail itself in following it rather than orienting to the many vertical cues provided by the stalks of the goldenrod stems. A portion of this diverging trail is shown in the photograph in figure 69. During the next two nights the rats gradually concentrated their travel along one of these trails until it all lay along a single route slightly SW of the trail which existed on the ground under the snow. Thus through trial and error a new trail developed to which the rats were able to respond directly by visual, tactile or olfactory perception.

Example No. 3: Trail to Passage 3 from a burrow exit beside the outside fence. The trail on the ground covered a distance of approximately 12 feet over the ground devoid of any vegetation or any other structures. As shown in figure 70, the trail followed a curved course for the first half of the distance from the fence. On the morning of January 25, 1948, there was a system of trails over the most curved portion of the trail. The conclusion is that without any tactile or visual cues, or possible olfactory ones, a rat is unable to reproduce

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Figure 69.—Initial orientation through a clump of vertical cues after a 5-inch snow. The goldenrod stalks in the upper right corner are that half of the clump shown in figure 68, which is nearest passage 1. When the trail is obscured by such a snow, rats are unable to duplicate a curved trail through closely spaced groups of vertical cues. Neither of the bifurcated trails duplicated the underlying trail. During the next two nights a single trail developed through this area slightly to the south of the original trail.

a curved trail. During the following two nights the rats concentrated their activities over two of the most peripheral of this aggregate of trails.

b. *Orientation under snow.* The 5 inches of snow which fell on January 24, 1948, lasted for 11 days without further addition of new snow. The severeness of the weather prevented this from melting significantly although there was a compacting of the snow until it formed an ice crusted layer 2 to 4 inches deep. Over this the rats

confined their travel essentially to the routes shown by the dashed lines in figure 71.

At 6 a.m. of February 4, 1948, it began to snow and continued steadily snowing for the following 18 hours until an average depth of 10 inches of new snow had fallen. On the morning of February 5 I climbed the tower for a preliminary survey before entering the pen in order to determine the reaction of the rats to this deep snow. The snow was completely unmarred and so I initially as-
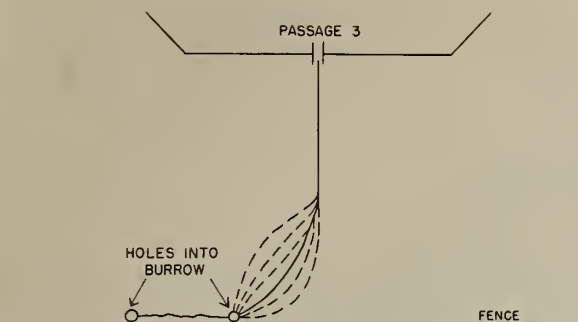
Figure 70.—The inability of rats to reproduce a curved trail in the absence of immediately adjoining visual or tactile cues. The solid line represents the position of the trail prior to the 5-inch snowfall of January 24, 1948. The dashed lines indicate in a diagramatic fashion the position of trails initially developed over the snow. During the next two nights activity was concentrated on two of these, neither of which coincided with the underlying original trail.

sumed that there had been a complete suppression of above ground activity. However, upon entering the pen and proceeding to the food hopper it was noted that three tunnels emerged from the snow into the food hopper which was protected overhead by a roof wide enough to prevent the drifting of the snow on top of the food.

This indicated that the rats were active under the snow. Beginning at the food hopper these three trails were traced outward by sectioning through the snow with a hoe at approximately 2-foot intervals. By this procedure the subnivian trail system shown by the solid lines in figure 71 was revealed. The thickness of the snow above the floor of these tunnels averaged 9.7 inches for 14 measurements. Eleven measurements were made of the height and width of the tunnels (compare with table 4). For each, these ranged from 60 to 75 mm., with each having a mean of 67 mm. There was no obvious extension of these diameters of the tunnels at the many other unmeasured points where the tunnel was sectioned. It is obvious from this that only one rat at a time had traveled any specific section of this system of tunnels.

The floor of the tunnel was formed by a thin compacted layer of the new snow. This was sufficiently thick to completely mask the muddy trail preexisting on the former snow at points where the subnivian trails and the former trails on top of the snow coincided. This indicated that direct visual perception of the trail was precluded. It is not known whether the rats could detect the

previous trail by olfactory means through the thin layer of compacted snow. However, we shall examine the data for enlightenment on this point. As had already been noted, there is considerable evidence that rats utilize vertical objects at a distance toward which to direct their locomotion. A typical distance between vertical objects is 5 feet. In order to detect an object 5 feet away and 2 feet above the surface of the tunnel would require seeing it through approximately 23 inches of snow. It seems rather unlikely that this could be accomplished at night. Therefore, it will be concluded that neither visual perception of the former trail nor visual perception of neighboring vertical cues were in operation.

By a cursory examination of the system of subnivian trails, the maximum number of sets of responses that is revealed by these data can be estimated. There were four boxes and five burrow systems (the latter counting the North Alley Burrow twice because of the two widely separated exits) in which rats were harboring, and there was one food source. Counting each segment of tunnel between harborages, between a harborage and the food source, or the blind tunnels as a response by a rat there is a maximum of 20 responses. In all probability a much fewer number of rats was involved in these initial responses. Once the tunnel was developed by one rat the response of other rats which followed it might be a simple tactile one to the walls of the tunnel. This was the only instance during the history of the colony for which conditions were suitable for the development of subnivian trails. Since the orientations shown during the development of these trails appear to be quite revealing as to the modes of orientation, separate sections of the trail will be commented upon separately. Figures 14 and 71 must be compared in order to follow the interpretations presented below.

A. The trail from Box 9 to Box 3. The movement without a doubt began at Box 9. There are three general directions toward which movement from Box 9 might be oriented: 1. Box 3, which served as a way station during travel, and the food hopper; both of these were in the same direction. 2. Box 1 and/or Passage 1; these are secondary points of orientation which lie along the route which has to be traveled in order to get to the main goal, the food source. 3. The South Alley Burrow. Animals from Area I occasionally stopped in this burrow system along the way to the Food
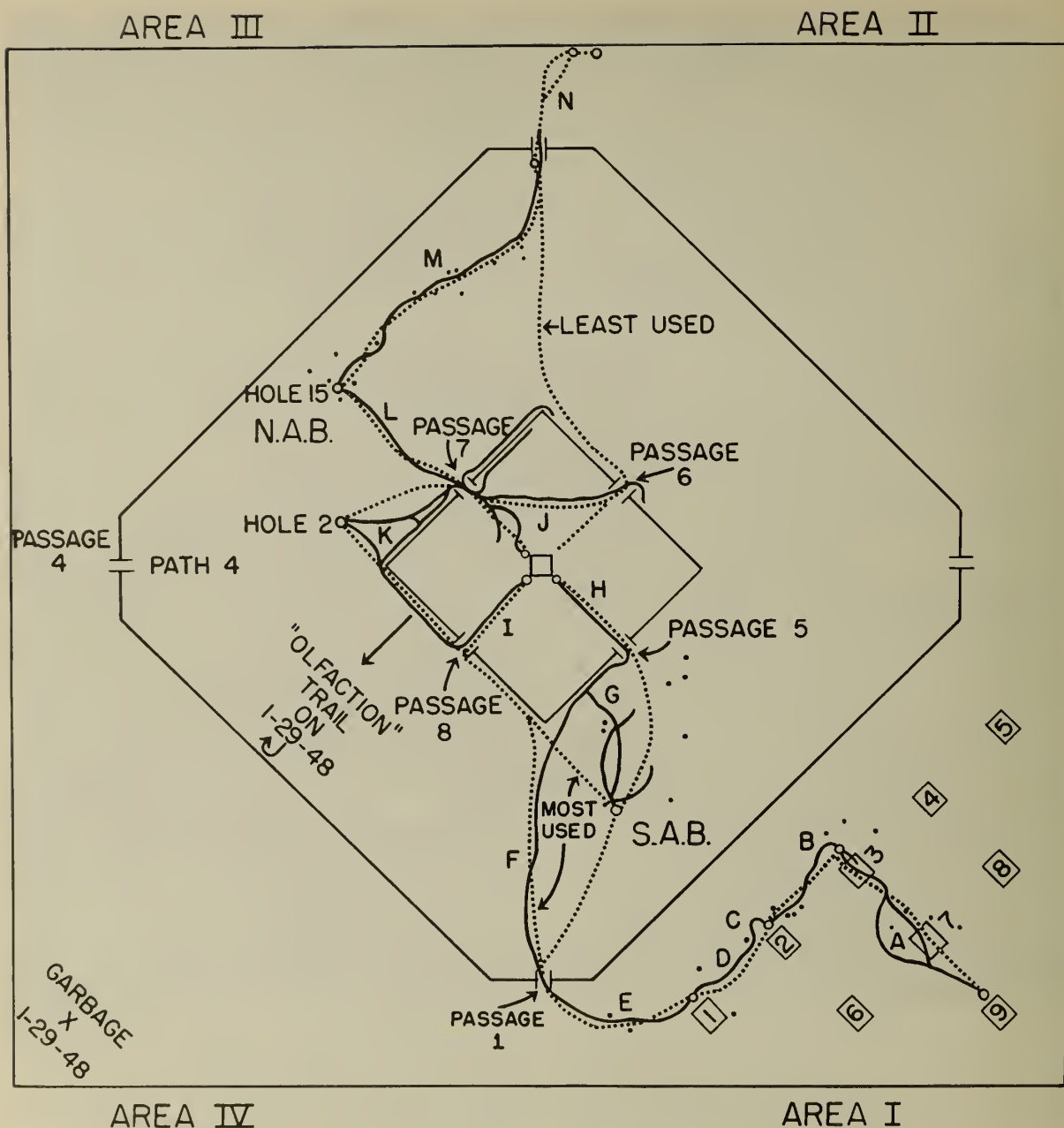
Figure 71.—Orientation of rats over and under snow. The broken lines indicate the trails over snow compacted to a depth of 3 inches and covered with a crust of ice. These were developed between January 24 and February 3, 1948. The solid lines indicate the subnivian trails that were developed through the 10-inch deep snow that fell on top of this ice-crusted snow. Letters refer to segments of the subnivian trails discussed in detail in the text. See figure 73B and accompanying text for further remarks on the "olfaction" trail of January 29. Dots represent positions of tree trunks.

Pen. Initially the subnivian snow trail departs from the prior route and heads in the general direction of the South Alley Burrow, but at about the place of Box 7 or just beyond it the trail turns back and follows along the preexisting route. I doubt that the orientation of the trail was influenced significantly by the South Alley

Burrow. The reason for believing this is that Box 9 at this time was inhabited by three socially low-ranking females (Nos. 17, 20 and 25) who utilized this burrow system as a way station much less frequently than did other rats harboring in Area I. It will be noted that the initial divergence comes fairly close to bisecting the angle between

the direction toward the other two sets of goals. It appears as though the nearness of Box 3 as a way station goal produced a sufficiently strong attraction to pull back the route of travel to conform with the previously existing route. Olfactory perception may have been operative in producing an exact conformity of the latter portion of the trail to Box 3. However, the fact that it was not initially operative indicates that kinesthetic—goal—directed behavior is dominant to the degree of olfactory perception possible under the present circumstances.

B, C, and D. The leaving of Boxes 3 and 2 with eventual arrival at the next way station. The interesting thing about the trail as it leaves both Boxes 3 and 2 is that there is an initial continuation straight in front of the box for about 18 inches beyond the end of the drain tile before the trail bends back and approximates the previous trail. It was as though the rats were initially attracted by the Food Pen, but that as the barrier fence was approached its negative value as a goal, operating simultaneously with the positive goal value of the next harborage box, which serves as a way station, was sufficient to overcome the attraction value of the Food Pen goal and cause the rat to return toward the nearest positive goal. The nearly total lack of comformity of the subnivian trail with the preexisting trail indicates no importance to olfactory perception in this instance.

E. Trail between Box 1 and Passage 1. The exact duplication of this arched trail presents a most puzzling situation. The easiest assumption is that olfactory perception of the previous trail was the single means of perception here operating. However, in the light of the indications of the previous orientations one might anticipate the direct orientation toward goals. One other possible speculation might be made. That is that the travel from Box 2 past Box 1 might be considered as inducing the rat to follow a trajectory route despite its goal directed attraction to Passage 1 or the Food Pen.

F and H. Trail between Passages 1 and 5. Prior to the formation of the subnivian trails most of the animals had been traveling to the Food Pen from Passage 1 directly down Path 1 and around to Passage 8, although a few animals cut across and used the South Alley Burrow as a way station. Thus, there were two routes of travel from Passage 1 to the food hopper and there were two goals. The

primary goal was the food hopper whereas the secondary goal was the South Alley Burrow. The position of the subnivian trail indicates that the direction of travel was essentially toward the food hopper goal but that there was sufficient attraction toward the South Alley Burrow to cause a deflection from the previous route. This deflection caused the animal to make an initial orientation between the two goals or routes of travel. However, as soon as the subnivian trail encountered the Food Pen fence the rat merely had to follow along the edge of the fence by tactile perception until the Passage 5 was reached. At this point there was protection in the channel of the activity recorder, which presumably also gave the rat some orientation toward the food hopper.

G. Trails between the South Alley Burrow and Passage 5. Three attempts were made to cover this route. The first attempt produced a short blind tunnel which overshot this route in the direction of Area I. It will be recalled that the rats harboring in the South Alley Burrow have an affinity to Area I as a secondary location for harborage. It is, therefore, assumed that the deflection of this first attempt is a result of the attraction toward this secondary goal. The second and third attempts, both essentially bisected the angle produced by the two prior routes to the Food Pen.

The unsuccessful attempt showed a deflection toward the least traveled of these two routes, whereas the successful attempt showed a longer deflection toward and parallel to the most used of these two routes. This indicates that the position of the preexisting trails are in themselves goals which influence orientation.

J. Trails leading into or around the Food Pen from Passage 7 in a southeast direction. We shall begin our considerations with the condition that the rat is already at Passage 7 after having come from the North Alley Burrow. It appears as though the tunnels along either side of the Food Pen fence were directed toward the trail up Path 3 and around the East Alley. I find it difficult to understand how a rat was able to follow exactly the less used and longer route between Passages 7 and 6 and yet become obviously confused in the shorter route from Passage 7 to the food hopper.

K. Trails from hole 2, North Alley Burrow, to Passage 7. The interesting thing about the two trails leading from hole 2, is that the ones pro-

duced under the snow are arched inward toward the food hopper. The interpretation is as follows: When visual perception was possible the rats leaving hole 2 of the North Alley Burrow made a direct orientation toward the nearest point along the route to the food hopper regardless of whether this route might be taking them temporarily away from this primary goal. However, as soon as the visual perception of goals becomes impossible there arises a conflict between the orientation of movement of the animal toward intermediate and terminal goals. One might also interpret the origin of the snow tunnels here as resulting from a conflict between the directions of the routes of travel, rather than the locations of goals.

L. Trail between hole 15, North Alley Burrow, and Passage 7. This trail most likely was initiated from North Alley Burrow hole 15. The remarkable approximation to the preexisting route on the ground is without clear explanation. According to the logic formulated for explaining routes A, G, and K, a rat heading out in the general direction of two spatially separated goals will actually move toward a point between these two goals. Presumably such orientation resulted from an averaging of the kinesthetic orientation toward these separate goals. But in the present case the rat has three possible choices from North Alley Burrow hole 15: (a) toward the food hopper, (b) toward Passage 3 along route M, (c) along an underground tunnel toward North Alley Burrow hole 2. I can only hazard the speculation that the opposite attractions toward b and c essentially cancelled each other, and left the rat unhampered in its then major orientation toward the food hopper via the intermediate goal, Passage 7.

M. Trail between hole 15, North Alley Burrow and Passage 3. Under the discussion of the previous sections of subnivian trails I have indicated the direction in which I believe it most likely that the tunnel developed. However, in this case it is just as likely that a rat started from hole 15 and went toward Passage 3 as it was for the reverse direction of movement. With the exception of that portion of the trail nearest the North Alley Burrow there was an exact duplication of the preexisting trail. In the light of several of the previously discussed segments of the subnivian trails it might be anticipated that regardless of whether the rat had started at hole 15 or at Passage 3 there would have been a deflection of the trail toward the Food Pen. Yet such was not the case. However, there was

one set of conditions characteristic of the location of this trail that was absent to a marked extent for the other trails. This condition was that there were eight trees scattered along the route of this trail. In figure 65 is shown a series of diagrams of the relationship of these trees and other conditions to the location of trails at different periods over the history of the colony through this region. The route traveled by the rats on the night of January 24–25 shows that they utilized these tree trunks as vertical cues for visual orientation. In observing the movement of rats along such trails it has been noted that the tendency to pause is greater at trees or other vertical objects. Although the rat may primarily utilize visual and tactile modes of perception in traveling to or by the next vertical orientation cue, the hypothesis is forwarded that at the same time the rat is becoming conditioned to a system of proprioceptive stimuli. Each time the rat alters its course by directing its movement toward another vertical cue, a different system of proprioceptive stimuli will be generated. When visual and tactile perception are impossible, each of the trees along the trail will act as an intermediate goal, toward which the rat orients by kinesthetic sensation. On arriving at one tree the rat then responds by moving in the direction indicated by the system of proprioceptive stimuli associated with that place. In so long as the vertical cues toward which the rat orients are not too far apart the orientation will not be significantly affected by other more distant, but also more terminal, goals.

N. Trail from limiting barrier fence to Passage 3. Due to the fact that there was no wind very little snow had drifted back under the 18-inch overhang. Over most of the way the rats used visual perception since they started on the preexisting trail and then gradually tramped down the deepening snow. This particular section gives no further information since the subnivian trail did not start until just before Passage 3.

c. *Summary of inferences concerning orientation during the formation of subnivian trails.*

1. Visual and tactile perception were inoperative during the orientations leading to the formation of the tunnels.

2. From the position in which a rat happens to be, more distant intermediate and terminal goals serve as points toward which the rat tends to direct its movement, even though it is unable to perceive the goal directly.

3. Attraction toward more distant goals occurs, even though no trails directly connect the place where the rat is and the goal at which it will eventually arrive. This applies even though there may be an insurmountable barrier along the line of the shortest distance between the rat and the goal.

4. When a rat is simultaneously attracted by two goals the degree of attraction toward each of them depends upon the distance of the goal and the value of the goal in satisfying some drive.

5. The reaction to two or more distant goals which can not be directly perceived requires that the rat possess the ability to conceptualize space-time relationships.

6. The direction of movement from one goal to another is primarily based upon the kinesthetic perception of an appropriate system of proprioceptive stimuli. Where two systems are in conflict the orientation of the animal will be to direct its movements in a direction between the routes indicated by the systems in conflict.

d. *Presumed order of dominance of the sense modalities of rats in determining spatial orientation.*

1. Tactile
    (a) To sides of tunnel.
    (b) To sides of trail through vegetation.
    (c) To a single wall.
2. Visual.
    (a) To the beaten trail itself.
    (b) To vertical objects (so long as they are spaced far enough apart that neighboring ones will not be confused with each other).
3. Kinesthetics. Goal directed (i.e., "cognitive-map" orientation).
4. Olfactory.

Certainly tactile and visual perceptions are of a higher magnitude of importance than are kinesthetic and olfactory perceptions. Although all four of these means of perception leading to spatial orientation may be operating, it is evident that the conditions existing when an animal finds itself at a particular position in space and time determines the extent to which each of these sense modalities are important. When a trap or other objects is placed near a trail, the shifting of the trail toward, and then along the object shows that visual perception must initially direct the rats toward the object although tactile perception may keep the rats against the object. When vision is impeded, as in rats just coming out of anesthesia, locomotion is completely random

until a trail through vegetation is encountered, whereupon locomotion becomes stereotyped by tactile perception in conformity with the trail itself, irrespective of where the trail may be leading. The following of subnivian trails just developed by other rats is a similar case. An instance of the dominance of kinesthetic "cognitive-map" (12) type of orientation in conjunction with visual orientation as having dominance over olfactory perception in orientation is exemplified in the experiment on the location of garbage (p. 82).

e. *Observed orientations of individual rats.* Upon release following trapping rats frequently took a circuitous route back to their location for harboring. This circuitous route usually took the rat through the Food Pen or around the Food Pen on the opposite side from its place of harborage.

Example No. 1 (fig. 72B): Female 43 was caught and released near Box 19 in Area III where she had a 16-day-old litter. Here as is usual the initial direction of travel was away from the observer. She was not anesthetized prior to release. Upon release she ran through the East Alley, crossed the Food Pen, and then went up Path 4 and over into the nearest harborage box, Box 23 in her home area. By taking this route of travel she was able to move away from the observer, avoid the more dominant female No. 42 which harbored in the North Alley Burrow, and reach a temporary harborage from which she could later in the day return to her young.

Example No. 2 (fig. 72A): Adolescent male No. 69 was trapped in the Food Pen. However, it was released in the East Alley opposite Box 11 while still exhibiting poor motor coordination following anesthesia. It followed a trail to the Food Pen, crossed it, and headed along a trail toward the North Alley Burrow. Along the way it ran into a box trap set facing down the trail and was caught. On release again it ran into the North Alley Burrow. This indicates that visual perception was poorly operating. It is assumed that tactile perception of the trail was the main means of orientation. Perhaps kinesthetic perception was also involved in the selection of the trail at points of juncture, and in guiding the rat across the bare Food Pen. At this period in the life of this rat, it harbored occasionally in the North Alley Burrow as well as at its place of birth in the South Alley Burrow.

Example No. 3 (fig. 72A): Male No. 87, who was born at the South Alley Burrow, was trapped
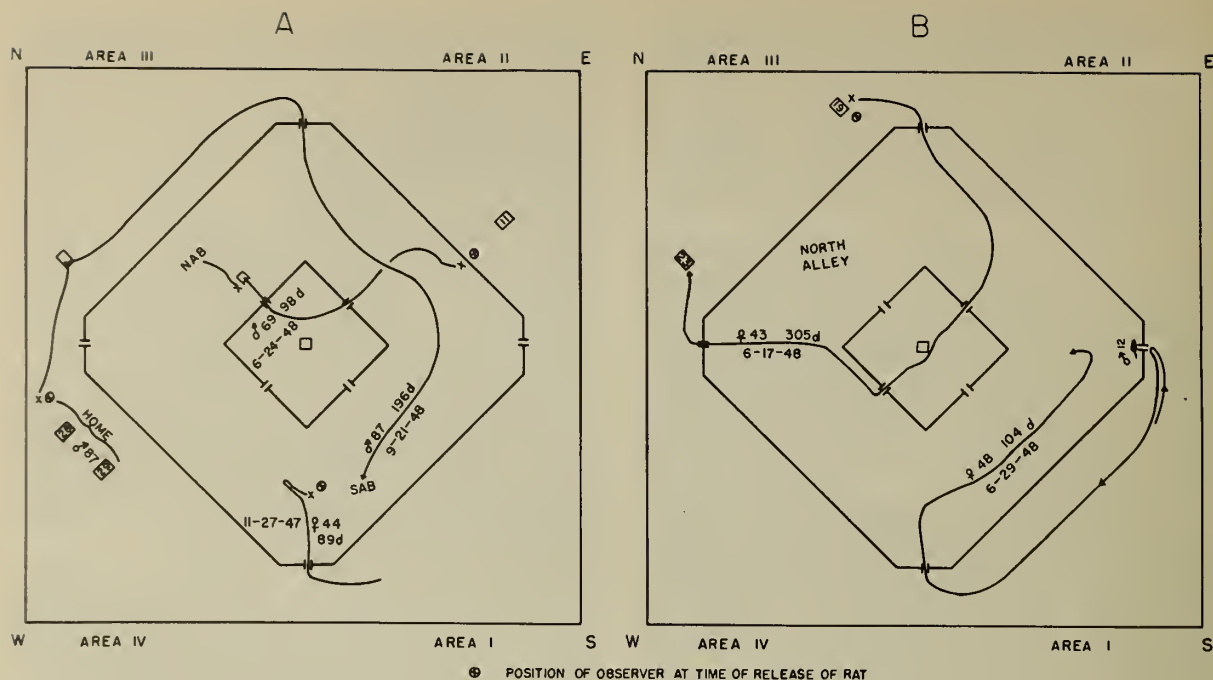
Figure 72.—Examples of observed responses with reference to movement through space. See text for details.
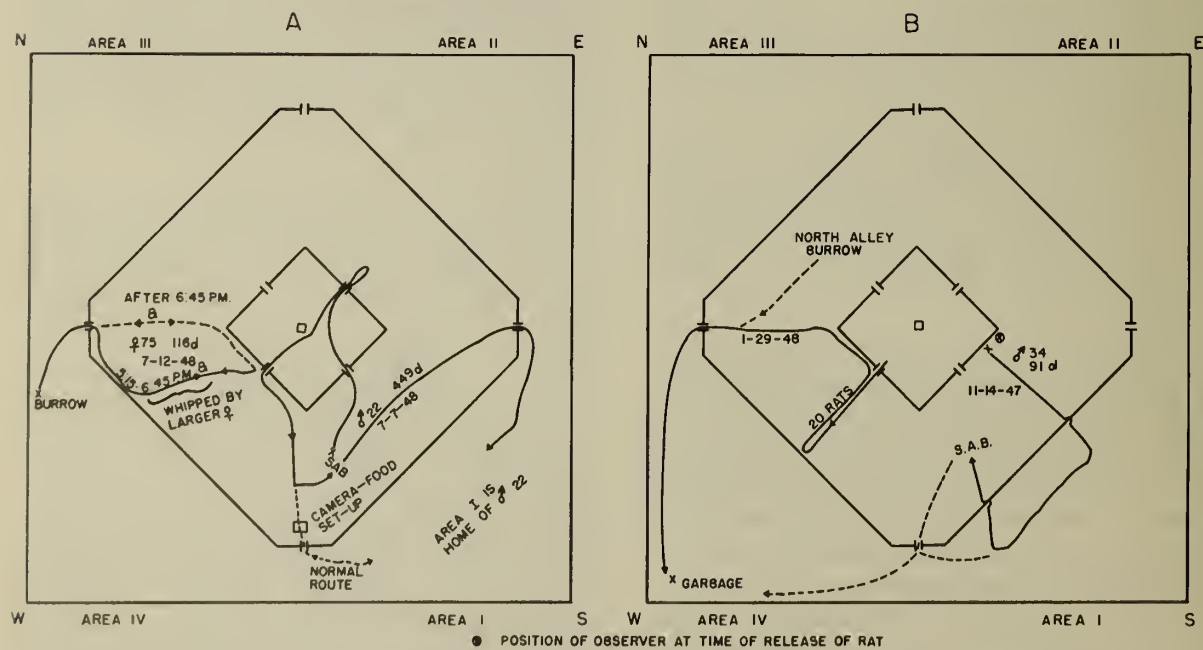
Figure 73.—Examples of observed responses with reference to movement through space. See text for details.

in Area IV at a burrow near Box 28 to which it had transferred its place of residence. The interesting thing about this observation was that immediately following release it made a long circuitous journey to its place of birth.

In a sense the above and similar examples also provide information relating to the ability of rats to select alternate routes to goals. This ability to utilize alternate routes of travel is much better exemplified in those instances where rats, undisturbed by the presence of the observer, have immediately selected an alternate route to a goal when they found their initial route blocked. Three examples of this commonly observed behavior are as follows:

Example No. 1 (fig. 72B): Adolescent female No. 48 on leaving Area I tried to enter Passage 2 but found the then dominant male No. 12 blocking the passage with its body. She then went back through Area I to Passage 1, crossed through the South Alley to Path 2, which she took toward the Food Pen. This rat was normally an inhabitant of Area II where she was born. The fact that she moved to the left on finding Passage 1 blocked is an indication that she was responding to the structure of one of these similar Areas, even though it took her away from her own home. She nevertheless, appeared to realize her departure from her home since she took a detour through the South Alley to return to a more customary route of travel up Path 2.

Example No. 2 (fig. 73A): A camera on a tripod had been placed over some garbage nailed to a board at a position in front of Passage 1. The shutter was operated by a string from the tower outside the pen. Normally male No. 22 harbored in Area I and utilized Path I and Passage 1 on its trips to the Food Pen. Occasionally it harbored temporarily in the South Alley Burrow. This was the case during the late afternoon of July 7, 1948, when the camera setup was placed along his usual route of travel. He left the South Alley Burrow shortly after 4:30 p.m. and headed to the Food Pen via Passage 5. As he returned up Path 1 toward Area I, he exhibited the strange object reaction by avoiding the new structure in its environment. This avoidance took him to and momentarily into the South Alley Burrow from which it proceeded to Passage 2, the alternate place of gaining access to Area I. Prior and later observations showed that male No. 22 most regularly used Passage 1 in departing from Area I, although when

the occasion demanded, he would immediately adjust to the use of Passage 2.

Example No. 3 (fig. 73A): Female No. 75 who was in the 14th day of her first pregnancy made a number of trips between 5:15 p.m. and 6:45 p.m. carrying food from the Food Pen via the West Alley and Passage 4. At 6:45 while on one of these trips through the West Alley she was attacked and chased by a larger female, who presumably was from the South Alley Burrow. On subsequent food storage trips, which began immediately after this encounter, she shifted her route of travel to Path 4. This shift to an alternate route is an example of the manner in which social action affects space utilization.

Both of the above sets of examples offer considerable evidence that rats learn the trails about their environment with sufficient detail to enable them to make immediate adjustments of selection of alternate or circuitous routes of travel. One might also interpret them as suggesting a general position awareness with reference to all points in their environment, with which they have had experience, even though they are unable to perceive those points from the position in which they happen to be. This awareness seems to be more than just a knowledge of the patterns of existing trails, although this is extremely important. Certain observations give evidence of this awareness, whose properties fulfill the requisites of the "cognitive map" postulated by Tolman (*12*).

Example No. 1 (fig. 72A): Female No. 44 was released headed into the West Alley near Path 1 opposite the South Alley Burrow. The South Alley Burrow was the place of her birth. She initially ran for 5 feet northward in the direction she had been headed by the observer. She then turned around and headed back toward the South Alley Burrow, but upon reaching Path 1 she became startled by a movement of the observer, whereupon she headed up Path 1 and over into Area I. The initial change in direction of movement is interpreted as giving evidence of the position of the South Alley Burrow, which she could not perceive. This still involves the use of prior trails.

Example No. 2 (fig. 73B): Male No. 34, which was caught at the southeast outside corner of the Food Pen, was released near its southeast outside corner. Upon release it wobbled about exhibiting considerable evidence of still being under the effects of anesthesia. Without utilizing trails at anytime it wandered over to the median barrier

fence and climbed over it. The charged wire on the top of this barrier fence was not in operation at the moment, but even so this was a highly unusual behavior since after the first few experiences with the electric fence, rats normally avoid climbing fences. After wandering around in Area I it again climbed over the barrier fence and went to its home burrow, the South Alley Burrow. This return home may have been purely a chance one. This orientation toward its home despite the reduction of utilization of tactile and visual stimuli is interpreted as indicating some means of orientation in which learned patterns of behavior are not necessarily requisite.

Example No. 3 (fig. 73B): This example involves the interaction of the sense of smell and conditioned routes of travel on the location of a new source of food. Details are presented in the following section.

f. *The interaction of the sense of smell and conditioned routes of travel upon the ability to locate a new source of food.* Between January 24 and 30, 1948, there was a continuous blanket of snow over the ground. As was usual when there was a cover of snow, the routes of travel and the places of residence became more restricted. During this period the place of living of the rats was confined to the west half of Area I, the South Alley Burrow, the North Alley Burrow, a burrow at Passage 3, the east half of Area III, and the north half of Area II. For all practical purposes there was a single trail developed from Area I, through Passage 1, by the South Alley Burrow, through or around the Food Pen, by the North Alley Burrow, to and through Passage 3 and thence over into both Areas II and III. With the exception of two round trip passages between Box 32 and Passage 1 there had been no movement into Area IV. This presented an excellent opportunity for an experiment on orientation by rats. To this end a small pile of garbage from my home was placed in the extreme west corner of the pen just west of Box 36. This was placed at 5 p.m. on January 29, 1948. The rats were not observed that night but the trails (fig. 73B) the next morning revealed the nature of their behavior. On the morning of January 30 there were well worn trails from Passage 1 to the garbage and from both the North Alley Burrow and the northwest outside corner of the Food Pen to Passage 4 and thence around through Area IV to the garbage. This might also apply to the South Alley Burrow rats since they frequently

made excursions over into Area I through Passage 1. However, one new trail developed during the night is most revealing in regard to the interaction of the responses which led the rats in the rest of the pen to the new source of food. From the outside west side of the Food Pen, at a point half way between Passage 8 and the northwest corner of the Food Pen, a trail traveled by at least 20 rats led directly westward across the West Alley to the median barrier fence. This line of travel was directly toward the new source of food. Since the rats had been conditioned not to climb fences there was no attempt at climbing over and continuing toward this new goal. One might have suspected that the rats would have followed along the median barrier fence to Passage 4, since this response would have kept the olfactory stimulation at the highest level. However, with only one exception this did not occur. Instead all but one of the 20 rats turned around and retraced their steps to the outside of the Food Pen. From here they proceeded to the northwest outside corner of the Food Pen, and thence over the snow up Path 4 before heading through Area IV to the garbage. In this behavior of the rats there was apparently an integration of two systems or interactions of the organism with its environment: A. There was the tendency of the rats to follow a gradient of odor to its point of origin. B. There was the tendency to adhere to customary routes of travel. Thus, the initial response of following the odor gradient was dominant until the rats met the barrier fence. At this point, without any wandering back and forth along the fence there was a suppression of this response to the extent that the rats returned to a known point of orientation, the northwest corner of the Food Pen, from which they could simultaneously respond to the gradient of olfactory stimulation while at the same time they were able to follow over a conditioned route of travel. However, it must be kept in mind that this previously traveled route had not been followed for at least 6 days. It will be helpful to refer to figure 71 in following this discussion. The dashed line in this figure shows the positions of the main trails existing on January 29. The arrow shows the direction of travel across the West Alley to the median barrier fence on the initial detection of the garbage. See figure 73 for additional detail.

F. *Utilization of Space by Rats.* Observations upon marked rats indicate that over extended periods of

time each utilizes either a single place of harborage or a few neighboring ones. From such centers of orientation the activities of the rats radiate in all directions. Some directions are favored over others because of the location of goals, such as sources of food. The general impression was obtained that there was a gradual decrease in the frequency of longer travels. However, it was impossible to obtain direct evidence of this. On the assumption that the outward travel from any point of orientation follows the same general principle, an approximation may be obtained by examining the distribution of feces adjacent to the outer limiting barrier fence. Rats passing outward through Passages 1, 2, 3, and 4 through the median barrier fence frequently traveled directly out to the outer limiting barrier fence and thence along it for varying distances toward a corner of the pen. Usually each rat would stop at some intermediate point prior to reaching the corner. When the rat again initiated travel, it would generally travel out into the area rather than continuing along the fence toward the corner. It is presumed that defecation occurred at these times when the rats stopped, since in the other regions of the pen the distribution of feces was such as to suggest that they were deposited at those points where the rats came at least to a momentary stop in their travel.

Surveys on six dates gave a total of 4,793 feces along the outer fence. The fence was arbitrarily divided into five intervals of 10 feet each from the point opposite the passage through the median barrier fence to the corner of the pen (see fig. 74). The number of feces in these five intervals was: 1,868, 975, 738, 545, and 667. The increase in the feces in the terminal group toward the corners of the pen presumably represents in part the feces that would have been deposited at points still farther away had the fence not terminated the outward travel. To the extent that the number of feces at any point were proportional to the number of trips taken to that point, conclusions can be drawn as to the utilization of space radiating out from a point of orientation. The number of feces within any one 10-foot interval along the fence only partially reflects the extent of use of that area. This is because the number of trips through this region will be proportional to the sum of all the feces in that region plus the total feces in regions farther along the fence, since rats normally passed through the nearer regions along the fence in order to get to the more distant ones. Therefore,
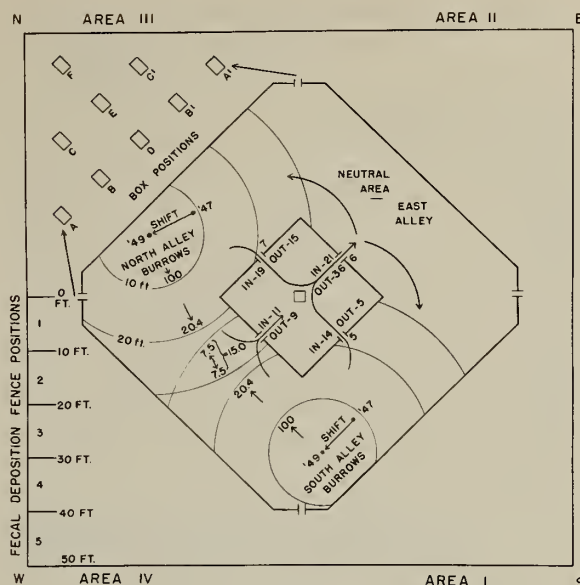
Figure 74.—Some indications of space utilization and orientation by the Norway rat. The "fecal deposition fence positions" are in terms of distance along the peripheral fence directly opposite the passages through the median barrier fence (see fig. 75). The isobars of space utilization about the North and South Alley Burrows were prepared under the assumption that the probability (table 8) of rats being at different distances from the centers of the burrows follows the same pattern of decrement with distance as revealed by the deposition of feces along the peripheral barrier fence. On the average there was a circular flow of movement from the burrows, into the Food Pen, and back again. This flow reduced the number of contacts of rats proceeding in opposite directions. Harborage boxes are lettered with reference to increasing distance from the passages through the median barrier fence. See table 18 for details of utilization of these boxes.

the accumulated totals of feces (4,793, 2,925, 1,950, 1,212, 667) for the successively more distant locations along the fence were utilized as a more accurate reflection of the frequency with which rats pass through points at successively greater distances from a point of orientation. Both the actual and the accumulated totals of feces at the five fence positions are shown in figure 75.

Although these accumulated totals of feces reflect the relative frequency of arriving at distances from a point of orientation, they do not reflect the intensity of usage of the environment. This arises from the fact that each band of equal width, w, about a point of orientation increase in area by and amount $2\pi W^2$ over the preceding band. Thus, as the amount of area in a band increases, the frequency of visitation to the band decreases.

DISTRIBUTION OF FECES ALONG THE PERIPHERAL FENCE
□ = PERCENT OF TOTAL (4793)
○ = PERCENT OF ACCUMULATED
TOTAL (11,547)

PERCENTAGE OCCURRENCE

1   2   3   4   5
(.1-10FT.) (10.1-20FT.) (20.1-30FT.) (30.1-40FT.) (40.1-50FT.)
FENCE POSITIONS FROM OPPOSITE TILE PASSAGE TO
CORNER OF PEN
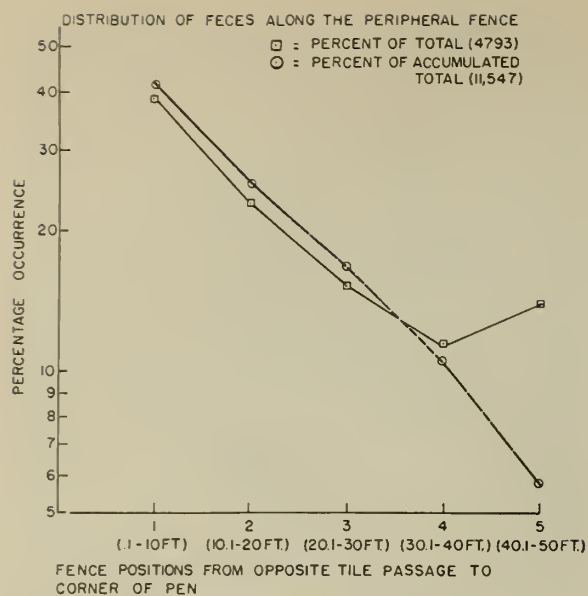
Figure 75.—Distribution of feces along the peripheral fence. From the point immediately opposite the passage through the median barrier fence, the 50-foot section of the peripheral fence was arbitrarily divided into 5 sections (fig. 74), and the number of feces in each was counted. Since rats normally defecate only after stopping, and after stopping along the peripheral fence they either returned along the previous route or moved out into the areas. The number of feces is probably proportional to the frequency of making trips of the distances at which the defecation occurred. The accumulated total of feces represents·an index of the probability of the rats passing through points with reference to the point of orientation, that is the passage through the median barrier fence.

Therefore, the relative usage of a given amount of space will decrease much more rapidly than the frequency of making trips of successively longer lengths. This is shown in table 8. This extremely rapid rate of decrement in the intensity of space utilization by rats at points of increasing distances from a point of orientation indicates that there can be very little effective interaction between the organism and its environment very far from the center of orientation.

If this table adequately reflects the intensity of utilization of space at increasing distances from the center of activity, certain inferences may be made regarding the manner in which different groups of rats interact in their utilization of space. Only two major burrow systems were constructed in the "Alley" about the Food Pen. The center of these two mature burrow systems with 10-foot isobars of space utilization about them are shown in figure 74. In the region where the isobars of

these neighboring burrows systems overlap there will be an increase in the space utilization equivalent to the sum of the overlapping bands. This suggests that this increase in the relative intensity of space utilization might limit or modify the movements of rats irrespective of any social antagonism which might exist between adjacent colonies.

TABLE 8.—*Relative intensity of use of bands of 10-foot width from a point of orientation*

Band	Distance to outer limit of band in ft.	Area of band in sq. ft.	Relative number of trips into band [1]	Relative visitations per 314 sq. ft. (i.e., equivalent area)
A........	10	314	100. 0	100. 00
B........	20	942	61. 2	20. 40
C........	30	1, 571	37. 5	7. 50
D........	40	2, 199	22. 9	3. 27
E........	50	2, 827	14. 0	1. 56
F........	60	3, 456	8. 6	. 78

[1] The relative number of trips into a band was determined on the basis of the fact that the decrement in accumulated total of feces at each position along the fence decreased on the average of 38.8 percent from that of the previous position.

Although this possibility was not recognized during the course of recording observations over the history of the pen, there were, nevertheless, accumulated certain observations which are relevant. These pertain to the 65 observations of known individuals, where the passage utilized to enter the Food Pen, as well as the passage used subsequently to depart from the Food Pen, was recorded. The number and direction of trips through each passage is shown in figure 74. It will be noted that for Passages 5, 7, and 8, the passages nearest the burrow systems, there are fewer exits than entrances. The deficit is made up through Passage 6 which leads into the East Alley. Here in the East Alley near Passage 6 the sum of the theoretical relative usage, as reflecting centrifugal movements in the absence of the food goal, would be 6.6 or less in contrast with approximate relative usages of 9.1 for Passage 5; 10.8 for Passage 7; and 15.0 for Passage 8. Thus, once rats were at the source of food their return journey home could be made with a greater avoidance of contacts with other rats, who were

approaching the food source, if they entered directly into the East Alley from the Food Pen. In figure 74 the main tendency of flow of rats through the the Food Pen is shown by the system of arrows. The development and utilization of trails through the central portion of the East Alley connecting back to the North and South Alley Burrows further substantiates this concept (see figs. 14 and 59).

Of course, rats living out in the triangular areas also moved through the alleys into and out of the Food Pen. However, it is believed that their movements were mainly determined with reference to rats living in the two main burrow systems in the alleys. Those rats living in Areas II and III primarily utilized Passage 6 adjoining the East Alley. Furthermore, rats living in Area IV predominantly utilized Passage 8 adjoining the West Alley. In their movement from Area IV to Passage 8 into the Food Pen these rats utilized trails which swung toward the center of the West Alley prior to being directed more directly toward Passage 8. The orientation of these trails through the West Alley was such as to insure a reduction of contacts with rats living at the North and South Alley Burrows (see figs. 14 and 59). Rats from Area I with their close social affinity to the members of the South Alley Burrow most frequently went directly down Path 1 and then at its base around to Passages 5 or 8 without much avoidance of the South Alley Burrow. Further avoidance of contact by area inhabiting rats with alley inhabiting rats was brought about through an altered periodicity of activity by which the area rats tended to utilize the periods of decreased activity by the alley rats for their own periods of increased activity (see pp. 117–119).

3. *The Strange Object or Strange Situation Reaction*

Wild Norway rats are frequently difficult to capture when use is made of many of the types of commercially available traps. The ineffectiveness of such traps is in large part attributable to the fact that they represent a new type of object in their environment. When the object has become somewhat familiar to the rat it may still elicit a similar avoidance response if it is placed in a new position, particularly a position which interferes with accustomed activities. The rat responds by avoiding the object or situation. Several situations were encountered which exemplify this reaction.

A. *Activity Recorders.* One class of strange objects was that formed by devices designed to record the activity of rats. The first device was a wire suspended along a trail or at a passage through a fence. This wire when moved to one side by the rat closed a circuit causing a light to flash in the observation tower. These wire rods were suspended from the center of a square of wood 4 inches in width. This square was supported by four wire legs and stood some 6 inches above the ground. On May 8, 1947, one of these recorders was placed at each of the four entrances to the Food Pen. The reaction to these recorders was invariably the same. The rat would cautiously approach it, jump back, bypass it while keeping a foot or two away, and then go look at another recorder until all four had been examined. No fighting was observed around the Food Pen, although rats met or passed each other frequently. Gradually the number of rats attempting to enter the Food Pen lessened. At this time there was considerably activity in the alley about the Food Pen. The rats did not keep to worn trails. One rat started to climb the fence into the Food Pen but only went up a foot. The interesting aspect of this situation was the reduction of social strife and the disruption of normal adherence to trails. At the beginning of the following night rats were closing the contact recorders without hesitation. This indicates that at some time during the previous night the rats had learned that no deleterious results accompanied brushing by the suspended wire rod.

A much more marked avoidance reaction was elicited by another type of activity recorder. As mentioned elsewhere (p. 112) these contained a photoelectric cell. When a beam of infrared light to this cell was interrupted a solenoid closed with a sharp clang. The apparatus was protected by a black metal tunnel approximately 9 by 12 by 26 inches. This tunnel formed a strange object, which if entered resulted in the production of a strange noise. On July 28, 1947, such recorders were placed on the inside surface of the Food Pen at each of the four entrances. A large amount of garbage was placed in the Food Pen as an additional inducement for the rats to enter. During an hour of observation following 6:30 p.m., 7 rats made 27 responses to these strange objects. The invariable response was to approach an entrance to the Food

Pen, look into one of the recorders without entering, and then to make similar responses at one or more of the other entrances before going elsewhere in the pen. These responses were exhibited by both 100-day-old rats born in the pen and the adult rats introduced the previous winter. Although the recorder tape jammed during the night, and thus there was no record of possible entrances, the fact that the garbage in the Food Pen had been undisturbed during the night forms a good indication that no rats had passed through the recorders into the Food Pen. During the hour of observation there was considerable fighting. This is in contrast to the presumed suppression of conflict which accompanied the presence of strange objects on May 8, 1947. During the second night two of the four recorders operated satisfactorily. These left a total of only 11 marks on the tape. Judging by the fact that the garbage was still undisturbed on the morning of July 30, all that had happened was that a few rats had entered the tunnel just far enough to break the beam. With the clang of the closing solenoid the rats must have turned around and run out of the tunnel. During a 20-minute observation period on the evening of July 30 beginning at 7:05 p.m. only five rats were seen active and only two of these even approached the Food Pen. They appeared quite nervous. Such a state was indicated by an interspersion of standing and sniffing, hesitant approaches, then short dashes, rather than the more usual continuous ambling or running between goals. On the morning of July 31 there was no evidence that any rats had entered the Food Pen. This is based upon the fact that food placed the previous night directly in front of the tunnels, on the Food Pen side of the recorders had not been disturbed. This consisted of bread in front of two tunnels, table scraps in front of another, and watermelon in front of the last. These are all quite preferred foods over the normal diet of Purina checkers. Also, there was no dew during the night July 30–31. The rats may have had a little stored food but they certainly had no other source of water than that in the Food Pen. The two recorders which were operating on this night showed only three marks, again indicating that rats which had come in far enough to break the beam were frightened away after the clang of the closing solenoid. Although this new object and situation was sufficient to prevent any rats from passing through for the first three nights, the following five nights saw the completion of the adjustment of the rats

to the point that they evidenced no difference in reaction to the tunnel and the clanging solenoid than they did to other aspects of their environment. Rats born in the pen following the conditioning of these first few rats never showed any sign of avoidance of or disturbance by this tunnel activity recorder. Rats just being weaned were observed passing through the tunnels with no more concern than the adults. This unconcern may possibly be attributed to two causes: (1) Any object toward which the rat has no inherent aversion, and which occurs in the environment into which the rat is born, is accepted by it. (2) A rat is less likely to become alarmed over new situations towards which it associates remain undisturbed.

B. *Food.* Food may initially elicit an avoidance response providing it is of a new type or at a new location. On October 3, 1947, a pile of garbage and a pile of cornmeal were placed in the Food Pen at 5:31 a.m. At 5:48 a.m. male No. 8 was the first rat to approach this source of food. It approached each of the piles slowly with neck outstretched and its tail protruding straight behind. After the initial approach without untoward consequences, later approaches were direct with no hesitation. This is the characteristic behavior of the initial rats encountering a new source of food. Normally rats, which encounter the food after prior rats have already made a satisfactory adjustment and are eating peacefully at this source, exhibit nothing of this hesitant approach. This same set of responses has been noted to accompany the encountering of small strange objects such as rulers, jars, etc. which the observer left temporarily in the pen.

C. *Birds.* Birds alighting in the pen normally caused no alteration in the behavior of the rats. Presumably this was of such frequent occurrence that birds were actually not strange objects. On only two occasions was a positive interaction noted. On June 22, 1947, as adult female No. 4 stood up on top of Box 6, a male yellow-breasted chat flew at it, whereupon she ran into the nearby weeds. On July 6, 1947, adult female No. 10 was entering the South Alley Burrow when a young house wren began taking a dust bath on the nearby Path 1. The rat turned around and ran at the wren as if in an attempt to catch it, but the bird escaped.

D. *Sound.* Disturbances outside the pen, which may be presumed to have occurred irregularly in the past, seem not to disturb the rats. These include both the scolding and hawk cries of the

blue jay, the caws of crows and the screams of cats. During the first summer the rats, which consisted mainly of those introduced into the pen, would run for cover upon hearing the click which occurred at the time of unlocking the observation tower door or opening the latch to the observation tower window.

Strange noises which occurred within the pen produced a more marked response. The click of a camera shutter is a good example. During July 1948 a camera was suspended about 6 feet above Path 1 over some food nailed to a board. Four hundred and forty-seven day old male No. 16, who had already become adjusted to eating at this new food source, was here alone when the shutter was first released. As the shutter clicked it jumped and dashed rapidly 20 feet to the South Alley Burrow where it stopped to turn around and look. A short while later a picture was taken after several rats had settled down to eating. Upon the shutter click the group of rats jumped in all directions as if there had been an explosion in their midst. This was the rats' first experience with this noise. During the spring of 1949, when the U.S. Army Signal Corps was preparing to take extensive moving picture footage of the rats, it was realized that this reaction to strange noises would interfere with the behavior of the rats. In order to overcome this difficulty, a nonsense sound track was prepared which included talking, motors, and miscellaneous mechanical sounds. This was played for 2 days before the filming began and nearly continuously during the night for the next 6 weeks while the filming was in progress. The rats rapidly adjusted to this nonsense sound and insofar as I was able to detect all activities occurred in a perfectly normal fashion. This even included responses which were elicited by the vocalizations of other rats. It was concluded that the rats were able to sort out these vocalizations from the miscellaneous noises on the sound track.

Such vocalizations by other rats may elicit a response similar to that produced by strange mechanical noises. As an example take the field note of June 28, 1948, 6:40 p.m.: "Some rat gave a loud squeal and all other rats ran into burrows or other hiding places. However, hardly a minute had elapsed before they began coming out."

E. *The "Chain-fright Reaction."* By July 1948 the increasing population size caused the rats to exhibit frequently what might be termed a "chain-fright reaction." Fights, chases, rustling of dry leaves, in fact anything that produced a sudden or unusual noise, made rats scatter even when they were some distance away.

This transfer of the state of being disturbed from one individual to another presented a means for a more continuous state of disturbance as the population continued to increase in size. The operation of this phenomenon is exemplified in the characteristic behavior of shifting the place of harborage upon being disturbed. This occurred when the disturbance was by the intrusion of another rat or by some outside agent such as the observer. In each case where an initial resident was joined by another rat, either one must leave or they both must make some mutual adjustment. Depending upon (a) the degree to which the incoming rat is disturbed, (b) the ability of the meeting individuals to make mutual adjustments, and (c) the distribution of other individuals through the environment, there will inevitably result secondary and other sequential disturbances. This general inference is based upon the following types of observations. Marked rats, who were undisturbed by the observer have been noted to enter a harborage box or burrow in which another rat was known to be at that time. Sometimes both rats remained in the harborage with no resultant disturbance having been detected by the observer. When this happened it was concluded that some mutual adjustment had been made despite the fact that this may have produced some stress. Very frequently though, the sounds of fighting within the harborage, or the squeals accompanying it, were heard by the observer in the tower. Even so both rats might remain in the harborage box although more often either the invader or the resident rat would depart. A similar sequence of events sometimes occurred again if the departing rats entered another harborage containing a rat. Similar events accompanied the release of trapped rats into portions of the pen outside their normal range. On their return home such rats entered harborages along the way. Usually they were chased out of these alien harborages, but at the same time one or more of the resident rats might also depart. On a number of occasions the observer opened all the harborage boxes and identified pelage marked rats without handling them. Although the area in which harborage boxes were initially opened varied it was customary to travel around the pen in a counterclockwise direction. It frequently hap-

pened that rats encountered initially in one area were found in another area by the time these later boxes were opened. Often the place of the second observation was outside the rat's normal range, and was with another rat with whom it infrequently associated.

4. *The Responses of Rats to Traps*

Traps, used to capture the rats alive, also elicited an avoidance reaction. So much data was accumulated with reference to the avoidance response of the rats toward the traps that various aspects of this phenomena are treated separately in this and the following sections.

Although wooden traps were normally used with fair success, a commercial Havahart trap was also tried out. These consisted of wire mesh walls and solid metal treadles and doors. Doors occurred at either end so that when the doors were propped open it was possible for a rat to travel through the trap. Two of these traps were received in December 1947. These were initially placed with doors propped open along well used trails. After 2 days the treadles were still shiny; that is there were no muddy foot prints on them as would have been the case had the rats passed through. A similar test was made on a later date. On this date the rats were intensively using a trail worn through the snow from the North Alley Burrow to the Food Pen. During the night that the trap was placed along this trail, with both doors propped open, the rats diverged around the trap and never disturbed the snow in the bottom of the trap (see fig. 76). These two traps were also set during the December 1947 trapping period. Yet the only rat caught was the socially very low-ranking female No. 25, and she entered one of these traps twice. During the next year and a half the few rats caught in this type of trap were invariably juvenile or socially low-ranking adults.

This tendency of socially low-ranking rats to exhibit a reduced avoidance of traps is so characteristic that it forms a portion of the syndrome of abnormal behavior discussed with respect to the extremely socially low-ranking rats in a later section (p. 195).

At irregular intervals (46.4 days, $\pm 2\sigma$ of 14.5 days) wooden box traps (9) were set. Traps were left set for 3 to 8 days during each of these periods of trapping (fig. 10). Groups of traps were concentrated about all the places of harborage, at the

passages through the barrier fences, and along the most frequently used trails. Thus all rats must have had several opportunities for entering traps on each night they were set. Furthermore, traps were in an adequate excess to insure the presence of many unset traps throughout the night. Therefore, any lack of capture indicates a failure of the rat to complete his response to the bait in the trap.

Bait placed in the traps included such items as sunflower seed, horse feed, sweet potato, bread, and oranges which were known to be highly attractive to the rats. When such food was made available in the Food Pen, but not in traps, the rats would ignore the Purina pellets at the hooper until this temporary type of food was all eaten or stored. This preferred food represented a reward or positive reinforcement of the response of entering the trap. Once trapped the rat was exposed to a series of events which served as a punishment or negative reinforcement of the response of entering traps. The following conditions contributed to the unpleasant aspects of the experience:

1. The door falls with a bang.
2. The door may fall on the rat's tail.
3. The rat is confined to a small space, usually for 10 or more hours, from which there is usually no escape. During this time the rat is prevented from engaging in the many activities in which it otherwise would have been participating.
4. The rat is exposed to the weather during the period of confinement.
5. The food supply is inadequate and no water is available.
6. When two rats are simultaneously trapped, intense fighting frequently occurs. This is even true of juvenile rats, who very infrequently engage in such fighting outside of traps.

Despite these unpleasant aspects of the experience rats do reenter traps. When this happens it must be concluded that the positive attraction of the trap exerts a greater influence than do the negative repelling aspects. The data on retrapped rats provides some insight into this balance.

Many observations of rats from the tower substantiated the inference from trapping data that rats do develop a marked avoidance behavior toward traps. The pattern of behavior was one of repeatedly approaching a set trap whose door was held open by the trigger stick. These approaches were followed by backing or turning

Figure 76.—Avoidance of a strange situation. A hole from the North Alley Burrow is in the left foreground. Prior to placing the two tunnel traps in the positions shown, the rats had developed two trails to the Food Pen from this hole. One went toward passage 7 in the left background. The other crossed toward the right center of the photograph in the direction of the northwest corner of the Food Pen. There were no tracks made by rats in the snow on either side of these two trails during the several nights preceding the placing of the two traps. There was a door at either end of these traps. These were propped open with sticks and placed over the trails so that it was possible for the rats to pass through without diverging from their previously established routes. Each trap contained a layer of loose snow. The next morning no tracks were visible over this snow within the traps. Instead the rats had diverged to either side of these traps as the tracks through the snow indicate.

away as soon as the rat's nose nearly reached the open door. Finally the rat would desist and engage in some other activity. I am also convinced that rats soon learned to detect whether or not a trap was set. Frequently traps were prebaited for 1 to 3 days before setting. At such times most or all of the bait was removed each night. When the traps were set three changes in appearance took place: (a) a wire trigger protruded down into the center-rear of the trap near the bait. (b) A wooden trigger extended parallel above the roof of the trap connecting the wire

trigger and the door. (c) The door stood up in its sliding groove and also obscured the upper one-third of the doorway. Then many traps remained set with the bait undisturbed, even though during the preceding days, when traps were unset, the rats regularly removed the bait. The reason that I believe that trap-avoidance is a learned response is that most young rats were captured during their first period of exposure to traps, in contrast to older rats who frequently avoided capture through an entire 3 to 8 day period of continuous exposure to set traps.

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A. *The Repeat Response.* Traps were left set for 3 to 8 days during each period of trapping. Any rat caught before the terminal day of a period of trapping had the opportunity of being trapped during a later date of that same trapping period. Such captures following the lapse of 1 to 7 days were designated as repeats.

Only 30 percent of the rats (195 out of 652), captured initially during trapping periods, repeated. For those rats which did not reenter traps during a trapping period, it may be assumed that confinement in traps comprised such an unpleasant experience as to override the attraction to enter the trap exerted by the bait. Even among those rats which repeated, (table 9) some delayed reentrance longer than did others. This suggests that, even among the minority who were quite prone to reenter traps, some were affected more by the experience than others. Furthermore, the decline in frequency of longer intervals before repeating suggests a possible regularity to the intensity of the effect of being trapped. Any such regularity was obscured by three variables in the manner of assembling the data: (a) Trapping periods were not all of the same duration, and thus the longer repeat intervals did not have the same opportunity of occurrence as the shorter ones. (b) Rats repeating once were released, and thus were subject to being captured a third time. (c) The number of rats available for trapping was not constant (see fig. 10).

TABLE 9.—*Frequency of repeat intervals* [1]

Interval length in days	Males	Females	Total	Expected frequency
1.....................	129 (126.0)	51 (56.0)	180 (182.0)	.7001
2.....................	35 (39.5)	22 (17.5)	57 (57.0)	.2193
3.....................	10 (10.7)	2 (4.7)	12 (15.4)	.0593
4.....................	5 (3.04)	1 (1.35)	6 (4.39)	.0169
5.....................	0 (0.74)	1 (0.33)	1 (1.07)	.0041
6.....................	1 (0.05)	3 (0.024)	4 (0.078)	.0003
Total.........	180	80	260	1.0000

[1] The numbers in parenthesis refer to the number of each interval calculated on the basis of the expected frequency.

In calculations not included here, these three variables were taken into consideration. It was found that for those rats which did repeat, the probability of the number of rats waiting 2 days before repeating was 0.50 of the number waiting only 1 day; the number waiting 3 days was 0.50 of those waiting 2 days; and so on. Empirically, a probability of 0.50 gave a better fit than did either 0.49 or 0.51. The observed and expected frequencies of repeat intervals (table 9) approximate each other so closely that confidence may be placed in the notion that there is a regularity to the change in frequency of intensity of response to traps among the members of the population. This regularity is probably that determining the right hand one third of the curves shown in figure 77.

B. *The Recapture Response.* When traps were left unset for 11 to 75 days (mean, 46 days) and then reset it was again possible for rats to reenter. A capture after such a lapse of time is termed a recapture.

A certain proportion (c.f. fig. 10 and first five points in fig. 78) of both males and females were represented by recaptures roughly parallel to their opportunity of being captured. However, certain individuals skipped some opportunities of capture—that is they avoided reentering traps. This resulted in a mean elapsed time between captures considerably longer than the mean interval between exposure to set traps (table 10). The actual mean interval between recaptures closely approximated 85.12 days rather than the 46.42 possible or the 67.37 calculated from the observed captures. This was because many individuals did not enter traps during the terminal or last few periods of trapping to which they were exposed.

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Figure 77.—The frequency distribution of a behavoir through the population. This behavior is the proneness of rats to enter traps. A rat with an index of zero always avoids traps. A rat with an index near two entered a trap at nearly every exposure.

TABLE 10.—*Comparative data on recapture intervals*

Sex	Period born	Number of individuals	Mean interval between captures in days	$\pm 2\sigma$
♂	1947..	31	88. 58	26. 90
♀	1947..	45	98. 66	24. 66
♂	March–May 1948.................................	167	57. 70	18. 46
♀	March–May 1948.................................	96	66. 44	20. 00
♂	June–October 1948..............................	91	63. 00	17. 40
♀	June–October 1948..............................	57	68. 00	18. 40
	Total......................................	487	67. 37	20. 34
	Total exposure intervals......................	893	46. 42	14. 48

POSSIBLE ....
MALES ——
FEMALES — —

FREQUENCY

INTERVAL BETWEEN RECAPTURES IN DAYS
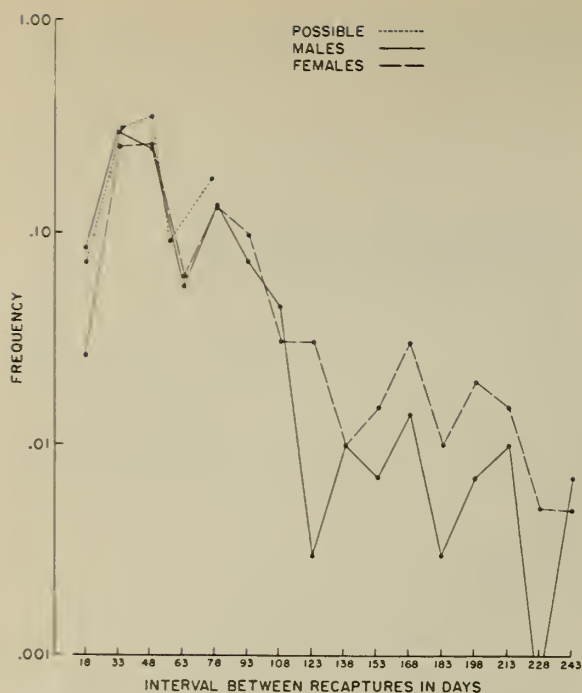
Figure 78.—The frequency of intervals between recaptures.
The frequencies are 3-point moving averages, except for
the terminal points, which are the observed frequencies.
Had every rat been trapped during each trapping period,
the dotted "possible" curve would have resulted.

Regardless of the length of the interval between
trappings, approximately half of the rats avoided
entering traps. This general statement forms the
major conclusion regarding the recapture response.
The results indicated no lessening of the avoidance
behavior toward traps between 18 and 78 days.
In fact, they indicate a slight enhancement of the
avoidance behavior. However, little confidence
may be placed in this difference, for, as may be
seen in figure 10, rats born during 1947 were pro-
portionately much higher represented by shorter
intervals (11 to 40 days) than were the rats born
during 1948. Thus this difference may, in some
unrecognized fashion, be related to time of birth.

Any rat, which avoided capture for 78 days,
must have lived through a period of trapping
without entering a trap. After 93 days (i.e. 86 to
100 days) only 17.1 percent of the rats still avoided
capture. Such rats which avoided capture for
86 to 100 days were exposed to at least one period
of trapping without being captured. Despite the
crudeness of these figures there can be little doubt
that the avoidance of traps became markedly
reduced once a rat went through an entire trapping
period without entering a trap. As may be seen

in figure 78, there was a gradual decline in the num-
ber of rats still avoiding entering traps after in-
tervals of time longer than 93 days.

C. *Summary of the Alteration of Trap Avoidance
Through Time.* After 1 day following last capture,
79 percent of the rats avoided reentering traps.
Days 2 through 6 following last capture had the
following percentages of rats still avoiding traps:
69, 64, 61, 60, 59. From 18 to 78 days dollowing
capture 52 to 66 percent of the rats still avoided
reentering traps. These two sets of data suggest,
that, regardless of the time intervening between
exposure to traps, there is little change in the
number of rats which will continue to avoid traps.
However, when a period of nonentering traps
between two other periods of exposure to traps,
there is a marked reduction to 17 percent of the
rats still avoiding traps. This percent gradually
declines between 100 and 300 days from prior
capture until practically no rats avoid capture
longer than this. These trends are summarized
in figure 79.

D. *Trap Avoidance as Influenced by a Rat's Asso-
ciates.* One female never entered traps over a
period of 14 months. Several other rats never
again reentered traps after their first or first few
exposures as juveniles, even though they lived for
a year or more. Young rats apparently are in-
fluenced by the avoidance behavoir (or lack of
it) exhibited by their older associates. See the
previous discussion (pp. 85–86) of entering
the activity recorders. I suspect that this same
process of mimicking the behavoir of older rats op-
erated in this trap-avoidance behavoir. If this is a
correct interpretation of the social influence on de-
termination or modification of behavior, it is quite
important in assessing existing or attainable states
of culture by rats.

E. *Sexual Difference in Frequency of Capture.* Four
hundred and twelve rats inhabiting several Balti-
more row-house blocks were trapped, marked, and
released. A number of these reentered traps during
the initial 5 to 10 day period of trapping (table 11).
Females repeated as frequently as did males.
The number of males and females available to be
captured was unknown. Therefore, the only valid
conclusion is that those females which entered
traps were as prone as males to reenter.

The population in the pen exposed to traps was
known. There were two methods of capture.
Rats trapped or removed from their places of
harborage should reflect fairly accurately the sex

Figure 79.—The alteration of an avoidance behavior through time. This figure was based upon three sets of data. The circles represent the lack of reentering traps within the consecutive days of setting traps within a trapping period. The squares represent the number of rats still avoiding traps in relation to the length of time between setting traps during consecutive periods of trapping. The triangles are based on those rats for whom one or more trapping periods intervene between two consecutive captures.

ratio of rats exposed to being trapped. This gave a nearly 1 to 1 sex ratio. Yet males entered traps much more frequently than did females (table 12).

TABLE 11.—*Frequency of repeating among rats in Baltimore residential blocks*

	Number marked	Number of repeats
Males.....................	219	75
Females...................	193	75

Chi Square = 0.321; p between 0.5 and 0.7.

Males in the pen also repeated more frequently than did females. However, for those rats which were prone to repeat more than once (2d, 3d, etc., repeats following an initial capture) females were just as prone to enter traps as were males (C with D comparison in table 12). This provides the clue as to the sexual difference in the response. It suggests that there is no inherent attribute of females, which prevents them from reacting the same as males with reference to an anxiety producing experience such as being trapped. One may infer that those conditions which bias rats' behavior toward a reduction of the avoidance behavior toward traps, occur with greater frequency or intensity with reference to males; but that once some thresh-

TABLE 12.—*Frequency of capture of males and females*

	Males	Females
A. From burrows or harborage boxes...............................	396	361
B. Captures and recaptures in traps................................	387	265
C. Initial repeats..	133 (0.34 of B)	62 (0.23 of B)
D. 2d, 3d, etc., repeats during same trapping period...................	46 (0.35 of C)	21 (0.34) of C)

A with B comparison: Chi Square=6.76; p=.01.
B with C comparison: Chi Square=4.59; p=.02.
C with D comparison: Chi Square=0.007; p=.95.

old of modification of behavior is reached, males and females respond similarly. This is discussed in more detail in the section, "Social Stress and the Proneness to Enter Traps", pages 95 to 99.

F. *Variability of the Trap-Avoidance Behavior.* Previous analysis suggest that some rats enter traps more frequently than others. In order to investigate this variability further, an index of the positive aspect of the behavior, i.e., proneness to enter traps was developed:

Trap-proneness index=Number of times captured/number of periods rat was exposed to being trapped.

This index varied from 0.0 to 2.0. A rat which never entered traps has an index of 0.0. One which enters once during each period of exposure has an index of 1.0. One which repeats occasionally, in addition to captures and recaptures may have an index over 1.0.

This trap-proneness index was determined for all rats which were born in the pen and who lived for at least 277 days (fig. 77). Seventy-three males and 64 females were included in this restriction of the population. It will be noted that for both sexes the distribution of this behavior approaches a normal one. This was the only behavior for which a quantitative analysis was possible with reference to its variability. As discussed in the following section the major variability of this behavior is assumed to result from the social structuring of the population rather than from genetic variability.

The degree to which rats enter or avoid traps has been discussed entirely upon the basis of their prior experience of having been confined in a trap. However, 38 percent of those rats which lived to 277 days of age were not trapped on their first exposure to traps following initiation of aboveground activity at between 25 to 30 days of age (see table 13). Of these a few rats were not cap-

tured until their third or fourth exposure to traps and three rats were never captured at all in traps' although each was exposed to being trapped during four to seven different periods. It will be recalled that the traps when not being used were left in piles scattered about the pen. Therefore, they can hardly be considered as strange objects, other than that they occurred at new locations when set. In order to preclude this change from eliciting a strange object reaction it was the usual procedure to prebait the traps for 2 or 3 days with the doors off so as to accustom the rats to entering the traps. Because of the large number of traps set and their distribution through the entire pen, the lack of rats entering a trap cannot be attributed to the lack of opportunity of encountering set traps. Therefore, it is concluded that the avoidance of traps by rats which had no prior experience of being trapped is probably attributed to their behavior being influenced by the behavior of their older associates, which evidenced an avoidance behavior toward traps. If this interpretation is correct, it is important because it indicates the possibility of cultural determination of behaviors without the individual having to experience the situation normally required to elicit the behavior.

TABLE 13.—*Period of exposure at first capture*

Trapping period	Number of rats	Mean age in days at capture	Standard deviation
First.................	85	48. 2	14. 9
Second.............	40	75. 6	15. 8
Third..............	7	118. 0	33. 8
Fourth.............	2	193. 0	....
No captures........	*3	....	....

*These 3 rats lived through a total of 15 trapping periods (4, 4, and 7 respectively) without ever being taken in traps.

G. *Social Stress and the Proneness to Enter Traps.* The demonstration that the avoidance response to traps approached a normal distribution was not anticipated. Had the population been composed of individuals with considerable genetic variability such a normal distribution would have been anticipated on the basis of its probable dependency upon multiple factor inheritance. However, in the light of the fact that the original stock had been selected in such a way as to insure the maximum restriction of genetic variability, it was believed that variability in this behavior was mainly attributable to environmental influences. Since the presence of food in the traps served as a reward or positive reinforcement in overcoming the avoidance response toward the trap, it might be presumed that the proneness to enter traps was associated with the degree of food deprivation. This cannot be ruled out, since data was not obtained on the food consumption of individuals. The general impression was gained that all individuals were able to procure all the food that they needed, but that the degree of social conflict experienced varied between individuals. Variability in social conflict is reflected in the number of wounds characterizing rats as of May 1949 (Tables 44 to 48, 50 to 55): Mean wounds for males 14.2 (σ, 11.5); for females 5.7 (σ, 6.6). Range for males 0 to 61, with a median of 11; range for females 0 to 26, with a median of 4.

Several lines of evidence indicated that the degree of stress became accentuated through later periods in the history of the colony. These periods have been arbitrarily designated: 1. Rats born during 1947; 2. Rats born from March through May, 1948; 3. Rats born from June through October 1948. Comparative data for the rats born during these three periods and which lived for at least 277 days are shown in table 14. For both sexes there are consistent trends toward an increasing proneness to enter traps as births occurred later in the history of the colony. With males there were consistent increases in the mean number of wounds per rat through these periods as well as consistent decreases in the rate of maturation. As discussed in a later section (pp. 220 to 221), slower rates of maturation are indicated by a higher Maturation Index. The frequency of being wounded is a very direct indication of social conflict among males and the resulting state of stress. The inhibition of rates of maturation is also considered to result from increased social stress. Among females the relationship of these two indices (wounds and rate of maturation) of stress do not bear as consistent a relationship with the proneness to enter traps as they do for males. Apparent trends, however, are consistent with the situation for males. At the younger age, 150 to 277 days of age, the lowest incidence of wounds characterized those females born during 1947, whereas the highest incidence of wounds for the older age, 278 to 400 days of age, characterized those females born during the later time. The picture for females was somewhat obscured by the fact that among the eleven females born during 1947 there

TABLE 14.—*The relationship between time of birth and (1) proneness to enter traps, (2) number of wounds, and (3) rate of maturation*

Time of birth	Number of rats	Mean number of periods of exposure to traps per rat	Index of trap proneness (median)	Number of wounds between age in days of:		Maturity index (median)
				150–277 (median)	278–400 (median)	
MALES						
1. 1947	10	11. 1	. 430	1. 0	5 0	I.55
2. March–May 1948	34	8. 0	. 817	2. 4	8. 1	I.67
3. June–October 1948	29	5. 0	1. 000	3. 4	10. 5	II.25
FEMALES						
1. 1947	11	13. 4	. 462	*0. 3	**3. 0	***I.67
2. March–May 1948	28	7. 4	. 714	1. 3	3. 0	I.50
3. June–October 1948	25	4. 9	. 800	1. 3	4. 5	II.25

Omitting females 17, 20, and 25 born during 1947: *0.7; **2.2; ***I.55.

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were three individuals, Nos. 17, 20, and 25, who received a greater degree of punitive action from their associates than might have been anticipated on the basis of the low population density. When these three atypical 1947 females are removed from consideration the trends for the wounds and rate of maturation through these three periods more closely resemble that of the males.

Each of these three periods of birth included individuals representing most of the range of the trap-proneness index. In order to separate the relationship between incidence of wounds or the rate of maturation and the proneness to enter traps from their dependence upon conditions associated with season of birth, the trap-proneness index for each sex was divided into low-, medium-, and high-class intervals, such that each interval was represented by approximately the same number of individuals. This analysis is shown in table 15. Shown in italics in this table are those trends which the author considers as being biologically significant. Thus with females the greater the proneness to enter traps the slower was the rate of maturation. The lack of any correlation between incidence of wounds and proneness to enter traps probably resulted from the fact that many of those females who matured rapidly were those which reared litters and engaged in considerable fighting during the time of lactation. This produced a higher incidence of wounds in this group than would otherwise have been the case. For males, which fight more than females, there is a good correlation between the proneness to enter traps and the degree of inhibition of the rate of maturation. However, it will be noted that the males which were most prone to enter traps had a more favorable rate of maturation than did those males with only a medium proneness to enter traps. This is due to the fact that a number of fairly rapidly maturing males continued to contend unsuccessfully for a higher social status, and in the process they received many wounds. The increased stress associated with this unsuccessful fighting probably produced this increased proneness to enter traps.

An understanding of the dependency of proneness to enter traps upon those conditions which affect the rate of maturation is facilitated by an examination of the figures 80 A and B in which the maturity index is plotted against the trap-proneness index. For each sex the rats plotted in these figures are separated into five constellations, A to E. For each sex the constellations A, C, and D are somewhat arbitrary divisions in a continuous distribution in which those rats with lower rates of maturation (i.e. higher maturity index) are more prone to enter traps. The interpretation placed upon this relationship is that those conditions of social stress which inhibit growth reduce the tendency of rats to avoid noxious stimuli or situations deleterious to them. Although there was no way of completely determining the degree to which a heightened food drive, that may be more characteristic of rats with socially produced inhibitions of growth, may account for the greater tendency of such rats to enter baited traps, the author nevertheless believes it is the altered emotional state accompanying stress, that accounts for variability in proneness to enter traps rather than the hunger drive.

TABLE 15.—*The relationship of number of wounds and rate of maturation to the relative proneness to enter traps*

Sex	Number of rats	Trap-proneness index (median)	Maturity index (median)	Number of wounds between age in days of:	
				150–277 (median)	278–300 (median)
Females.....	22	.434	*I. 71*	1.3	5.0
	20	.691	*I. 90*	0.5	3.5
	22	1.448	*II. 10*	2.0	3.0
Males.	23	.400	I. 50	*1.3*	*6.9*
	27	.800	II. 17	*2.3*	*8.8*
	23	1.286	I. 86	*4.4*	*9.8*

(Figures in italic represent those trends deemed by the author to be significant.)
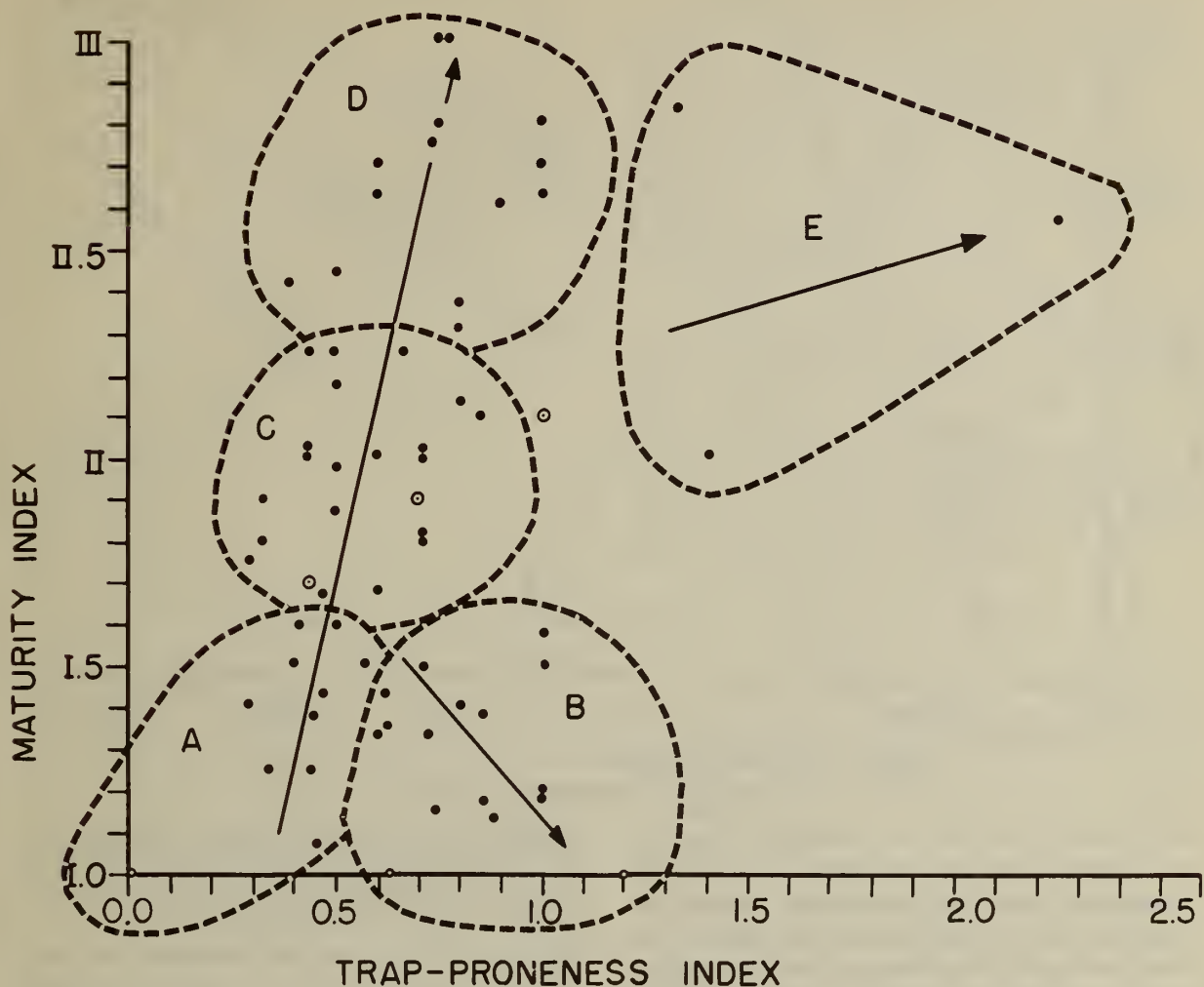
Figure 80A (females).—The relationship between physical maturation and the proneness to enter traps. A high maturity index represents markedly inhibited growth. Individuals which have lived under the most favorable circumstances are those represented by dots nearest the intersection of the ordinate and abscissa. Arrows indicate trends away from such more optimum conditions. The constellations A through E represent aggregates of rats with similar histories. The increased proneness to enter traps characteristic of constellation B and E are related to indications of an augmented anxiety state during adult life. The circled dots in figure 80A are the mean maturity indices for rats having the lower, middle, or upper trap proneness indices.

A reason for believing this becomes apparent upon a closer scrutiny of those individuals forming the B constellation for males. The discreteness of this clump of individuals may be seen in figure 80B. The status of this group of males is shown in comparison with the other constellations of males in table 16. In this table, in addition to data on wounds, there is shown a birth rating score, which depicts the author's opinion as to the degree of favorableness of the conditions surrounding the early life of these rats. The basis of this rating score is shown in table 17. It takes into consideration: (1) Birth during periods of higher population density (i.e., later in the history of the colony) was characterized by conditions unfavorable to both physical and social maturation; (2) Birth close to the food source (i.e., alleys versus areas) was more favorable; (3) Birth on the south side of the pen was more favorable than on the north side (i.e., due to the cultrual concomitants of the first high-ranking
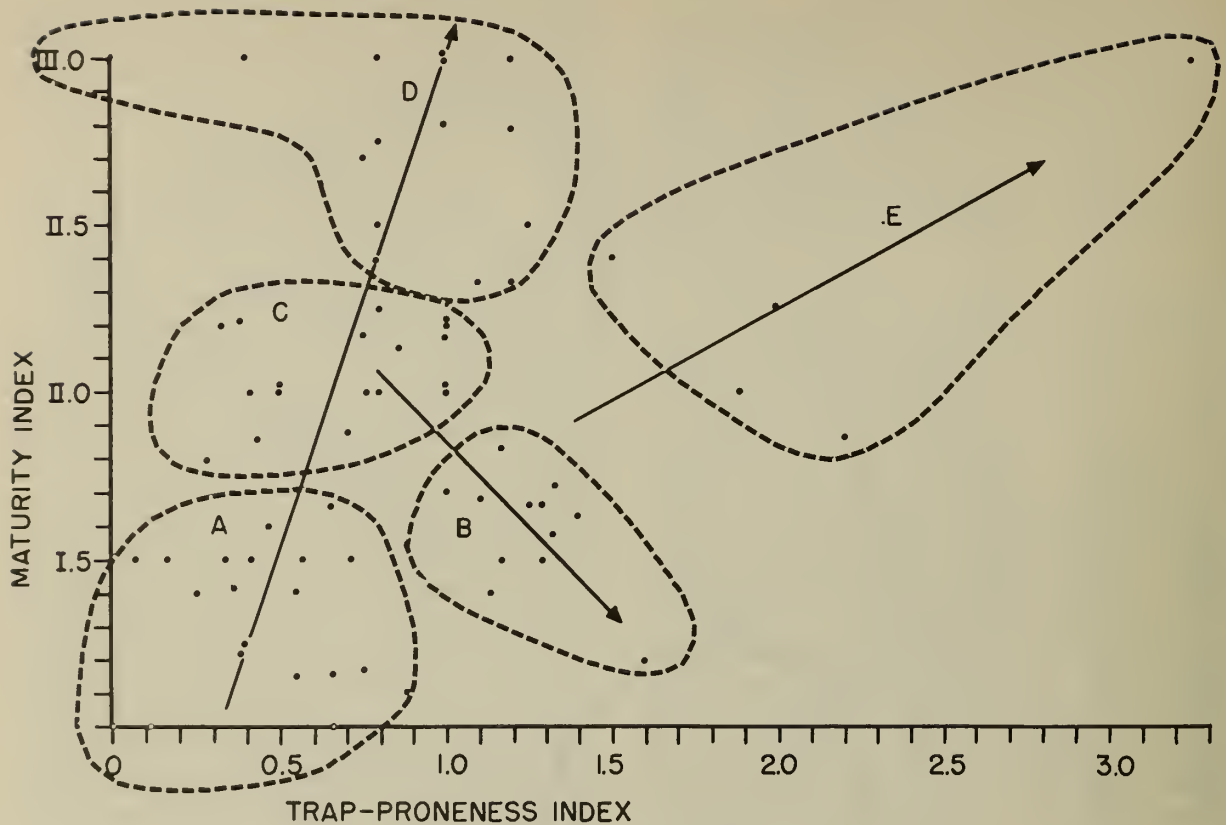
Figure 80B (males).—See legend for fig. 80A.

female having her litter on the south side of the pen). Despite the fact that members of the B constellation were born under more unfavorable conditions (mean birth rating score: 6.67) than either the A or C constellations (mean birth rating scores: 4.15 and 5.94 respectively) they exhibited a rate of physical maturation only slightly less rapid than did the A constellation males. It is probable, that with their greater size at an earlier date in comparison with their litter mates, that these B constellation males were the more dominant members of their repective litters. Thus with the experience of success in priority of action over their litter mates, it became inevitable that these rats would be the ones which further contended for dominancy status with their larger associates, who in general had been born under much more favorable conditions. Their contention was in general unsuccessful. Its lack of success is reflected in the fact that this group of males had the greater number of wounds, particularly during early adulthood, than any of the other constellations. The opinion is held by the author that it is the

stress arising from this unsuccessful contention for social rank which reduces the degree of avoidance of traps among the B constellation males.

TABLE 16.—*The relationship between (a) the stress associated with fighting or the conditions surrounding early life, and (b) the membership in constellations having similar attributes of proneness to enter traps and physical maturation*

Constellation*	N.	Median number of wounds between ages in days of:		Time and place of birth rating score (median)**
		150–277	278–400	
A..............	20	1. 8	8. 3	3. 0
B..............	12	6. 2	11. 0	6. 5
C..............	18	2. 0	6. 5	6. 0
D..............	15	2. 3	9. 0	8. 0
E..............	5	2. 3	7. 5	8. 0

*See figure 80B for delineation of these constellations of male rats.

**See table 17 for details of rating score.

TABLE 17.—*Rating scale[1] of presumed degree of social stress associated with time and place of birth in terms of the sum of the rating for place of birth and time of birth*

Place of birth	Place rating	Time of birth		
		1947 and March 1948	April and May 1948	June–October 1948
		Time rating		
		2	4	6
South Alley Burrow	1	3	5	7
Areas I and II	2	4	6	8
North Alley Burrow	3	5	7	9
Areas III and IV	4	6	8	10

[1] The lower the rating scale the less the stress experienced.

For constellations A, C, D there are consistent trends of: (1) decreasing rates of maturation; (2) increasing proneness to enter traps: (3) more unfavorable social conditions surrounding early life; and (4) in general a greater frequency of wounds. The exception to the latter (i.e., 8.3 wounds for A constellation males between the ages of 278–400 days) is attributable to the fact that these more dominant males were involved in fights with all the other groups of males and could not avoid being wounded some of the time, although they usually won.

The E constellation of males presumably represents those few individuals who, for a variety of reasons, remained under exceptional stress during their entire life span. Presumably the B constellation for females is just as real a group as it was for males, but an analysis similar to that for males, as shown in table 16, was not prepared since the discreteness of this group was not so apparent in figure 80A.

The trend of the evidence suggests the following formulations:

1. The trap may be considered as a particular example of those goals which possess both positive and negative attributes affecting the degree of response elicited from the individual.

2. The degree to which the negative or unfavorable aspects of the goal situation elicit avoid-ance of the goal is inversely related to the degree of emotional disturbance or stress experienced by the individual. Another way of phrasing this statement is that individuals who have unavoidably experienced many disturbing situations also seek out other punishing situations such as represented by capture in traps (see pp. 281 to 283).

3. The social stress experienced by the individual during early life, which determines physical maturation, also modifies the degree of avoidance of the trap.

4. Social stresses, which arise after the rate of maturation has been determined, and which are frequently unrelated to food attainment, may produce a marked decrease in the avoidance of traps.

These formulations should be considered as hypotheses, which need further verification under more rigidly controlled conditions than were possible during the history of this colony.

5. *Food, Water and Elimination.*

A. *The Sources of Food.* The sources of food for the rats were (1) a nearly continuously and abundantly available supply of Purina Laboratory checkers, (2) an occasional small amount of garbage, and (3) a few natural food stuffs available in the environment.

The Purina checkers were placed in a hopper directly in the center of the pen. This hopper would hold 100 pounds, and so with the exception of the last few months of the study it was easy to keep an adequate supply of this food always available. Even when this supply was temporarily exhausted at the times of high population density, it was usually possible to replenish the supply before the food caches formed by the rats were exhausted. On a few occasions during periods of trapping, food was purposely withheld for periods of 3 or 4 days in the hope that this might increase the hunger drive sufficiently to make the rats more liable to enter traps. Even during these periods, stored food appeared to be sufficient to sustain the rats in good health.

The garbage placed in the pen rarely exceeded 5 to 10 pounds at any one time. With few exceptions when this food was available the rats ignored the Purina checkers and concentrated on eating and transporting the garbage until it was all gone.

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On several occasions a raw unbroken hen's egg was placed in the Food Pen. Although the rats rolled it about on the ground they were never able to break the shell. There are many popular reports relating to the ability of rats to break or transport hen's eggs. If there is any validity to these reports it is likely that the behavior is a culturally developed behavior which has a low probability of spontaneous origin.

Natural food stuffs occurring within the pen played an insignificant role in the nutrition of the rats. On a few rare occasions rats were observed to eat blades of grass. Bark from the trees also served as an occasional source of food. Dogwood, Virginia pine and black locust were the only trees of any abundance in the pen. Of these the locust was the only one which seemed to be eaten to any extent. Many of the locust trees were severely damaged, even far up in the branches, although few trees were killed. Even so this bark supplied only a minute portion of the diet of the rat. Otherwise, when the population was high, these trees would all have soon been killed. On two occasions the groups of fasicles forming the tips of pine boughs were mixed through caches of Purina checkers in such a manner as to indicate that their transportation was a food storage behavior, even though no evidence was ever obtained that the rats ate pine needles or stems. On one of these occasions several hundred such tips of branches were mixed through a huge cache of 2200 Purina checkers, the composite mass of which completely filled a harborage box. This depositing of pine fasicles among actual particles of food is interpreted as a disruption of discrimination by chronically disturbed rats. The rats involved in this aberrant behavior were female 43 and members of her three litters described on pages 147 to 148. These same rats were those excluded from Area III by more dominant rats in the formation of Colony e during the early spring of 1949 (see pp. 207 to 209). Also see pages 195 to 196 for details of this and related behaviors of the rats involved.

During the spring of 1947 when there were 10 or less adult rats, small piles composed of 1 to 8 earthworms were found in the harborage boxes. In most cases only parts of each earthworm were present.

Other than these few instances, the rats were forced to depend entirely upon the supply of Purina laboratory checkers provided for them directly in the center of the Food Pen.

B. *Behaviors about the Source of Food.* The dimensions of the Purina checkers were approximately 10 by 18 by 20 mm. These were removed one at a time at the time of eating or transporting. Occasionally the rats would rake out small piles with their forefeet much in the manner of excavating dirt from burrows. This behavior became highly exaggerated on one occasion when a smaller sized food particle was provided. This commercial food was in the shape of small cylinders approximately 5 mm. in diameter and 15 mm. long. The use of this food had to be discontinued since the rats excavated the entire 100 pounds the first night so that it formed a concave mound about the hopper. Under these conditions the rats responded more to the food as materials for excavation than as items of nutrition.

Invariably any object of food picked up was initially grasped with the teeth. Occasionally an upward raking motion with one forepaw might be used to facilitate the grasping of larger objects by the teeth. However, this use of the forepaws never appeared to be very effective. With smaller objects, such as the Purina checkers, there would be a transfer to the forefeet, as the rat sat on its haunches. The rats rotated such objects proficiently while eating. Regardless of the size of the food object, rats frequently just nibbled on it in the position which the food happened to be lying.

Rats were never observed to transport more than one Purina checker at a time. On only one occasion was a rat seen to attempt to transport two pieces of food as large as a Purina checker. This rat grasped a piece of meat, shook it back in its mouth and picked up a roll. Halfway to its burrow it dropped the roll and had to return. With small objects such as dry corn meal the rats will transport them by the mouthfull. Objects the size of a slice of bread or a carrot are picked up with the teeth, and with the head slightly tipped back on the shoulders the rat runs forward. When the rat reaches a passage through a fence or an entrance to a burrow with such a piece of food it drops it, goes through, turns around, comes back, and then pulls the food through. Objects too heavy to carry, and these may weigh as much as the rat, are dragged along as the rat grasps them with its teeth and backs along.

As soon as the population had increased to 30 individuals it was not uncommon to see 10 to 15

rats grouped about the source of food. Observation of such groupings has led me to conclude that what appears to be rather complex interrelationships among members of such groups can actually be broken down into paired relationships. Frame by frame examination of several thousand feet of movie film supports this conclusion.

The following are the major types of paired relationship about the food:

1. Two rats approach the food and begin eating without apparently paying any attention to each other, even though they may move so close together that their sides touch.

2. The two rats may approach each other in the recognition behavior of extending their bodies and heads until their noses nearly touch. This may develop into:
   a. Rats eat side by side paying no attention to each other.
   b. Both rats run away. When this happens, the two rats may very shortly come back and begin eating while paying no attention to each other.

3. When one rat is eating and is approached by another, the first rat may initially run away and avoid the second rat. This behavior of the first rat may be the simple one of retreating from an object in motion. This retreat may occur even though the approaching rat is socially subordinate.

4. The behavior of the rat that avoids the approaching rat, must be qualitatively different depending upon social rank. Normally the approaching rat does not give chase to the avoiding rat unless the approaching rat is a dominant one and the avoiding rat holds a subordinate position. The implication of such observations is that many conflicts, which occur near the food source, do not arise as a competitive action over food. In fact, where both rats are socially relatively high ranking, the frequency of avoidance is less and the likelihood of a chase being precipitated by the avoidance is also decreased.

5. When two rats come in contact with each other by chance movements or as a result of a restriction of the distribution of the food, pushing behaviors frequently arise. This takes the form of pushing with the forefeet, kicking with the hind feet, or swinging the posterior end of the body at the other rat.

Both rats may continue eating while engaging in this pushing. Following this pushing one of the rats may walk away from the food, although sometimes upon receiving a push a rat will jump sidewise or backward from the food.

6. This pushing may develop into a conflict, which interrupts the feeding of both individuals to the point that they rear up in the sparring position and engage in a tumbling fight. One rat at least leaves the food source and the other may give chase.

These latter two categories of behavior may be considered as different intensities of intolerance to crowding rather than to conflicts resulting from the food objects themselves. Considering these six categories as having covered the basic relationships which may exist between two rats, it is apparent that as the number of individuals, which assemble simultaneously as the food source increases, there will be an increased likelihood that any specific paired interaction will become more aggravated. Furthermore, the opportunity for sequential reactions becomes enhanced. This happens when one animal, which jumps away from the approach, push, or bite of another, accidentally lands on a companion, who in turn may swing aside and bump into another rat. At times a group of 10 to 15 rats appears to explode.

There are a number of factors which predispose a paired relation toward complete amicableness or aggressiveness. These will be discussed in more detail later in the sections relating to social behaviors and social organization (pp. 179 to 198), since paired relations may occur at many points other than at the food source. Nevertheless, my notes are replete with instances of rats in groups of from 2 to 15 eating amicably together.

It was stated above that conflicts arising at the food source do not arise over competition for the food objects themselves. The following two instances are typical examples which further support this belief:

1. June 28, 1948: Male 22 (440 days of age; weight 532 grams) has been transporting food to Area I where he is the dominant male. At 5:50 p.m. he brought a piece of cake up Path 1, but along the way it fell and crumbled. This caused him to make several trips to retrieve it. On one of these trips back into Area I he encountered male 30 (317 days of age; weight, 474 grams) who had just invaded

Area I. Male 30 normally inhabited the adjoining Area IV. Male 22 chased male 30 out of Area I. By the time male 22 got back to the pieces of cake on Path 1 male 30 was there eating. Male 22 joined him and they ate amicably.

2. May 19, 1948: Female 37 (276 days of age) has a litter in the South Alley Burrow. Her littermate, male 34, who had been living at the South Alley Burrow but shortly shifted his harborage to other places in the pen, and female 28, another littermate whose home was now in Area I, both approached the South Alley Burrow. Both were chased away by female 37. A few minutes later these three rats were seen to be eating amicably together at the pile of garbage in the Food Pen.

The point which I wish to make is that conflict arises not over the food object itself but results rather from crowding. About the place of customary harborage the threshold of tolerance to crowding is low, with the resulting expression of territorial defense. At a distance from the harborage, such as at the food source, the tolerance to crowding is so high, that normally physical contact, followed by pushing, is requisite to initiating conflict to the extent of fighting. An intuitive hypothesis derived from such observations is that the threshold of tolerance to crowding is directly proportional to the distance from the harborage

The home range of each animal may be thought of as being gourd-shaped with the neck of the gourd ending over the Food Pen. Where other conditions have enhanced the expression of territorial defense about its harborage, there is a tendency for this heightened aggression to be expressed about the approaches to the Food Pen as well as within the Food Pen itself. Details of this type of aggression are given later in the paper (pp. 183 to 184).

In my notes there are only five records of simultaneous attention to a single piece of food by two rats. These occurred after one of the rats was already in possession of the food:

1. A 102-day-old male from the North Alley Burrow took a piece of food away from a 316-day-old female at the South Alley Burrow. She relinquished the food and walked away as if nothing had happened.
2. A 105-day-old male took a piece of cake away from 443-day-old male 22 at an entrance to

the Food Pen with no show of antagonism upon the latter's part.
3. At the North Alley Burrow 282-day-old lactating female 42 ran out and had a tug-o-war with a young rat which was attempting to transport a piece of food away from the burrow entrance.
4. Female 37, who was in estrous, took a roll away from an adult male as he was approaching one of the passages through the Food Pen. The male was probably a sib of female 37 and both lived at the South Alley Burrow. No antagonism was shown by the male.
5. An adult rat dragged a ham bone to the South Alley Burrow but it was too large to be taken down into the burrow. A much smaller rat approached the bone every time the adult went down in the burrow but retreated each time the larger rat came back out.

The meagerness of these observations indicates the infrequency of joint action over a piece of food. In the Food Pen several rats frequently ate simultaneously from a large piece of garbage.

A socially low-ranking rat, while transporting food to its harborage, may be chased by another. Usually the rat being chased drops its food. Occasionally the rat doing the chasing may return to eat or transport the food to its own harborage, but more often the food will be left until such time as some other rat encounters it. Involvement of food in the conflict situation appears to be coincidental rather than causal. See pages 179 to 180, 182 to 183, and 194 to 195 for description of the behaviors of subordinate rats which tend to elicit attack.

C. *Shelter Storage.* The simplest behavior of rats with regard to food is to consume it at its source. The next increase in complexity is to transport the food a short distance before eating it. This slightly more complex behavior arises from the tendency of rats to seek shelter, which provides protection both above and to the sides. At each of the entrances of the Food Pen there was a metal tunnel which housed the photoelectric cell and the mechanism for recording the passages of the rats. This type of shelter was probably utilized by all of the rats for eating food they had transported from the center of the barren Food Pen. Although I have no quantitative data on this point, it is my general impression that as great a quantity of food was actually consumed in these four recorder

shelters as at the hopper itself. With many rats this "transportation-to-shelter-for-consumption" behavior evolved into a "transportation-for-storage" behavior in which piles of food were left in the recorder tunnel. Such food caches were usually ignored by the rat which assembled them, although they then became a secondary source of food for rats subsequently coming to the Food Pen. Even though most rats engaged in this type of shelter storage of food, this behavior became accentuated among socially low-ranking rats to the point that it formed a typical segment of a syndrome of abnormal behavior (p. 196).

A typical record: Female 7; 324 days of age; October 3, 1947; 2:19 to 2:45 p.m. She made 23 trips carrying garbage into the recorder tunnel at Passage 6. During the 12½ hours of light sufficient for observation, 10 other rats made 31 storage trips into the recorder shelters, 4 trips for eating in these shelters, and only 5 trips of storage into harborages.

To a lesser extent caches of food were formed under the protective cover of the small trees and other vegetation just outside the Food Pen in the alleys. Such food caches were used by other rats as well as by the one which did the transporting to that site. This food might be eaten at this location or transported elsewhere. Occasionally food was dropped just outside the Food Pen without any reference to shelter. This abandonment of food being transported was at times the result of the rat being pursued by another, but at other times the food was abandoned for no apparent reason that the observer was able to detect.

There is a characteristic series of developmental stages in the maturation of storage behavior to the point where food particles are transported over the greater distance to the burrow or harborage box. These stages are:

a. Food is eaten directly at the source.
b. Food is transported into a recorder shelter at the entrance to the Food Pen, or into the shrubbery just outside the Food Pen where it is then eaten.
c. Food is transported and deposited into discrete piles or caches in the recorder shelters or in the vegetation just outside the Food Pen.
d. Food is transported and deposited into discrete piles or caches in and at the greater distances at which the harborages were located.

There is considerable evidence that a rat in motion while transporting a particle of food is attracted into the first harborage it passes unless the presence of some other rat prevents its entry. In my notes there are records of 21 rats making 68 trips from the Food Pen with food into harborages boxes whose positions were recorded (see table 18). 0.74 of the trips terminated in the two boxes nearest the passages through the barrier fence (i.e., box positions A and A^1, see fig. 74). 0.25 terminated in the four boxes (B, B^1, C, C^1) which required that the rats at least pass by one other box (i.e., A or A^1). However, only 0.015 of the trips terminated in the three boxes (D, E, F), which required that the rats pass by at least two other boxes.

TABLE 18.—*Proportionate distribution of objects or acts through the areas*

Position of box [1]	389 rats	3969 feces	4272 food pellets	68 enterings with food
A..............	.075	.083	.029	.324
B..............	.105	.098	.012	.015
C..............	.085	.075	.014	.074
D..............	.175	.121	.084	.000
E..............	.067	.107	.001	.000
F..............	.072	.167	.017	.015
A^1..............	.123	.124	.220	.412
B^1..............	.157	.074	.609	.132
C^1..............	.141	.156	.015	.029
A+B+C.......	.265	.256	.055	.413
$A^1+B^1+C^1$.....	.421	.354	.844	.573

[1] See fig. 74.

On the night of September 14–15, 1948 six box traps were left unset and prebaited with sunflower seed about each of the Passages 1 to 4, through the median barrier fence. No other prebaited traps were present in the areas. By the next morning most of the seed had been removed from all of the traps. All the harborage boxes were opened to determine where they had been transported. Hulls from the seeds were only found in harborage boxes 1, 5, 13, 19, 23, and 32. Except for box 13, these represent the nearest box that the rats would encounter in the process of transporting the sunflower seed to a sheltered place to eat. Actually box 13 was not an exception since the nearer box 14 was unavailable, since it was filled with a huge colony of *Formica exsectoides* ants. There were many other records which showed that food from prebaited

traps was transported into the nearest harborage box whether or not it was immediately eaten.

However, the actual count of Purina checkers in the harborage boxes (see table 18) indicates a much greater number in those boxes lying farther away from the passages through the barrier fence than would be anticipated on the basis of the above behavior of deposition in the nearest shelter or harborage. The explanation of this lies in the fact that once a food cache is formed it may serve as a secondary source of food which will then be transported to other places. In this way the food becomes rather generally distributed through the environment in all available harborage sites, irrespective of whether the harborages were being utilized by the rats as place of retreat during their inactive periods. The independence of the usage of harborage sites for food storage from their usage as a place of retreat is revealed in table 19 which was derived from several inspections of the harborage boxes.

TABLE 19.— *The independence of the place of termi-nating a food storage trip from the place of habitation*

Food in boxes	Rats or nests in harborage box	
	Present	Absent
Present.................	76	66
Absent.................	170	166

The Chi square for this distribution is 0.2350 which has a probability of chance occurrence between .5 and .7

Up to this point we have reached the general conclusions that (1) there is a tendency to deposit food in the nearest harborage shelter, and that (2) both initial and subsequent transfers of food are made irrespective of the use of harborages as places of retreat during times when the rats are inactive.

This food dispersal through the environment was an important aspect of the life of the rats. It made the food, which was originally available only in the center of the Food Pen, rather generally available over the whole pen. This must have reduced considerably the frequency of conflicts which would otherwise have arisen at the single source of food. Although one rat may remove the food from the cache formed by another rat near this rat's place of harborage, one probably is not justified in designating this behavior as "stealing". Practically all

the evidence points to the fact that there is a complete unawareness of property rights or value of the food object (see p. 108).

The following are a few examples of the events which transpire during the social dispersal of food:

1. April 20, 1949, 1:45 a.m. At the South Alley Burrow a rat entered and departed from a burrow entrance with a piece of garbage just taken in by another rat, and carried it into another nearby entrance.

2. May 9, 1947. A rat took a piece of garbage from the Food Pen into Box 28. Just after it left another rat entered and took it to Box 19.

3. May 18, 1947. Garbage had been placed near the food hopper. Between 6:33 and 6:45 p.m. a male rat made seven trips taking garbage through Passage 7 into the North Alley where he formed two food caches; four trips into a clump of shrubs, and three trips into an unset trap just outside Passage 7. Between 6:45 and 6:50 another male rat took the food from the cache among the shrubs and transported it down Path 3 over to and into a burrow beside the outside fence opposite Box 19. While he was doing this, the first rat took the food from the cache he had formed in the open trap and transported it down into the North Alley Burrow. Between 6:50 and 6:55 p.m. the second male made two trips taking some of the crumbled garbage from the open trap over into its burrow opposite Box 19 and then he made two trips carrying food from the Food Pen to his burrow. At 7:10 p.m. two other rats from somewhere in Area III entered this burrow and took food past Box 20 to a point that I could not see.

4. January 21, 1948. A rat carried food from the Food Pen into hole 9 of the South Alley burrow. One of three rats standing nearby immediately followed and, without going in far enough for me to loose sight of its tail, it backed out with the food.

5. March 4, 1948, 6:50 to 7 p.m. Several rats have made trips from the Food Pen carrying carrying food into hole 3 of the South Alley Burrow. A rat coming from Passage 1 went down this hole, took some food and ran back through Passage 1 into either Area I or IV.

6. May 24, 1948. One rat took a piece of bread through Passage 8 of the Food Pen and left it just outside in the West Alley. Another rat took it out among a clump of small trees

in the West Alley. Then female 20 took it to near Passage 4. At this point she dropped it upon being chased by another rat. Thus, this food after transportation by three separate rats was available for a fourth rat.

7. June 28, 1948. Female 28 (316 days of age) took a cookie that another rat had left at Passage 5 of the Food Pen and carried it up Path 1 and over into Area I. Along the way up Path 1 some of the cookie broke off and then Male 82 (112 days of age) came by and cleaned up the crumbs. One-hundred and two-day-old female 75 also came by and ate some of these crumbs.

This food dispersal becomes so extensive during the night that on the next day it may be found in locations where no rats are harboring even near by. Twice a considerable number of Purina checkers were found in Area I, where they had been transported during the previous night, although during the hours of daylight no animals were inhabiting this Area.

During November and December 1948 a record was kept of the rate of removal of Purina checkers from the hopper. Eight-hundred pounds were removed during 37 days. Approximate data:

Number of rats.............. 144
Mean weight................ 400 grams
Grams of food removed per
  rat per night.............. 60.5
Purina checkers removed per
  rat per night.............. 20 plus (the checkers av-
                               eraged less than 3 g.
                               each)

Since occasionally 1 to 3 days elapsed between the time each 100 pound lot of food was removed from the hopper and the next was placed, there actually was a period of 52 days between the provision of the first 100 pounds and the removal of the eighth 100 pounds. Considering this span of time, an average of 47.6 grams of food was removed per rat per night. This is equivalent to 0.119 grams of food per night per gram of rat. This includes both food consumed and food wasted.

Dr. Olaf Mickelson (Laboratory of Nutrition and Endocrinology of the National Institutes of Health) informs me that 0.05 grams of food (of the Purina chow type such as I used for the rats in the pen) per gram of body weight approximates that used each day by 400 gram rats. Considering the fact that over twice this amount was removed by the rats and dispersed through the pen, the likelihood was that all rats secured adequate food.

D. *Factors Affecting the Intensity of Storage.* No rats under 40 days of age were observed to transport food from the Food Pen. Between the ages of 25 and 40 days most of the explorations of the young were confined to within 10 feet of the home burrow or harborage box. Very shortly after the 40th day of life most of the young reach the Food Pan. Coincident with this arrival at the food source the behavior of transporting food immediately appears quite well developed, but its orientation with reference to harborage sites is poorly developed. For example:

July 11, 1947. In the evening I entered the observation tower at 6:15 p.m. At that time a 42-day-old Litter 3 rat whose home was in Area III was carrying Purina checkers from the Food Pen into the East Alley. At 6:28 p.m. I began counting the trips: 6:28 to 6:47, 36 trips; 6:55 to 7:00, 10 trips. It dashes from the weeds in the East Alley to the tile at Passage 6; there it pauses for 3 to 10 seconds with its head protruding into the Food Pen. It then dashes to the food tray, gets a Purina checker and dashes back into the East Alley through the tile at Passage 6 without pausing. It began raining lightly at 6:22 p.m., but this did not seem to disturb this little rat. There is an abundance of fresh garbage in the Food Pen toward which this rat paid no attention. This is the first Litter 3 rat that has been seen in the Food Pen. The next morning 42 checkers were found in the East Alley where this rat had been going. There were three piles: 30, 11, 1.

Between the 40th and 60th day of age most of the food transported is left as caches in shelters either at the passages into the Food Pen or just peripheral to it. Beginning with the 60th day there is a gradual elaboration of the storage behavior so that by the 100th day this behavior is in essentially its adult stage in so far as the likelihood of reaching a harborage with the transported food is concerned. The 60th day of age approximately marks the time when the young become independent of their mother to the extent that they may shift their center of activity elsewhere. It also marks the time when they begin to lose the juvenile pelage. On the other hand the 100th day of life falls roughly at the time of the completion of the adult pelage and the expression of adult sexual behavior.

Both sexes store food from that time until death. However, males store considerable less frequently than do females. The increased storage activity

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of females is primarily associated with lactation. Presumably the habit of storing during lactation may become sufficiently fixed that transportation of food for storage will continue at an increased rate even after the termination of lactation. Other conditions being equivalent animals of lower social rank engage in more storage activity than do higher ranking individuals. Storage of food in harborages occurs at all seasons of the year. My notes are inadequate to indicate whether there is any effect of seasonal changes in the weather on storing. These statements summarize the general conclusions regarding factors affecting intensity of storage activity. The following are samples of the types of observations upon which these conclusions were based:

Age and storage:

1. June 1, 1948. The first Purina checkers in a week were available tonight. All ages of both sexes except the month-old young of female 37 have been seen to transport food.
2. Although prior food deprivation no doubt affected the storage activity noted above, a subsequent checking of my notes showed that rats of all ages stored at other times as well. For 87 records the mean age was 259 days, when only those rats between the ages of 100 and 500 days were included. Age and number of storage trips: 125, 6; 175, 12; 225, 5; 275, 23; 325, 18; 375, 10; 425, 11; 475, 2.

It must be noted that most of my notes on food transportation by recognized individuals came during the first (1947) breeding season. Once I had become satisfied that food transportation was a rather general phenomenon most of my notes concerned social interactions between individuals. Therefore, the data which I have on food transportation is not nearly as adequate from a quantitative standpoint as it might have been. Nevertheless, the few records on recognized individuals provide a basis for a few general statements. Each record includes all the observed instances of storage by one rat on a particular date.

Concerning males:

1. Low social rank definitely was associated with increased storing. Male sibs 57 and 59 of Litter 13 who had a very retarded growth rate (fig. 139) and who all during their lives were frequently subject to the punitive action of their associates stored food. Likewise one of the original males No. 8 exhibited storing. This rat was particularly subject to punitive

action from the more dominant original male 12. However, the social status of male 12 gradually shifted as he aged so that by the time he was approximately 600 days of age many other rats dominated him. For the final nearly 200 days of his life he was repeatedly seen to transport food to distant harborages, although he was never noted to do so earlier. Sixteen of the 41 records of recognized individuals transporting food are encompassed by these 4 rats.

2. Low social status, however, is not a prerequisite for inducing storing behavior. Attainment of a high social status is correlated with the exhibiting of a rapid rate of growth to a relatively large mature size (pp. 203 to 236). Twenty-one of the remaining 25 records of storing by males were for those individuals having such favorable growth rates.

Concerning females:

1. Thirty-eight of the 55 records for recognized females refer to individuals for whom the age of their last litter was known (see table 20). It will be seen from this tabulation that storing practically ceases by the end of the fifth 10-day period of age of the young. This roughly coincides with the time at which young rats have been noted to begin their storing activity.

TABLE 20.—*Storage of food by females in relation to the age of their last litter*

Age of last litter in days	Number of records of storing behavior
1–10	9
11–20	9
21–30	3
31–40	3
41–50	9
51–60	1
61–70	1
71–80	2
81–90	1

2. Eleven of the records refer to females, 7, 20, 25, and 58; all of which have long histories of much punitive action from their associates. Most of the instances for storage included in the records for females 7 and 58 were of the nonharborage type discussed under the head-

ing "The Syndrome of the Social Outcast" (pp. 195 to 196).

3. Two records are for females aged 116 and 161 days respectively both of which were in their first pregnancy.

4. Four of the records concern individuals for which there is insufficient data to warrant any comment regarding associated factors.

In all the above comments a record refers to all the storing activity engaged in by one individual during a single night, although in most cases each individual noted made several storing trips. Transportation of food occurred during all months of the year. Surveys of the harborage boxes during December 1948 and February 1949 showed as wide a distribution of food as occurred at other seasons. During these winter months there was no reproduction.

E. *The Position of Food Caches in the Harborages.* The sunken harborage boxes provided were greater in volume (12 by 14 by 28 inches) than were the cavities (table 4) which the rats excavated in their burrows. Normally the nest covered not more than one-sixth of the floorspace and was located in one corner. Food brought into boxes containing nests was deposited in discrete piles, usually in an opposite corner of the box. Only rarely was food deposited on the edge of the nest or eaten in the nest. In the burrows piles of food were scattered along tunnels in small enough amounts so that the rats could get by them, or they were placed in separate terminal cavities in which there was no nesting material.

F. *An Extreme Development of Cache Formation.* During the breeding season of 1948 female 43 had 4 litters in Area III. This was the most litters had by any female during a similar period of time. While rearing these litters she formed larger food caches than were noted elsewhere in the pen.

1. April 3, 1948. Box 20. The young of litter 8 are 20 days old. There are several hundred Purina checkers and an apple in the box.

2. April 16, 1948. Box 28. As I opened the box, female 43 ran back into the burrow which led through the wall of the box. One of her 33-day-old Litter 8 young ran with her. Her 10-day-old Litter 13 young are in the burrow. In the box are 140 Purina checkers carried from the Food Pen last night. Minimum round trip distance of 120 feet between Food Pen and Box 28. Therefore, this

female traveled at least 16,800 feet during this one night while transporting food.

3. April 28, 1948. Box 21. Female 43 is nursing her Litter 13 young. She has transported at least 100 Purina checkers to this box.

4. June 2, 1948. Box 19. Nine to 12 Litter 18 young born to Female 43 last night. Twelve Purina checkers in corner opposite nest.

5. June 4, 1948. Box 19. There are now 40 Purina checkers in cache.

6. June 8, 1948. Box 19. Female 43 now has her 7-day-old Litter 18 young in the front nest. I counted 100 Purina checkers and estimated the remainder of the food cache at over 400.

7. June 12, 1948. Box 19. Food cache now nearly completely covered by dirt excavated by female 43 from a tunnel system leading through side of box.

During the fall of 1948 female 43 as well as many of her young remained in Area III. Twice two huge caches were observed. It was not known to what extent these were the work of female 43 or to what extent she was assisted by her young.

1. October 6, 1948. Box 20. Over 2,000 Purina checkers in box. I removed all of these and replaced them in the Food Pen.

2. December 10, 1948. Box 20. In this box there were 2,200 Purina checkers as well as several hundred pine shoots. These branches were scattered at random through the checkers as if they were food. This indicates that their cutting and storage was a food storage behavior pattern. However, I have never seen any evidence of rats eating these branches. Rats in burrow leading from box: Males 56, 57, 59, 696, 657, and 669; females 58 and 370. Only two of these eight rats showed a more than average rapidity in rate of growth. This retardation of growth may have been a factor in the accentuation of the storage behavior. However, since six of these rats were the young of female 43 there exists the possibility that their storage behavior was enhanced through a cultural learning process from the association with their mother.

G. *The Nonrecognition of the Value of Food.* Periodically the rats clean out their tunnels in conjunction with the enlargement of the burrow system. At this time dirt, feces, food caches, and nesting material are thrown out on the mound. In most

instances there is no attempt by the rats to salvage the food—even if it is fresh. The scattered cache is merely covered with dirt or left exposed to the weather. Occasionally this excavated food is retrieved: On December 2, 1947, 177 Purina checkers were excavated from holes about the North Alley Burrow. All were gone on December 4. Furthermore, food caches may be destroyed by the rats within their harborages. In a number of instances rats have assembled food caches in harborage boxes and then subsequently begun a burrow through the side of the box. In these cases the dirt from the burrow was excavated out into the box until it covered the cache. The food was in no instance uncovered later. It merely remained covered and decayed.

As mentioned previously female 43 had by June 8, 1948, assembled over 500 Purina checkers in the harborage box with her week-old young. Yet, during the next few days she completely covered over this cache with dirt she was excavating from a burrow leading from the box. One of the greatest values of stored food is that it may be available to the young rats at the time of their weaning. Thus, the mother destroyed food that could have maintained her litter for a week or 10 days after they were weaned. It, therefore, appears that the behavior of transporting and storing food is entirely dissociated from its usage. This is another line of evidence that the rats attribute no significance to the food object itself. It reinforces the belief that food objects are rarely factors in the initiation of fighting (see p. 102).

H. *The Food Acquisition Component in the Syndrome of the Social Outcast* (see p. 196). There are six aspects to this behavior which were observed to hold in part or in entirety for several rats:

1. There is an increased nonharborage storage immediately outside the Food Pen.
2. There is an increased storage in the activity recorder shelters at the entries to the Food Pen.
3. There is a storage of food or eating in the corners of the Food Pen. This was only observed for the few rats which exhibited several of the characteristics of the syndrome. (In all three of the above storage activities the food might be left and not used by the rat involved.)
4. There is an avoidance of other rats who come into the Food Pen even though these rats may pay no attention to these avoiding rats.

5. There is a hesitancy to enter the Food Pen even though no other rats are about. This behavior take the form of repeated approach-withdrawals before finally entering the Food Pen.
6. The acquisition of food by these rats becomes concentrated during the light hours of the day when most other rats are inactive.

All the rats which exhibited all or most of this constellation of behaviors had much in common in their history. The following are brief sketches of these histories, which list those factors which it is believed have relevancy to the development of the above behaviors:

Group 1. Female 7 and male 8. Each was the smallest of the five rats of each sex introduced into the pen in February 1947. Each was subject to considerable punitive action from its associates. They were dominated by those rats which were introduced with them into the pen as well as by many of the rats which were born later. At an estimated age of 1 year each fell into the Maturity Index Group III. As pointed out in the later section on growth this means that with respect to the rest of the population these rats grew very very slowly and attained only a very low mature weight and size.

Group 2. Original male 12 and male 83 born at the North Alley Burrow. The common factor here was that each rat enjoyed a much more favorable status earlier in life than they did later on when the abnormal behaviors relating to food acquisition appeared. During 1947 male 12 dominated the other introduced males, and he also maintained this status with reference to the males born in 1947. However, in the spring of 1948, as he reached an estimated age of over 600 days, he began to lose weight and began to be dominated by the males born in 1947. Coincident with this shift several of the behavior in the above list appeared. Male 83 during the first 3 months of life exhibited a very rapid growth, but during the next 3 months there was a considerable inhibition of his growth rate. As an adult he was not only frequently whipped by other adults but he also tended to associate in harborages with other rats with equally unfavorable histories. At 403 days of age he was seen to eat and form a cache in a corner of the Food Pen.

Group 3. This is the largest single group of rats with somewhat similar histories. It consists of the three Litter 3 females (17, 20, and 25) as well as the six members of Litter 13 (males 54, 56, 57, and 59,

and females 58 and 60). They were characterized by a moderately inhibited growth (see figs. 139 and 141). The average Maturity Index for the group was II.46 (where I is the most favorable and III the least favorable). Seventy-three percent of the rats in the pen exhibited a more favorable growth than this (see fig. 142). The mother (female 11) of Litter 3 was not only younger than the other original female (No. 10) which reproduced, but her growth was more inhibited (Maturity Index III). This litter was born at a point quite distant from the food source and at a time when they had to compete with rats born a month and a half earlier in the much more favorable South Alley Burrow location. Furthermore, at the age of 2½ months they were subjected to the rather severe punitive action of a lactating female at the North Alley Burrow whom they had to pass on their way to the Food Pen. It was at this time that their rate of growth became considerably inhibited (to the Maturity Index III level). Litter 13 had a roughly similar history with the additional factor of competition with older sibs who were still dependent upon their mother (No. 43). This was the only litter born in the pen which was conceived on the day

following the parturition of the previous litter, and which survived to compete with their older sibs.

Concerning these few individuals with abnormalities of feeding behavior for whom extensive data on their histories is available we may conclude that:

1. Where marked inhibition of growth or loss of weight is associated with the receiving of extensive punitive action from their associates, feeding abnormalities are likely to appear.

2. The more unfavorable factors, with respect to social and physical maturation, that are associated with the early life of the rat, the greater is the likelihood of developing abnormalities of feeding behavior.

I. *Summary of Hunger Satisfaction and Storage Behavior.* Normally hunger is satisfied either at the source of food or after food has been transported to the nearest shelter. Once a food cache has been formed the behavior of the rats toward it is essentially the same as at the primary source of food. In the diagram below X_1 to X_2 etc. represent ever more distant locations from the food source, Y.

Source
of   Ever farther distances, X, to which food is transported
food
Y X_1 X_2 X_3 X_4 X_5 X_6 X_7

------→Immediate satisfaction of hunger drive.

------------------→   Cache formation by young rats and also occasionally by older rats. These
   or   caches are usually in sheltered but non-harborage locations. This behavior
------------------------→   frequently immediately precedes transportation of food into harborages.

------------------------------------→——→——→——→——→etc.
                                 Cache formation by most adult rats. Locations are nearly invariably associ-
                                 ated with protected harborages such as the burrows or the sunken harborage
                                 boxes.

------------------------→——→ Cache formation and eating by many socially low ranking adult rats.
                                 This type of behavior in an individual does not preclude the expression
                                 of the previous more highly developed behavior. As likely as not these
                                 caches may be in completely exposed locations.

J. *Availability of Water and Behaviors Relating to Drinking.* One to four watering fountains such as are used for chickens were always available. They were placed in the corners of the Food Pen. Each held 2½ to 5½ gallons. When one of these containers was inverted the water became available in a shallow trough surrounding the edge of the bucket. At times 10 or more rats would crowd about one of these circular troughs with their sides touching. Open conflict as a result of crowding developed much less frequently about the water

source than at the food source. However, when one rat was drinking and another approached, the first rat frequently retreated temporarily from the approaching rat. This avoidance was accentuated among socially low-ranking rats. In fact, the very low-ranking rats tended to go only to those fountains not being used by other rats.

An example of the relationships between two individuals which may be exhibited at the fountain is shown in the following. May 12, 1949: Male 690, the second most high-ranking male in the pen,

was alone at the water fountain drinking. He was shortly joined by the dominant male 49. They drank amicably together, nearly side by side, for a moment. Then male 49 turned toward male 690. With this signal of intent to approach by male 49, male 690 jumped and ran away.

There is some evidence that the thirst drive holds dominance over the hunger drive.

1. November 25, 1947. 5:45 to 6:30 p.m. Although 5 days of accumulation of garbage from my home had been placed in the pen this afternoon rats paid surprisingly little attention to this food and none at all to the Purina checkers. However, hardly a rat entered the pen without taking a long drink at one of the fountains.

2. October 7, 1948. 12:30 to 3:45 p.m. All rats which came into the Food Pen drank, whether or not they ate.

3. In my notes there are 16 records of recognized individuals who after entering the Food Pen both ate and drank before departing.

In 14 of these 16 instances the rat drank before it ate. There are many records of rats just eating or just drinking when they entered the Food Pen. However, the few records above presumably pertain to those individuals in which both the hunger and thirst drives were sufficiently high to require satisfaction before returning toward the harborage.

At an open water source the obtaining of the water is by one of two methods. The rat either bends over and laps the water directly with its tongue, or it will first dip in its forepaws and lick off the water. Probably the former is the more frequent behavior. In either case grooming frequently follows drinking. In this process the rat sits on its haunches and extends a forepaw backward to and around the ear, dorsally over the head, across the eye, and toward the mouth. The hands are rotated alternately and rapidly with an occasional licking of them. Upon completion of the grooming of the head the rat bends to one side and begins grooming the fur of the back, sides and abdomen with both paws and mouth. This is followed by a cleaning of the genital region. With one or both forefeet on the ground a hind leg is extended forward and groomed with the mouth. The tail is picked up with the forefeet and licked. With some variation this in general depicts the order of grooming. Although grooming may occur at practically any point where the rat has stopped

momentarily, it is most frequently associated with drinking.

Dew and rain on the foliage served as accessory sources of water. The habit of licking off this moisture was noticed among the initial rats introduced into the pen as well as later when the population was quite dense. Presumably, the utilization of this occasional source of water may have reduced the social conflicts associated with the approach toward the Food Pen. However, this was probably of little import. At least on several occasions in the early morning hours rats were seen to congregate about the water fountain despite the presence of extremely wet, to the point of dripping, foliage.

K. *Elimination Behavior.* The actual act of defecation or urination was seldom observed. However, the distribution of spots, where urine could be seen or where there were feces, provided considerable indirect insight into these behaviors. Regarding feces:

1. Defecation occurred wherever the locomotion of the rat was temporarily inhibited. This is the most important generalization regarding the place of defecation. Most of the additional statements concerning locations of feces are merely corollaries of this.

2. Few feces occurred along the 3-foot wide paths from the corners of the Food Pen to the passages through the median barrier fence, except at the points where the trail down this path was intersected by a trail entering from the adjoining vegetation. At such points aggregations of feces might occur in a perfectly clear and unsheltered place. It will be recalled that these 3-foot wide paths were kept cleared of vegetation to facilitate observation.

3. Along trails through the vegetation the greatest concentration of feces occurred at intersection of trails. However, even along trails away from intersections more feces occurred than along similar stretches on trails over the cleared paths. This presumably resulted from the effect of the overhead shelter of the vegetation in temporarily halting locomotion.

4. Along the trails immediately adjacent to the outer limiting fence feces were no more concentrated at intersections of trails leading out into the areas than they were at any points intervening between such intersections. Characteristics of the situation and the behavior of the rats themselves suggest possible processes

producing this exception to a general rule. Vegetation was kept cleared for 12 inches away from the fence to prevent a shorting of the adjacent electric barrier wire. Rats most usually ran along this cleared pathway in the direction of the corners of the pen. While so traveling their heads were usually bent slightly toward the fence as if they were attending to stimuli outside the pen. Then the rat would stop. Presumably defecation took place at these times. All I can say here is that it always looked as if the rats were halted by some event random in onset with reference to the outward motion of the rat along the fence. Once the behavior of motion was interrupted, the intervening stopping was followed either by a retracing of the prior route along the fence or a turning out into the adjoining area as soon as an intersecting trail was encountered. Feces in piles adjacent to the outer fence were often in greater number, up to 100, than would be deposited by a single rat at a single period of defecation. This further suggests that though initial defecation here is on a chance basis, each defecation biases the probability of recurrence at the same spot. It is this sequence of behavior which leads to the decreased frequency of defecation with increases in distances from a center of orientation as was discussed under the topic of orientation and shown in figure 75.

5. Feces tend to be concentrated on either side of the passages through the fences. Stopping here is the consequence of two related behaviors. One is that a dominant rat spends a considerable amount of time at passages where it prevents others from passing through. As a result of having received punitive action near these passages the subordinate rats hesitate before going through.

6. Feces becomes concentrated in any sheltered area, particularly if there are vertical objects toward which the rat may orient. Thus, the activity recorder shelters at the passages into the Food Pen and the harborage boxes themselves became foci for defecation.

7. Defecation which occurred in the harborage boxes was normally away from the nest. Occasionally feces were found on the edge of a nest. In only one harborage box, No. 36, did defecation on the edge of the nest regularly occur (see fig. 54). However, in this case the

rats regularly relined the nest and kept it clean. When the number of rats inhabiting a single nest exceeds five or six adults, there is a beginning of cessation of maintenance of repair of the nest, and an accompanying deposition of both feces and urine in the nest. With aggregates of 15 or 20 adults the harborage site becomes extremely foul.

The presence of feces recorded on the surface of the ground has been utilized by the group at Johns Hopkins to assist in their sign-survey technique of estimating the abundance of rats. Although different workers can make very close estimates of the number of rats present, the actual number of feces were rarely recorded. In this pen study, however, both accurate counts of feces and close estimates of the number of rats alive are available (table 21).

TABLE 21.—*Variability in the number of above-ground feces per rat*

Date	Number of weaned rats	Feces per rat
June 1947	15	12. 6
September 1947	13	40. 4
November 1947	26	72. 7
January 1948	25	3. 8
May 1948	66	52. 5
November 1948	147	72. 2
February 1949	135	8. 8

It is quite obvious that the actual number of feces is quite misleading with reference to any relationship to population density. One factor that is involved is the severity of cold weather. The January 1948 survey includes only those feces left on the snow-covered ground during two nights following the snowfall. At this time when the minimum temperatures dropped below 15° F. there were only approximately two feces above ground per rat per night. The February 1949 survey also occurred when there was a snow cover. However, the count was made after only one night had elapsed following the termination of the snowfall, and at a time when the minimum temperature was only slightly less than 31° F. Thus, with the warmer air temperature approximately four times as much defecation occurred per night above ground. At other seasons of the year the attempt was made to count only those feces which were probably no older than 1 to 4 days. However,

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conditions of the weather with reference to the decay of the feces probably introduced so great an error as to preclude any usefulness of such counts. The conclusion is therefore, made that in the sign estimation of population density, the presence of feces must remain as a rough qualitative index.

With the exception of the very few observations of wet spots along trails, etc., which appeared to be distributed much as were feces, I have very little direct information regarding urination behavior. However, rats were frequently observed to rub their bodies against passages through fences, tile entries into harborage boxes, or over clods of dirt, rocks, or the entries to burrows. Defecation does not occur during this activity. It is assumed that some urination actually occurs during this rubbing process or that scent passed out with the urine and adhering to the fur is rubbed off. Details of this behavior are presented in the discussion (pp. 152 to 158) of sexual behavior of which it forms a component part. That the scent leaves the body with either the feces or urine is shown by the following. The feces and dried urine accumulating in the tray under the cage of a laboratory strain of the Norway rat was preserved by washing the tray with 50 percent alcohol. When this solution was poured over objects in the pen and allowed to dry it attracted the wild rats and elicited from them similar but somewhat more intense inspection and sexual behavior than normally followed the leaving of such sign by one of the rats in the pen. Such activity by the rats in the pen served to form sign posts which attracted the presence of other rats.

Urine and feces adhering to the feet of rats becomes spread along trails. This serves to support a rich algal growth to the extent that the trails stand out as shown in figure 62.

6. Activity

A. *Fluctuations in Intensity and Periodicity of Locomotor Activity.* Even the most casual observation of wild rats reveals that they tend to be nocturnal. However, when sources of food, such as garbage about homes or food for domestic animals, are temporarily available only during the day hours, rats readily adapt to these situations and exhibit an increase in diurnal activity sufficient to insure adequate use of these temporary sources of food. In the preparation of sign surveys of rats in city blocks one also gets the impression that meteoro-

logical conditions affect the amount of aboveground activity. At the beginning of this study of the rats in the pen, I held few preconceived notions regarding specific ways in which surrounding conditions might alter periodicity or intensity of activity. The following discussions summarize the results of analyses of these observations.

An objective measure of intensity of activity was obtained through the utilization of photoelectric cells placed within a protected hood (see fig. 63 and 76) at each of the passages through the Food Pen fence. Upon the breaking of a beam of light to the photoelectric cell by the passage of a rat, a pen was activated to make a mark on a strip of paper moving at the rate of 1 foot per hour. Each mark on the tape was designated as a unit of activity. There was a separate pen for each of the four passages. Although activity was measured only in terms of movement in and out of the Food Pen, it was observed that whenever a particular group of rats emerged from their harborages at least a portion of them were involved in the movement in and out of the Food Pen. In fact, the general impression was gained that the total aboveground activity was proportional to the activity in the Food Pen.

We shall first examine a sequence of records of the distribution of activity through the 24-hour period (figs. 81 to 90). In each figure there was represented what might be designated as the general pattern of the 24-hour rhythm. Each of these general patterns was determined by obtaining the percentage of activity which occurred during each half-hour interval over a period of 10 days. With each such general pattern there is given as contrast the rhythm of activity for 2 separate days. The activity cycle for a particular day is often quite different from the general pattern resulting from lumping the data for a series of days.

As a background for some of the interpretations that will be given to these figures, it will be necessary to consider some of the experimental work on activity rhythms in laboratory strains of the Norway rat. A review of rhythms in the Norway rat is covered in pages 373–378 (1945), and 208–209 (1946) in a general review of 24-hour periodicities in the animal kingdom (13). The following excerpt suffices for the present interpretations:

"The pioneering work of Slonaker (1907) on the white rat is the first thorough study on the diel (24-hour) activity cycle of a mammal. In this and his later (1912) study, adult rats showed a

single major activity period lasting from 7 p.m. to 3 a.m. The existence of a single nocturnal peak of activity has been since confirmed by many workers (Richter, 1922, 1927; Shirley, 1928; Holmgren, 1936; Browman, 1937, 1942; Hemmingsen and Krarup, 1937; Herring and Brody, 1938; Levinson et al., 1938). The development and modification of this nocturnal pattern seems to be an attribute of age (Slonaker, 1907, 1912; Richter, 1922, 1927). At the time of weaning short activity periods are equally distributed over the entire 24-hour period but is concentrated in the hours of 7 p.m. to 3 a.m. The accentuation of nocturnalism is continued through the seventh month so that by the eighth month practically all activity is confined to the night hours."

"This marked nocturnalism continues through the 11th month, but after this time there is a general leveling of the activity curve and a shifting of the major period of activity so that by the 21st month it occurs between 3 p.m. and 3 a.m. The loss of rhythmicity is accentuated from the 24th month until shortly before death, when activity is nearly completely arrhythmic. During old age, the periods of activity are of short duration and are separated by long periods of rest. As the white rat assumes its adult nocturnal activity pattern, it also reaches its peak in the total amount of activity expressed per day. The age of assumption of maximum activity has been variously calculated at 75 to 105 days (Browman, 1942); 87 to 120 days (Slonaker, 1907); 175 days (Richter, 1922); 210 days (Shirley, 1928) 240 to 270 days (Slonaker, 1912); 270 to 390 days (Slonaker, 1926). Despite the variations in results, they mostly fall within the period of maximum nocturnalism and have been preceded by the assumption of the ability of the muscle to do maximum amounts of work at the age of 90 days (Steinhaus, 1941). According to Anderson and Smith (1927), rats stunted by insufficient diet do not show the change in intensity of activity with age shown by normal control rats."

During Period 1, November 1947, when the population was low, 26 rats, there was little evidence of nocturnal variability of activity between 6 p.m. and midnight (fig. 81). The absence of the marked bimodal nocturnality observed during periods 2 and 3 may be attributable to the fact that the majority of the population consisted of rats no more than 3 months of age. According to the experimental studies cited above rats of this age

have not yet developed the complete adult rhythm of nocturnal activity.

Periods 2, December 1947 (fig. 82) and 3, January 1948 (fig. 83) may be considered as representative of the rhythm which mature rats (4 and 5 months and over) exhibit in the absence of the increased competition which accompanies sexual activity and increased population density. The general pattern for each of these periods is that of a bimodal nocturnal rhythm with the premidnight period being the one of greater intensity of activity. Such bimodal activity rhythms follow the typical pattern exhibited by most animals which possess an endogenous 24-hour rhythm of activity, regardless of whether it is diurnal or nocturnal (13). It is suspected that the unimodal nocturnal rhythm typical of laboratory rats is in part dependent upon their domestication and living in isolation. However, the expression of a unimodal peak of activity appears to be determined mainly by the periodic replenishment of their source of food and water. This latter has been shown by Richter (14) and Shirley (15) to result in a marked increase in activity, during the several hours just preceding feeding.

With regard to the day to day variability in rhythms of activity, the rhythms for each of the two separate and consecutive days for each of these periods reveal little in common as to the exact timing of local periods of intensified activity. One must conclude that, whereas there is a basic underlying endogenous rhythm, local and temporary biological or meteorological events may modify its exact expression. Similar variability of the day to day activity from that of the general pattern is revealed by the pairs of days diagramed for each of the following seven periods.

During Period 4, February 20 to March 7, 1948, there was an abrupt shift in the character of the activity rhythm (fig. 84). Although the population was low, 24 rats, this was a time of heightened sexual activity. Several females conceived during this time. Two factors regarding sexual activity contributed to the greater tendency toward nocturnal arrhythmicity during Period 4 in contrast to the midwinter striking nocturnal bimodality of Period 2 and 3. On those nights when females are in estrous several males continuously follow her throughout the night. Although some of the males may temporarily leave her to go into the Food Pen the others give her little opportunity to rest and also follow her when she goes into the Food Pen

Periodism of activity as revealed by the number of passages in and out of the Food Pen. Ten sets of figures are shown for successively later periods in the history of the colony. An inspection of the series will reveal the following:

1. There is a tendency toward a bimodal periodism with the major period before midnight and a minor period after midnight.

2. As the population increased there was a tendency for the activity of the population as a whole to become more arrhythmic. For example, compare periods 2 and 3 with periods 9 and 10.
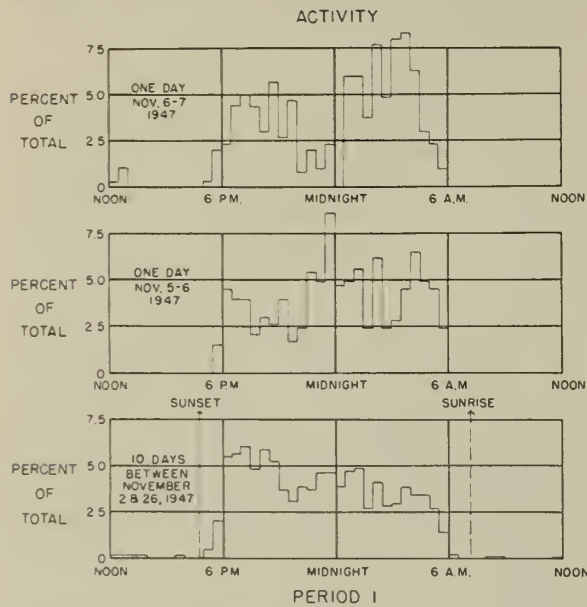
Figure 81.—Activity period 1; November 1947; 26 rats present in the pen.

Figure 82.—Activity period 2; latter third of December 1947; 25 rats present in the pen.

Figure 83.—Activity period 3; January 1948; 25 adult rats present in the pen. This was a time of inhibited sexual activity
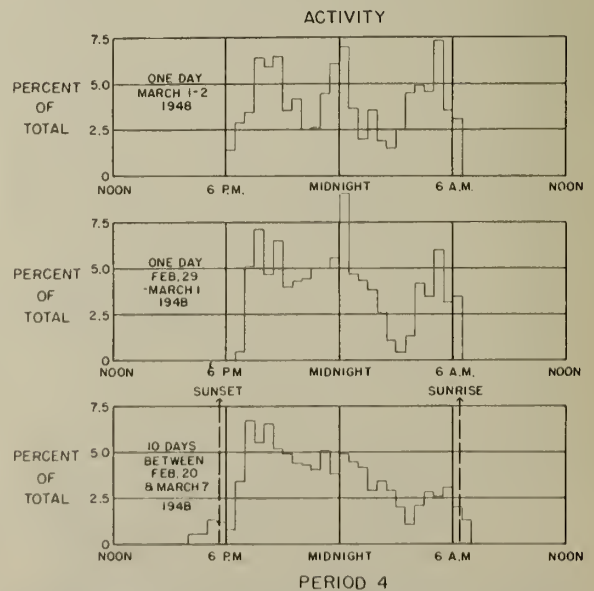
Figure 84.—Activity period 4; February–March 1948; 24 rats present in the pen. The 1948 breeding season began about February 13.
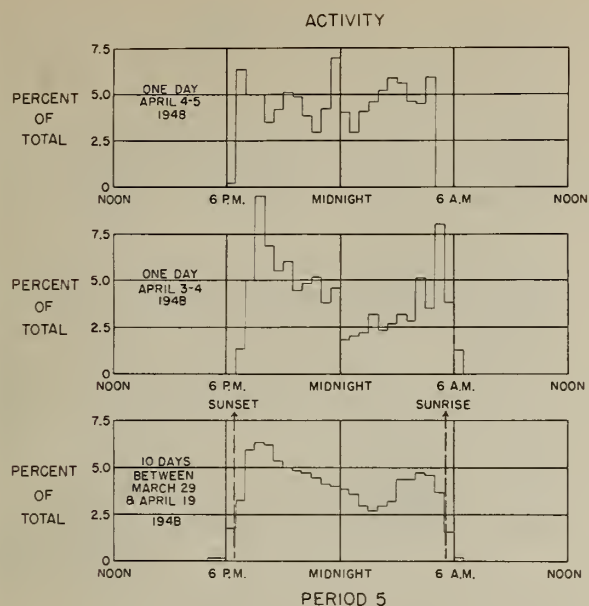
Figure 85.—Activity period 5; March–April 1948; 24 adults and 21 young that were being weaned contributed to this record.
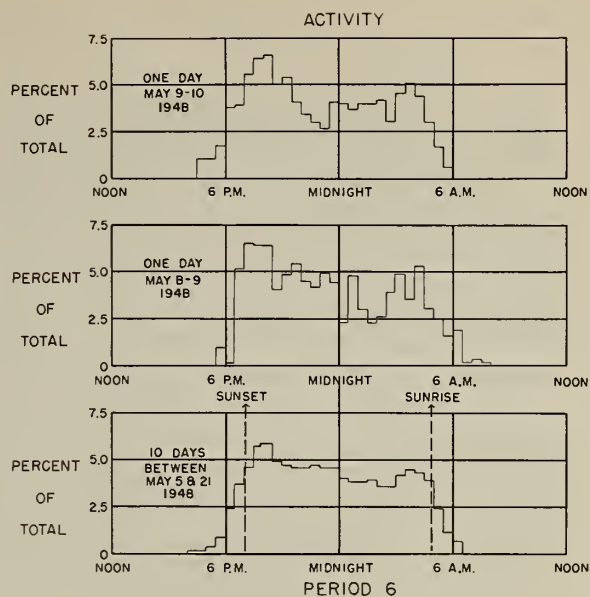
Figure 86.—Activity period 6; May 1948; 23 adults and 63 juveniles in the 30- to 60-day age range contributed to this record.
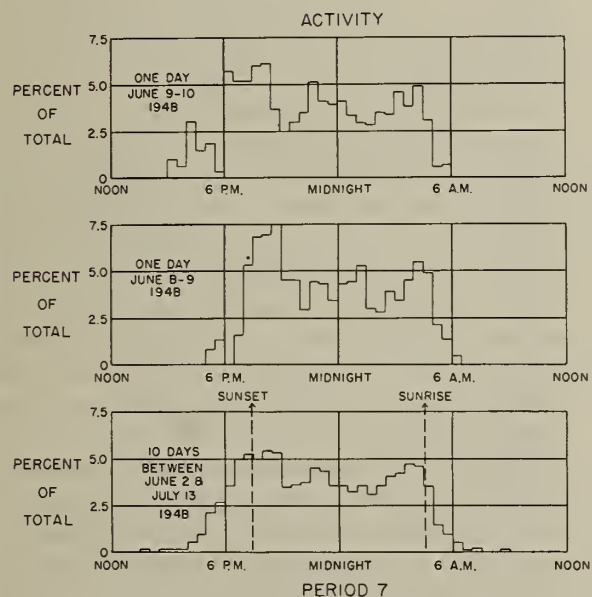
Figure 87.—Activity period 7; June 1948; 22 adults and 64 juveniles in the 30- to 90-day age range contributed to this record.
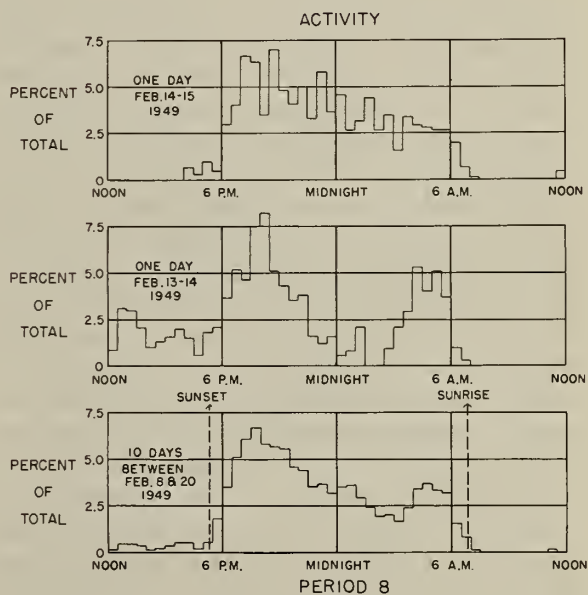
Figure 88.—Activity period 8; February 1949; 135 adult rats present in the pen; this time just precedes the initiation of the breeding season.

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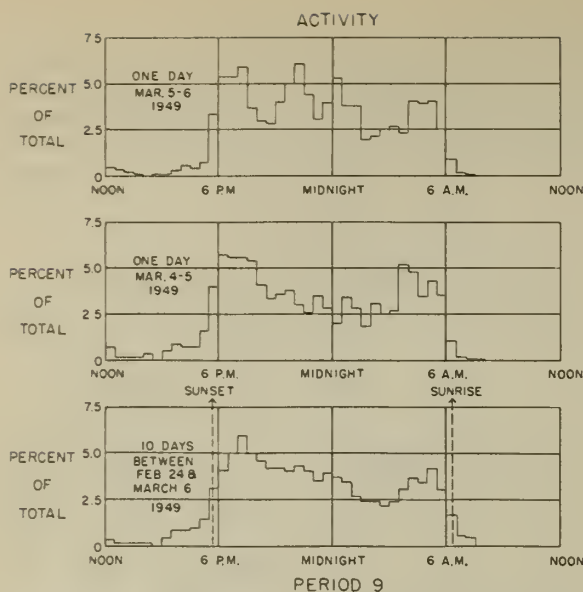
Figure 89.—Activity period 9; February–March 1949; 127 adult rats present in the pen; this is the time of the initial sexual activity of the breeding season.

Figure 90.—Activity period 10; March–April 1949; 126 adult rats in pen; juveniles were not yet exploring as far as the Food Pen.

and attempts to eat or drink. In addition, there is a heightened aggressiveness among males beginning with the descent of their testes and the onset of the breeding season. This aggressiveness is accentuated at the time a female is in estrous. Whenever aggressiveness is accentuated, there is a greater likelihood of a rat being repelled by a more dominant individual when it attempts to enter the Food Pen and thus it must attempt reentry at a later period during the night. These relationships are discussed in more detail later in the paper (pp. 183 to 184), but mention of them here is requisite to an understanding of the shift in the activity periodism toward increased arrhythmicity. Despite this trend toward nocturnal arrhythmicity the premidnight activity is still accentuated.

Periods 5, March to April 1948 (fig. 85), 6 May 1948 (fig. 86), and 7, June to July 1948 (fig. 87) may each be considered as representing different examples of the same set of conditions which modify periodicity of activity. In addition to continued sexual activity there are three additional factors which contribute to the trend toward increased arrhythmicity of the population. The storage of food by lactating females becomes markedly increased. This affects the ease with which other rats gain access to the Food Pen. And finally, during most of these three periods over half the population consisted of recently

weaned rats, whom presumably all had the arrhythmicity of activity demonstrated for juvenile laboratory rats.

Unfortunately the activity recording machine was not in operating condition from August 1948 through January 1949, when the large group of rats born during 1948 were attaining sexual maturity. Fortunately the machine was back in operation during February 1949, the month before the beginning of the 1949 breeding season. Period 8 (fig. 88) thus represents a time with a high population density, 135 rats, of mature but sexually inactive rats. Because of the later inception of sexual activity during 1949 (see fig. 94), Period 8 in 1949 is most nearly comparable to Period 3 during 1948, insofar as the physiological condition and the age of the majority of the rats is concerned. In comparing these two periods it will be noted that there is a greater degree of arrhythmicity of nocturnal activity during 1949. Even though both groups of rats were essentially sexually inactive, the presence of 135 rats in 1949 in contrast with only 25 in 1948 produced more competitive action between individuals for entry into the Food Pen and thus forced a greater proportion of individuals to enter the Food Pen later during the night.

The inception of heightened sexual activity during 1949 is represented by Period 9 (fig. 89),

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February 24 to March 6, and is most comparable to Period 4, February 20 to March 7, 1948. Again we find an increase in arrhythmicity of nocturnal activity during this later period. In this instance the increased population density accentuated the antagonism which accompanies sexual activity.

During the final Period 10 (fig. 90), March 20 to April 3, 1949, the action of lactating females in accentuating the arrhythmicity of nocturnal activity, when superimposed upon the increase of antagonistic relationships accompanying the increase in numbers of mature and sexually active rats, resulted in a nearly complete arrhythmicity in the general patterns of nocturnal activity. This increase in arrhythmicity of nocturnal activity also held true for individual days.

We may summarize as follows those conditions which modify the basic bimodal rhythm toward arrhythmicity:

1. Increase in density of mature rats (i.e. those over 3 to 4 months of age).
2. Increase in sexual activity.
3. Increase in the number of lactating females.
4. Increase in the number of juvenile rats (i.e. 25 to 30 through about 90 days of age).

The degree of shift from the bimodal nocturnal activity with its major premidnight peak toward a complete arrhythmicity of nocturnal activity may in part be considered as an index of the degree of stress experienced by the members of the population.

Another modification of the 24-hour activity rhythm, which accompanies the increase in intensity and frequency of social interactions, is the spreading out of activity into the daylight hours. From Periods 1 through 6, November 1947 through May 1948, when the population density was low or contained a large proportion of juveniles, there was essentially no activity before 6 p.m. or after 6 a.m. However, by Period 7, June and July 1948, when the juveniles born during March 1948 were beginning to attain sexual maturity, there was an augmentation of activity in the afternoon between 3:30 and 6 p.m. During the three terminal Periods 8, 9, and 10 of the winter and spring of 1949, when the density of adults was high, there was an increase in the afternoon activity in contrast to comparable Period 3, 4, and 5 to 7 of 1948. Thus the increase in intensity of social interaction produces a greater utilization of the daylight hours

as well as increases the arrhythmicity of nocturnal activity.

It is difficult to sort out the specific effect of light intensity on limiting activity from the counter effect of the spreading out of activity into the daylight hours resulting from social interaction. The effect of light intensity may best be judged by comparing Periods 2 and 3 with Periods 4 and 5. During the former two periods the sun set before 5 p.m. and rose after 7 a.m. With these conditions there was considerable activity during the hours: 5 to 6 p.m. and 6 to 7 a.m. However, in the latter two periods when sunset and sunrise were near 6 p.m. and 6 a.m., the length of the activity cycle had made a comparable contraction of 2 hours so that very little activity was exhibited during the hours of 5 to 6 p.m. and 6 to 7 a.m. During most of the later history of the colony, Periods 5 to 10, the intensity of social interaction was sufficient to override the limiting effect of increased light intensity.

By equally weighing the activity rhythms for each of the 10 Periods an average picture (fig. 91) of the activity rhythm for free ranging rats may be obtained. The bimodality of the nocturnal rhythm stands out.

The four passages through the Food Pen fence were fairly consistently utilized by different groups of rats. Therefore, the data for particular passages provide insight into alterations in activity associated with the social structuring of the colony.

South Passage (No. 5): Used mainly by the socially high-ranking rats of the South Alley Burrow. It was also used considerably by the rats inhabiting Area I. These rats had considerable in common with the South Alley Burrow rats with regard to their social and genetic history. It was also occasionally used by the middle social strata of Area II.

East Passage (No. 6): The greatest amount of usage was by the socially low-ranking rats of Area III. It was also used mainly by the Area II rats who were fewer in number.

North Passage (No. 7): It was utilized the majority of the time by the socially moderate to low-ranking rats of the North Alley Burrow. It was also utilized considerably by the Area III rats and by the socially moderate to low-ranking rats of Area IV.

West Passage (No. 8): The utilization of this passage was quite varied through time. Initially it was used most by North Alley Burrow rats.

SUNSET   SUNRISE

PERCENT OF TOTAL

7.5
5.0
2.5
0

MEAN ACTIVITY CYCLE

NOON   6 P.M.   MIDNIGHT   6 A.M.   NOON

(PERIODS 1–10 EQUALLY WEIGHTED BY AVERAGING THE HALF–HOUR PERCENTAGES OF ACTIVITY FOR ALL OF THE TEN-DAY PERIODS.)
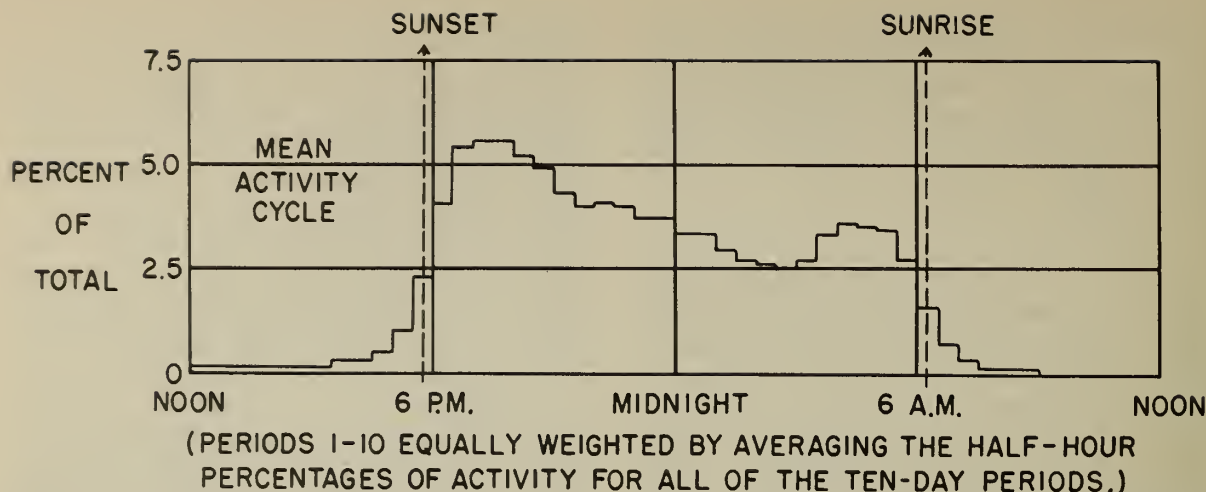
Figure 91.—Typical activity periodism exhibited by a colony of wild Norway rats. It is typical in the sense that the range of conditions, which contribute to variability from the more basic activity cycle as shown in figure 82, are represented by the samples from which this figure was developed.

Later on it was mainly used by Area I rats as well as those expelled into Area IV. During the last few months of the study it was mainly dominated by South Alley Burrow rats and Area I rats. However, a few Area IV rats still utilized it.

Although every rat probably utilized each passage at least occasionally, the above gives a sufficiently accurate picture of the differential usage of the passages with reference to the social stratification of the population.

The activity through each of these passages near the height of social interaction, March 1949, is shown in figure 92 for 2 consecutive days. With regard to intensity of activity, the total number of times rats went through the North (No. 7) and East (No. 6) Passages was greater than through the other two passages, which were dominated by the socially high-ranking rats. This is a direct reflection of the ability of higher ranking rats to prevent more subordinate ones from utilizing certain place in the environment. Differential utilization of time is also revealed in these figures. The South Passage (No. 5) shows the greatest amount of premidnight activity. Thus, the more dominant rats were able to express more nearly the basic bimodal nocturnal rhythm with its major premidnight peak. On the other hand, the North Passage (No. 7) exhibits an arrhythmicity of the activity through it by the lower ranking rats. This arrhythmicity of activity by the lower ranking rats only partially results from the immediate

actions of the more dominant rats during the same night. What had happened, was that a large portion of the population had previously been conditioned to utilize the North Passage and to avoid the South Passage. This avoidance of the South Passage, as a result of conditioning, occurred even when the more dominant rats were inactive. Among the many socially lower ranking rats there was further competition for the use of the North Passage, such that some individuals were forced to be active mainly after midnight. Activity through the East (No. 6) and the West (No. 8) Passages tended to fall intermediate between the North and South Passages with regard to both intensity and rhythmicity. This is as might be expected, since these passages were utilized more equally by lower and higher ranking rats.

Because of the marked contrast between the activity through the North and South Passages, detailed comparisons of them were prepared. These are shown in figures 93 and 94. The first analysis relates to the time distribution of activity. It utilizes the percentages of activity occurring after midnight as an index of the degree to which there is a modification of the periodicity of activity. For most of the course of this comparison 5 to 10 percent more of the activity through the North Passage (No. 7) occurred after midnight than was the case for the South Passage (No. 5). This is further evidence of the permanency of the greater social stress experienced by the rats utilizing the North Passage into the Food Pen. During the early spring of 1948 and 1949 there was a marked

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Figure 92.—Social modification of intensity and periodicity of activity. Two typical days near the time of maximum competition. Each activity unit represents a passage in or out of the Food Pen. The south passage (No. 5) was used by the fewer number of socially higher ranking rats, while the north passage (No. 7) was used by a greater number of lower ranking rats.

increase in the differential of postmidnight activity between the North and South Passages. This is further evidence of the importance of the beginning of the breeding season on the future history of the life of a colony of rats.

There were three occasions (circa Nov. 15, 1947, Jan. 4, and Apr. 28, 1948) during which the post-midnight activity through the South Passage exceeds that through the North Passage. These three exceptions to the general rule appeared to result from a time lag of some other underlying periodicity. Only a tentative hypothesis may be forwarded concerning this periodicity, which is so marked that it produces a doubling in the amount of postmidnight activity from the minimum to the maximum phase of the rhythm:

During the winter of 1947–48 there were three clear cycles of this rhythm. The peaks of each approximately coincided with the time of the new moon, that is reduced nocturnal luminosity, whereas the minima occurred during the light phase of full moon. This is interpreted as meaning

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SOCIAL MODIFICATION OF PERIODICITY OF ACTIVITY
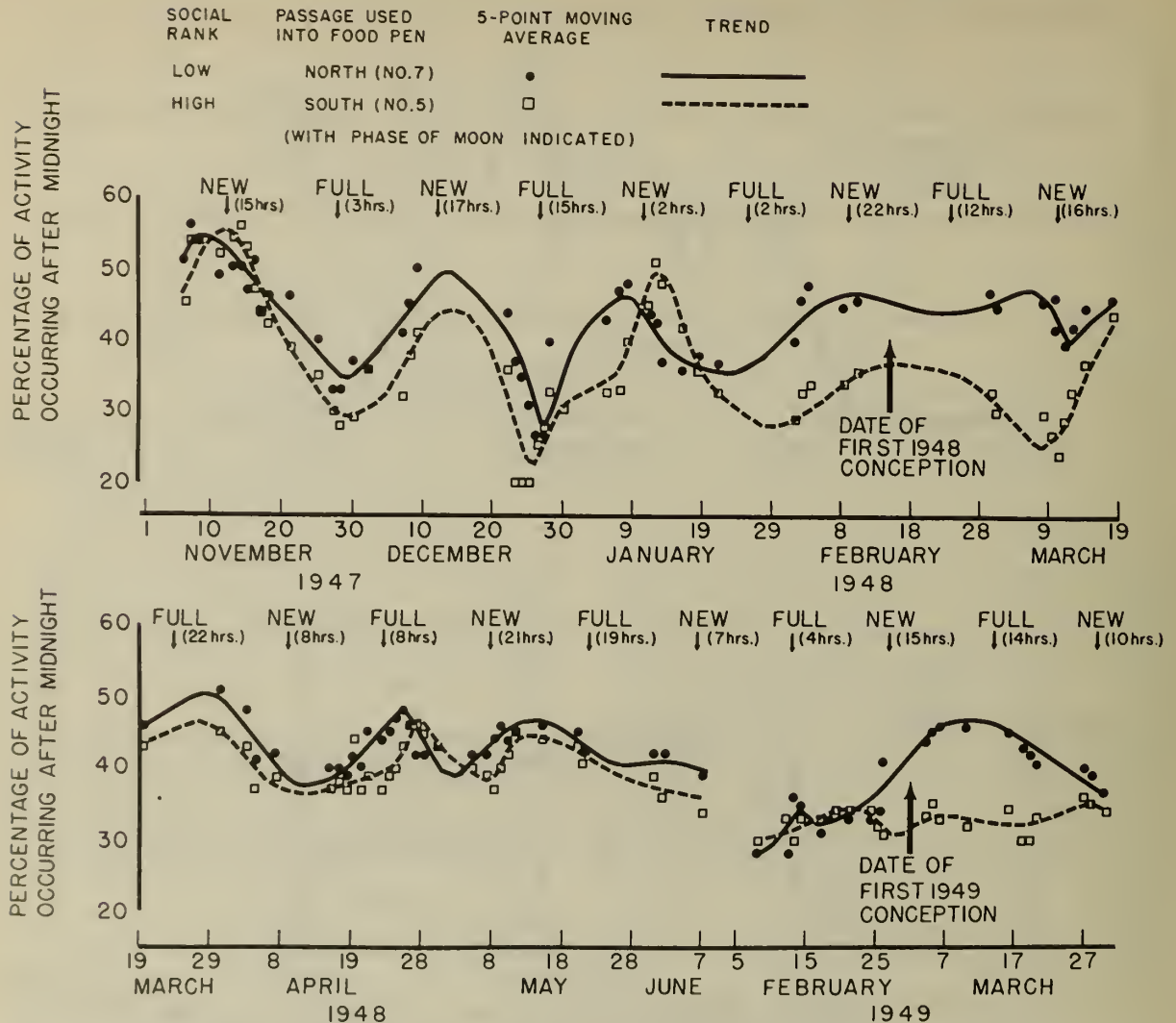
Figure 93.—Social modification of periodicity of activity. Five-point moving average of the percentage of post midnight activity. With few exceptions the lower ranking rats showed relatively more activity after midnight.

that when there are moonlight nights the rats must be active for at least a portion of the night in order to meet their nutritional requirements. This activity occurs during the first half of the night when their hunger and thirst drives are at a maximum. Coincident with the reduction of the hunger and thirst drives the light from the full moon is enabled to exert its full inhibitory effect upon activity. As the new moon phase approaches, the inhibitory effects of increased light intensity during the night declines and so postmidnight activity again increases.

For the remainder of the data this lunar periodicity of activity was either completely absent or out of phase with the moon itself. However, in the light of complicating social events which occurred after January 1948 this was not at all surprising. It will be recalled that the period of November 1947 through January 1948 was the time of minimal social tension. During the period of minimal social tension, we must assume that the lunar periodicity of activity had become endogenous. As the onset of the 1948 breeding season occurred the increased activity associated with sexual behavior prevented the decline in postmidnight activity that would have occurred about February 24. Following this, the maintained level of increased social tension reduced the amplitude of

the lunar periodicity and also prevented it from regaining its timing with the actual moon cycle. This effect of continuous high social tension on the lunar activity rhythm is quite analogous to the effect of continuous light upon the endogenous 24-hour activity rhythm of nocturnal animals or of continuous darkness upon the endogenous 24-hour rhythm of diurnal animals (13). In these instances the continuous presence of the inhibitory condition prolongs the onset of activity and thus increases the length of the activity cycle to something greater than 24 hours.

When only the total amount of activity occurring through the North and South Passages was considered, it was possible to calculate for each day the percentage of the total activity occurring through each of these passages. These calculations are shown as reciprocal curves in figure 94 through the period that data were available. We shall first examine the relative intensity of activity of the more dominant rats utilizing the South Passage (No. 5). During the 3 winter months of November 1947 through January 1948, when factors influencing increased competition were at a minimum, there was an increase in activity during times of low intensity of moonlight and a corresponding decrease in activity during periods of increased moonlight. These correlations between activity and moonlight were quite clear for five out of the six moon phases over this period. Since this inverse relationship between nocturnal light intensity and activity occurred for the more dominant rats, it was concluded that this was the basic relationship where other conditions modifying intensity of activity are absent.

On the other hand, the relative intensity of activity of the lower-ranking rats, utilizing the North Passage (No. 7), showed the opposite relationship to nocturnal light intensity. The interpretation placed upon this was that there was sufficient social interaction between these two groups of rats, that the augmentation of the activity of the more dominant rats inhibited that of the more submissive ones. These reciprocal rhythms exhibited by rats of opposite rank, which appear to be correlated with the phase of the moon, are rhythms of relative intensity only. Whatever effect lunar luminosity may have on activity, it may be masked by other conditions which modify intensity of activity. That this is so may be seen in figure 95 in which the trend of the actual number of passages through the South Passage is graphed.

During the winter months (November, December 1947, January 1948, and February 1949 as shown in fig. 94) there was a consistently greater amount of activity through the North Passage, even at times when there was a relative inhibition of activity by the rats involved. This is interpreted as being a direct reflection of the fact that more adult rats usually inhabited the north side of the pen. This is just another line of evidence to that presented later in the paper, that socially lower ranking rats are subjected to conditions which impose a greater frequency of contacts between individuals.

As the 1948 breeding ensued there was a disappearance of the apparent correlation between the lunar cycle and the relative amount of activity through the North and South Passages. Likewise the consistently greater amount of activity through the North Passage disappeared. It is not possible to offer a rational explanation for the near equality of activity through these two passages during February 1948, the beginning of the breeding season. However, those fluctuations, which occurred during March through June 1948 (fig. 94) were apparently dependent upon the number of lactating females and the number of weaned young present in the north and south sides of the pen. Coincident with the presence of three to four lactating females and then their 30-weaned young on the south side of the pen there was a period of 3 weeks in March and April 1948 during which there was for the first time a greater amount of activity through the South Passage than through the North Passage. This relationship between intensity of activity and place of entry into the Food Pen changed twice more during April to June 1948. First a group of 19-weaned young from the north side of the pen altered the balance in density. Then a second group of weaned young from the south side of the pen made their appearance, and they produced a second period of greater activity through the South Passage (No. 5). Because of the greater reproduction occurring on the south side of the pen one might have anticipated that at future dates there would have been a maintenance of greater activity through the South Passage. However, by February 1949 there was again nearly twice as much activity through the North Passage as through the South Passage. This was a result of the fact the many of the young born on the south side of the pen were forced to migrate (see table 30) to the
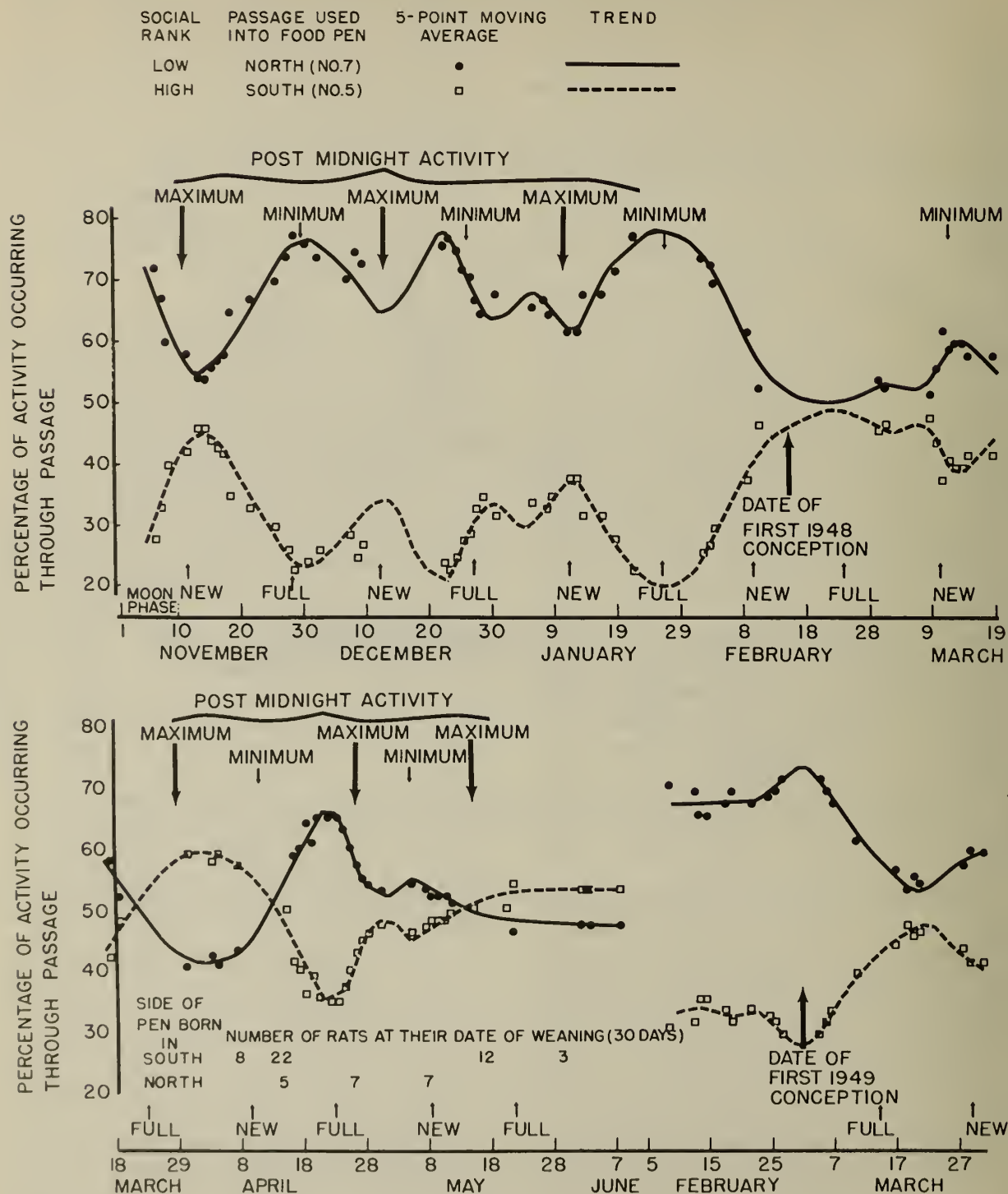
Figure 94.—Social modification of the relative intensity of activity. The activity through only the north and south passages is here considered. Thus the percentage of the total activity through one passage is the reciprocal of that through the other one. Arrows indicate the times of maximum and minimum postmidnight activity as shown in figure 93.

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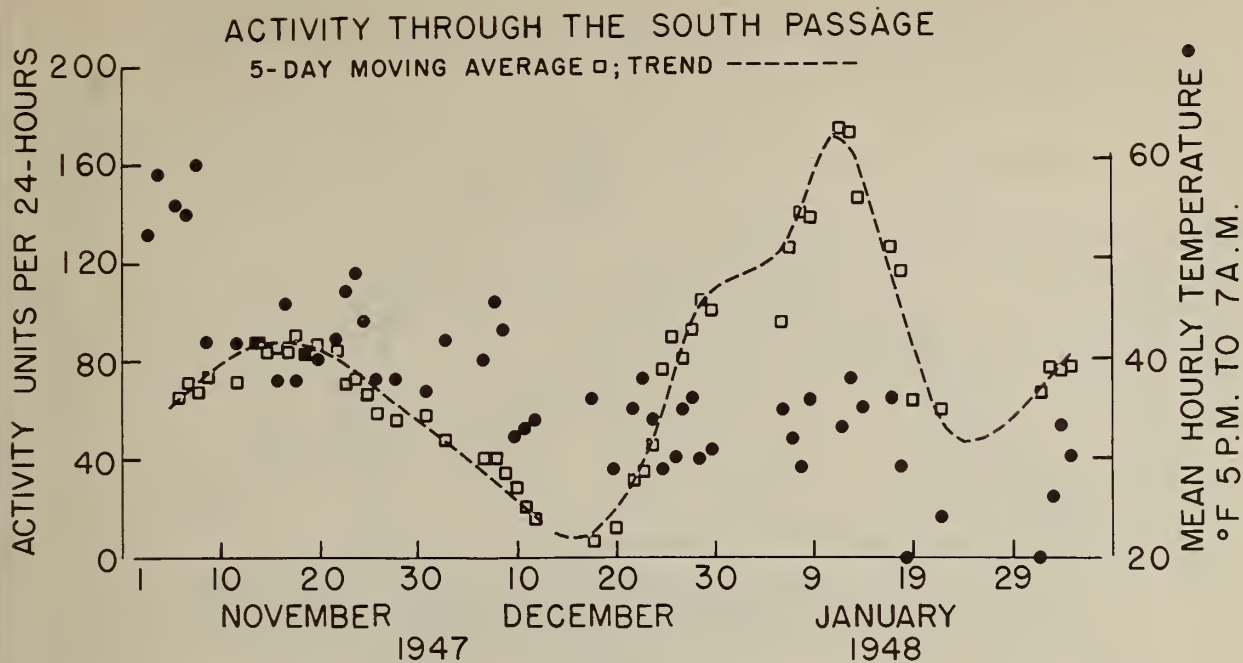
Figure 95.—Activity through the south passage of the Food Pen. In this case there is no apparent relationship of intensity of activity to temperature. Likewise by comparing this figure to figures 93 and 94, it may be seen that there is also no apparent relationship of intensity of activity to fluctuations in amount of postmidnight activity or to the amount of activity through this passage in comparison with that through the north passage.

north side of the pen as they approached sexual maturity. Thus, as is documented later in the paper, the disproportionate density between the two sides of the pen was reestablished. Table 22 further documents the conclusions that, in comparison with the South Passage which was utilized by socially higher-ranking rats, there were more socially lower-ranking rats utilizing the North Passage, and that these latter rats were more active after midnight. Furthermore, intensity and periodicity of activity through the East and West Passages was in general intermediate between that of the North and South Passages.

B. *Time-Space Utilization by Rats in Relation to Population Growth.* In order to obtain a more accurate index of such arrhythmicity than is afforded by a mere inspection of the figures 81 to 90, the 100 days represented in this sample were examined with reference to the variance in the percentage of activity among the half-hour intervals of each night. As a background to this analysis there first will be presented certain observations and inferences concerning activity rhythms.

For any individual day each of the two major periods of activity consists of shorter intervals of increased activity separated by periods of decreased activity. While the colony was small, there were

frequently periods in which no animals were active. This fact does not show on the graphs (figs. 81 to 90) since arbitrary half-hour periods are considered rather than the actual periods of activity. From observation of the activity of the rats it has been frequently noted that nearly simultaneously many of the rats became active regardless of the locations of their places or harborage. Two factors were probably involved in the initiation of this simultaneity of behavior:

(1) The physiological rhythms of each individual which induces initiation of activity following rest is similar.

(2) There is some means of social communication whereby the first few individuals which become active transmit this fact to rats living in other locations, whereupon these also become active. It is suspected that vocalization-audition is the mode of communication, although there is no conclusive evidence for this assumption.

The reason for making this second inference regarding communication is as follows: Slonaker and Richter have shown [see review by Calhoun (13)] that the relative lengths of periods of inactivity and activity vary with age. Despite this fact, rats of all ages, when living as members of a colony,

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A

Median date	Number of days	Mean number of activity units per day	Mean percentage of the total activity				Range high percent minus low percent
			North	East	South	West	
Nov. 14–15, 1947.	13	411	39. 9	18. 8	18. 3	22. 9	21. 6
Dec. 24–25, 1947.	11	432	40. 5	19. 9	14. 3	25. 3	26. 2
Apr. 17–18, 1948.	15	1, 539	24. 4	26. 0	17. 3	32. 4	15. 1
May 8–9, 1948.	13	2, 057	22. 8	25. 2	22. 2	29. 8	7. 6
Apr. 12–13, 1949.	4	2, 941	37. 0	25. 1	16. 9	20. 9	20. 1
Mean.	. . . .	. . . .	32. 9	23. 0	17. 8	26. 3	

B

Median date	Number of days	Mean percentage of postmidnight activity					Range high percent minus low percent
		Mean of all passages	North	East	South	West	
Nov. 14–15, 1947.	13	37. 3	45. 2	34. 7	35. 0	34. 2	11. 0
Dec. 24–25, 1947.	11	34. 8	38. 6	36. 9	32. 4	31. 1	7. 5
Apr. 17–18, 1948.	15	43. 8	44. 1	45. 6	39. 5	45. 9	6. 4
May 8–9, 1948.	13	42. 4	41. 7	41. 8	41. 6	44. 3	2. 7
Apr. 12–13, 1949.	4	38. 9	44. 3	40. 0	30. 8	40. 3	13. 5
Mean.	. . . .	. . . .	42. 8	39. 8	35. 9	39. 1	

time their periods of activity and inactivity more or less in unison. The coincidence of activity despite differences in age and place of harborage augers for the influence of a social influence by communication upon inception of activity. Termination of activity periods by all members also was frequently rather abrupt.

This pattern of coincidence of activity shown by members of different local colonies is assumed to be the basic biological pattern characteristic of the species. However, as the total colony increased in number through time, there was a gradual alteration of this pattern to one in which all portions of the night were approximately equally utilized. This is particularly well in evidence by the last period analyzed, Period 10—March and April 1949 (fig. 90). What this means is that when the population was high there was essentially no periods during the night when the Food Pen was not being utilized to the maximum capacity that the rats would tolerate.

This maximum capacity of utilization of the Food Pen was in the order of magnitude of 15 to 20 rats. This was so whether the colony was small, as it was in the fall of 1947, or when it was large as in the spring of 1949. Thus, as the colony increased in size, it was possible for a smaller and smaller proportion of the colony to exhibit the basic pattern of activity in evidence when the colony was small. As the colony increased in size more individuals were forced to utilize those periods of time left vacant by other rats. As indicated in more detail elsewhere in this section on activity, it was the socially lower-ranking rats which more frequently utilized the predusk and postdawn periods, when most other rats were resting in their places of harborage. These observations provide additional support to the belief that the socially low-ranking rats were the ones who altered their activity pattern during the night. We may schematically represent the situation as shown in figure 96. Although this is quite schematic, it

Figure 96.—Hypothetical origin of arrhythmicity of colony. By the time the colony approached a carrying capacity density, all periods of the night were nearly equally utilized, and in addition there was a considerable spread of activity over into the daylight hours. Despite the overall appearance of nocturnal arrhythmicity, the socially higher ranking rats retained the biologically preferable nocturnal bimodality. On the other hand the socially lower ranking rats were forced to be most active before and after these two peaks.

reveals the probable means through which space-time utilization became equalized during the night hours and how some of the activity spreads out into the lighter portion of the 24 hours.

Since most of the activity always occurred between the hours of 6 p.m. and 6 a.m. the variance about the mean half-hourly activity should provide an index of the degree of social tension existing among the rats of the population. The greater the variance, the less will be the competition over space-time utilization of the source of food and water.

$$\text{The variance, } \sigma^2 = \frac{1}{NT^2}\left[\left(\sum_{n=1}^{N} X_n^2\right) - \left(\frac{1}{N}\right)^2\right]$$

where

$N=$Total number of half-hour periods between 6 p.m. and 6 a.m. (i.e. 24).

$n=n$th half hour

$X_n=$number of activity units during the nth half hour

$T=$total number activity units during the 6 p.m. to 6 a.m. period

This formulation of σ^2 is in terms of the percentage of activity for each half-hour period with respect

to the total activity units during the 6 p.m. to 6 a.m. period within which it falls. The σ^2 was calculated for each of the 6 p.m. to 6 a.m. intervals of the 10 days which were utilized in each of the major Periods 1 to 10 (fig. 81 to 90) analyzed for activity periodism, and the results are shown in figure 97. The range in the variance from day to day is considerable, even within a single period of 10 days. Nevertheless, the trend, represented by the medians for each Period, follows a course consistent with the other lines of evidence. It will be noted that there is an overall trend of decrease in variance through time superimposed upon midwinter increases in variance when there is reduced sexual activity. If the variance in Periods 8, 9, and 10 are compared with the variance in the comparable Periods 3, 4, and 5 to 7 respectively, it will be found that the variance (degree of rhythmicity) for the 1948 periods is 1.7, 3.0, and 4.4 times that of the similar periods during 1949. If, as we suspect, the degree of stress is inversely proportional to the variance in activity, it is quite understandable that the observed decline in growth rate and reproductive rate, which is documented later on in the paper, should have arisen. Furthermore, it is interesting that the difference in variance becomes

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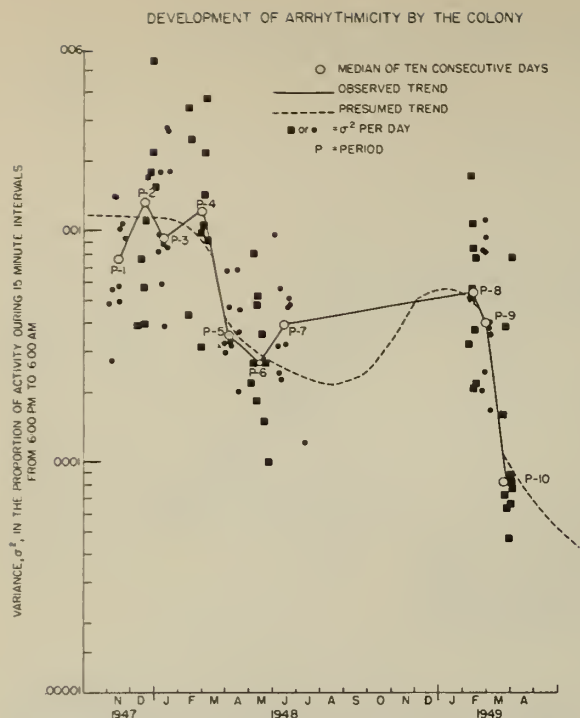
Figure 97.—Development of arrhythmicity of activity by the colony. As the number of rats increased, the variability in the amount of activity among comparable intervals of time decreased.

greater for comparable seasons of the two years as the progression is made from (1) midwinter reduced sexual activity through (2) inception of sexual activity, to (3) addition of juveniles to the population. This is in line with the evidence that the more factors there are which exert stress upon the social relationships between members of the population, the greater will be the arrhythmicity of nocturnal activity.

C. *The Relationship of Temperature and Barometric Pressure to Intensity of Activity.* From the previous analyses it is apparent that there are many factors which influence the intensity of activity. These make it difficult to utilize absolute indices of activity for the investigation of the role of meteorological conditions upon activity. The most valid comparison is that between two adjoining days since conditions other than the one being investigated are most likely to be similar. Utilizing this concept of paired days, an index of the effect of temperature upon activity was developed as follows:

$UD/HD \div TD$—Relative amount of change in activity per 1° change in temperature.

Where:

UD=Difference in activity units between the pair of days.

HD=Activity units on day of higher activity.

TD=Difference in temperature between the pair of days.

Sign of index:

$+$=Increase in activity with decrease in temperature.

$-$=Decrease in activity with decrease in temperature.

The results for 96 pair of days are shown in figure 98. It is apparent from the wide spread of points that temperature can be only one of several factors affecting intensity of activity. Nevertheless, the trend exhibited by the median activity changes certainly suggests that temperature does exert an important effect. Above 61° F. an increase in temperature exerts an inhibitory effect, and below 61° F. a decrease in temperature exerts an inhibitory effect. Below 48° F. there is apparently a rather constant effect of temperature in exerting a 2.25-percent reduction in activity with every degree drop in temperature. Since changes of 5° in the mean nightly temperature between adjoining nights were common below 48° F., temperature exerted an influence, which if operating alone would have caused approximately a 10-percent change in intensity of activity. Other factors influencing intensity of activity were sufficient either to accentuate greatly or to override completely the effect of temperature.

The influence of temperature upon absolute activity was also investigated, although it might be expected that there would be considerable more variability in the results. The total number of passages per rat per night into and out of the Food Pen was taken as this index of activity, and the influence of temperature upon it is shown in table 23. Although the variability among the means of activity within the seven temperature class intervals is significantly well below the 1 percent level of confidence, the actual trend of the means only partially validates the conclusions arrived at in the previous analyses. About all that may definitely be said is that with reference to the temperature range, 30° to 60° F., a decrease in temperature generally produces a decrease in activity, while an increase in temperature usually brings about an increase in activity.

If the mean number of activity units (25.13) per rat shown between 55.0 and 74.9° F., is an accurate

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Figure 98.—Influence of temperature on intensity of activity. The reason, that at any specific temperature, a decrease in temperature may be accompanied by either large increments or decrements in activity, is temperature accounts for only 13 percent of the total variability in activity. Even so, the median changes in activity with 1 degree Fahrenheit decreases in temperature probably reflect accurately the effect of temperature on intensity of activity.

index of the activity at the mean temperature of 63.7° F., the amount of activity expected at lower temperatures may be calculated by utilizing the trend of change in activity with each degree change in temperature shown in figure 98. These calculations along with the observed mean activity at each temperature are shown in figure 99 and table 23. Because temperature determines only 13 percent of the variance in activity (see table 23) the observed points in figure 99 poorly fit the

calculated changes in activity. Nevertheless, a crude estimate may be made from table 23 which does indicate the effect of temperature upon intensity of activity. The mean temperature for the 149 nights ranging between 15° and 45° F. was 35.2°, and the mean number of activity units per rat was 17.9. In contrast to this, the mean temperature for the 122 nights ranging between 45° and 75° F. was 57.6°, and the mean number of activity units per rat was 23.8. There was thus a

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TABLE 23.—*Influence of temperature upon activity*

	Mean nightly temperature (range in degrees Fahrenheit)						
	15. 0 to 24. 9	25. 0 to 34. 9	35. 0 to 44. 9	45. 0 to 54. 9	55. 0 to 64. 9	65. 0 to 74. 9	75. 0 to 84. 9
Number of nights................	7	58	84	54	43	25	2
Mean activity units per rat per night.	16. 57	19. 38	15. 74	22. 07	25. 33	24. 80	18. 00
Estimate of variance squared........	14. 29	90. 24	50. 24	135. 92	146. 84	60. 17	0

F = 6.70; significant below the 1 percent level of confidence.

Squared correlation ratio = 0.131 (i.e., 13 percent of the total variance is attributable to the effect of temperature). Statistical tests by Dr. Ardie Lubin.
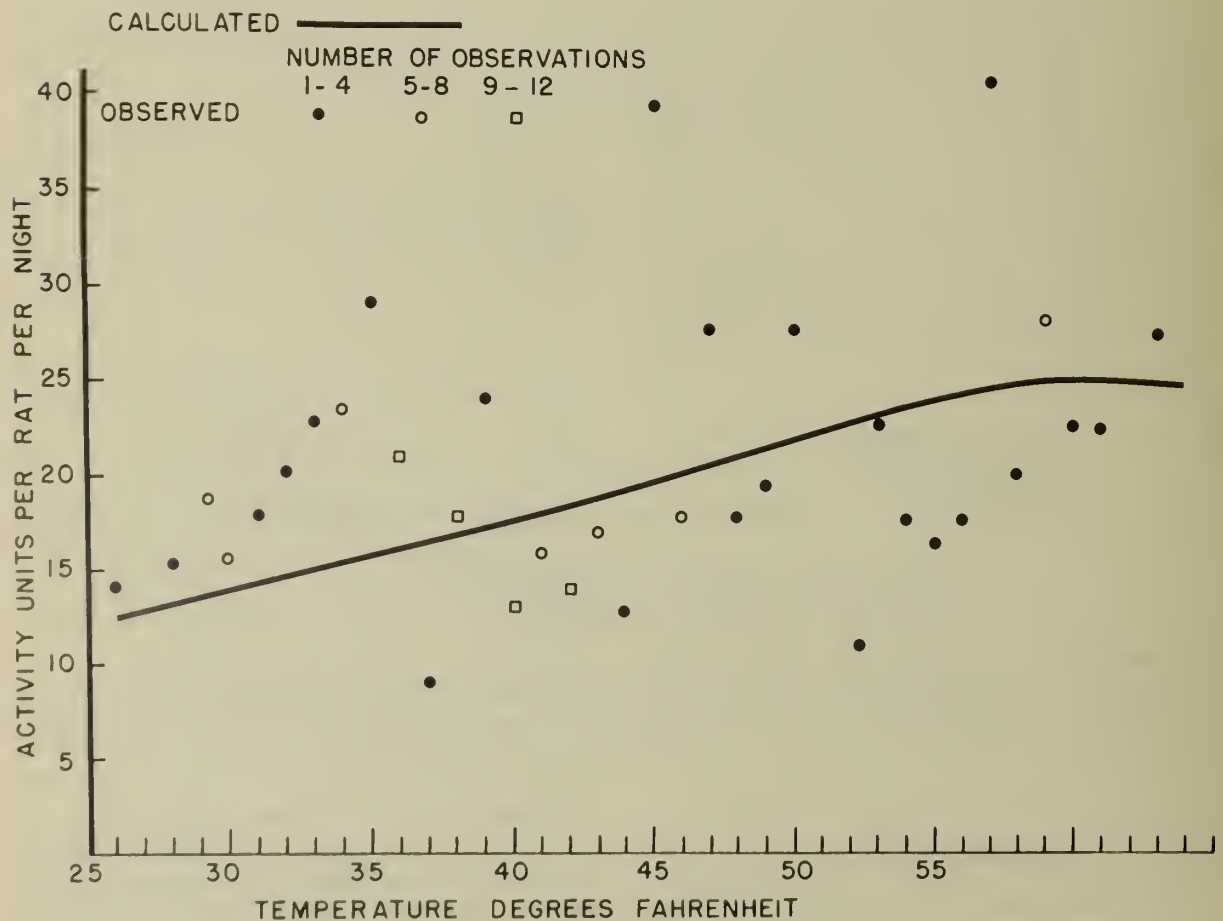
Figure 99.—Observed and calculated (i.e. expected) intensity of activity in relation to temperature.

25-percent reduction in activity with a 22 degree drop in temperature. This decrease in actual intensity of activity accompanying the decrease in temperature was nearly as much (25 percent instead of 33 percent) as might have been anticipated on the basis of the analysis of the relative change in activity between pairs of days.

The influence of barometric pressure upon activity, independent from that exerted by temperature, is difficult to determine because there is generally an inverse relationship between the direction of changes of these two factors. In examining the meteorological records for individual days it was noted that there were certain nights during which barometric pressure continuously decreased whereas on other nights it continuously increased. By comparing the mean change in meteorological conditions on these days with the mean activity rhythms on the same group of days, the character of a possible influence of barometric pressure upon activity should be revealed. These calculations are shown in figures 100 and 101. For the six pairs of nights during which the temperature was above 55° F. there is no apparent differences in the activity rhythms. In fact, the pre- and post-midnight activity was nearly identical despite the marked difference in pre- and post-midnight barometric pressure on these days. Nor is there any evidence from the more extensive series of data when the mean nightly tenperature was below 55° F. that barometric pressure affects intensity of activity. There is only a slightly greater slump
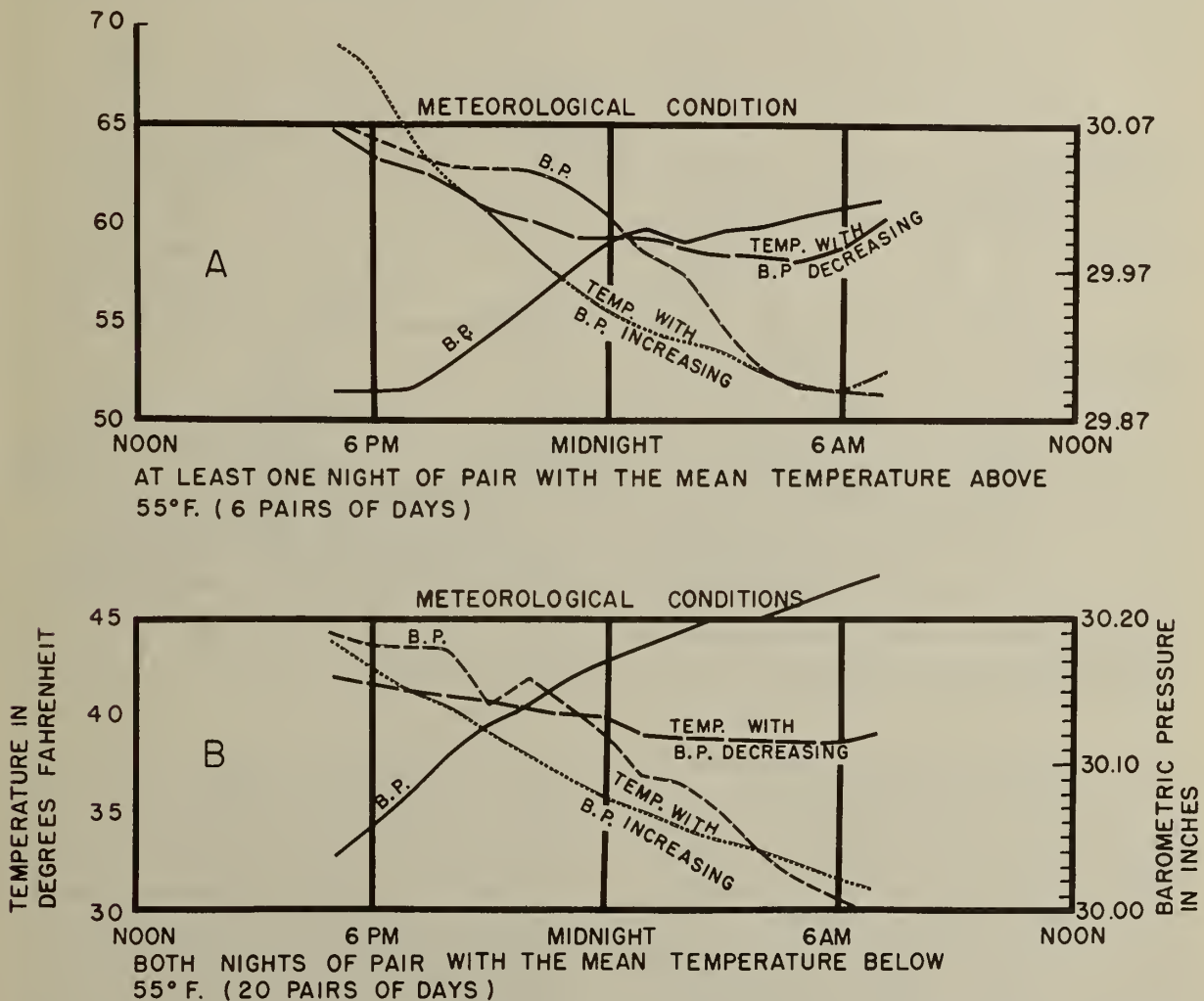
Figure 100.—Nocturnal changes in temperature and barometric pressure. Nights having continuously rising barometric pressure are compared with those having continuously falling barometric pressure. In either case there is a drop in temperature from 6 p.m. to 6 a.m. However, note that the drop is much greater on nights of rising barometric pressure.

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ACTIVITY

AVERAGE

PERCENT

OF TOTAL

A

15.0

10.0

5.0

| DAYS EACH |
| 2 NOV. 47 |
| 2 APR. 48 |
| 1 MAY 48 |
| 1 JUNE 48 |

NOON — 6 PM — MIDNIGHT — 6 AM — NOON

AT LEAST ONE NIGHT OF PAIR WITH TEMPERATURE ABOVE 55° F.

——————— 6 NIGHTS OF INCREASING BAROMETRIC PRESSURE

--------- 6 NIGHTS OF DECREASING BAROMETRIC PRESSURE

ACTIVITY

AVERAGE

PERCENT

OF TOTAL

B

15.0

10.0

5.0

33% BEFORE 8:00 PM

27.6% BEFORE 8:00 PM

| DAYS EACH |
| 3 NOV. 47 |
| 3 DEC. 47 |
| 2 JAN-FEB. 48 |
| 5 MCH-APR. 48 |
| 4 FEB. 49 |
| 3 MCH. 49 |

NOON — 6 PM — MIDNIGHT — 6 AM — NOON

BOTH NIGHTS OF PAIR WITH TEMPERATURE BELOW 55°F.

——————— 20 NIGHTS OF INCREASING BAROMETRIC PRESSURE

--------- 20 NIGHTS OF DECREASING BAROMETRIC PRESSURE

Figure 101.—Periodicity of activity during nights of continuously increasing barometric pressure in contrast to that during nights of continuously decreasing barometric pressure. Barometric pressure appears to affect activity much less than does the accompanying changes in temperature.

in activity after midnight on the nights of increasing barometric pressure, but this may be entirely accounted for by the greater decrease in temperature. The only possible effect that barometric pressure might exert is that activity changes are induced to vary in the same direction as barometric pressure. If this is true it might account for the lack of a greater inhibition of post-midnight activity by the greater decrease of temperature on those nights with a continuously rising barometric pressure (figs. 100B and 101B). An indication of this type of effect may be from the fact that, on

13 out of the 21 pairs of days between which there was less than a 2.0° difference in mean night temperature, but 0.1 inch or more difference in barometric pressure, the change in intensity of activity varied in the same direction as barometric pressure. It will probably take carefully controlled laboratory studies to determine whether or not changes within the normal range of barometric pressure affect activity.

Precipitation also appears to have no effect upon intensity of activity. For 35 nights during which 0.15 or more inches of rain fell and for which

activity records are available, there were wide fluctuations of both increase and decrease in activity from a day immediately preceding or following it, but on which no precipitation fell. The median change in activity on the night of rainfall was exactly zero percent.

During nine of these nights 0.4 or more inches of rain fell within 12 hours or less. In four of these cases there was significantly less activity during the time of rain than during a similar period of the adjoining day when it was not raining. On the other hand on 2 days there was significantly more activity during the rain. There is a basic criticism of this data. This is that the metal tunnels which housed the activity recorders, probably attracted the rats as a place of escaping downpours. This would tend to increase the number of closures of the photoelectric cell while it was raining. For this reason, I am inclined to place greater weight on the following more qualitative observations as reflecting the effect of rain upon rats.

September 15, 1947: Traps were set last night but no rats were caught. It rained hard all night. The traps were left set during the day. By 5 p.m. 6 of the 29 rats in the pen had been caught in traps during the day after 9 a.m.

October 5, 1948, 5:30 to 6 p.m. Raining and high wind: By 5:45 p.m. there were at least 20 rats at a time in the Food Pen. Their activity was confined to eating and drinking. Although there were avoidances between rats, there were no fights. In other parts of the pen activity consisted of running rapidly between burrows, harborage boxes, and the Food Pen. It appears as though the rain inhibited extraneous activities such as sexual, fighting, or investigatory, and restricted them to the essential ones relating to ingestion.

September 9, 1948, 6 to 6:30 p.m. Raining steadily. There is a much smaller proportion of the total rats out than is usually observed at this time of day. Although there seems to be a tendency to engage in less wandering activity, the rats which are out appear to pay little attention to the rain, and one male even engaged in a sexual roll at a burrow entrance.

D. *Effect of Snow on the Amount of Above Ground Activity.* During the history of the colony numerous surveys were made of the distribution of feces. The general conclusion from these surveys was that the number of feces at any one point was a reflection of the frequency with which the rats visited that

place. The data for June 5, 1947, will serve as a basis for comparison when the weather was mild and without snow. On this date there were 22 rats in the pen. On this date a count was made of the feces which were still sufficiently fresh and glistening from contained moisture to indicate that they had been deposited within the previous 2 nights (see table 24). This gives a mean of 6.75

TABLE 24.—*Feces recorded on the June 5, 1947, survey*

Place of deposition	Number of feces
On surface in areas.....................	96
In boxes in areas......................	44
On surface in alleys....................	95
In burrows in alleys....................	*44
In food pen...........................	18
Total...........................	297

*The estimate of the number of feces deposited in the burrows was made on the assumption that the belowground and aboveground feces in the alleys was in the same proportion as in the areas.

feces per rat per day, and a mean of 4.75 aboveground feces per rat per day. 2.38 times as many feces were deposited above ground as below ground. On January 31, 1948, when there were 25 rats in the pen, a survey of the aboveground feces was made. During the previous 5 nights the temperature was continuously below freezing and the surface was covered with snow. During these 5 days there was a total of only 96 feces deposited on the surface of the snow. Thus, there was less than one aboveground fecal bolus per rat per day deposited during this period (see table 25).

TABLE 25.—*Feces per rat per day*

Date	Above ground	Below ground	Percentage of total defecation on surface
June 5, 1947.....	4.75	2.00	70
Jan. 31, 1948....	.77	*5.98	11

*The belowground estimate is based on the assumption that the mean number of feces per rat per day was the same for the two periods.

Probably the major source of error in this comparison lies in the subjective ability of the author to judge the age of feces during the June 1947 period. I can only say that I am convinced that this judgment is fairly accurate. Even if the feces on June 5 had been deposited during the previous 4 days, rather than on the 2 previous days, as I believe to be true, there would still have been three times as much aboveground defecation in June as during January. Thus, even when considerable latitude is allowed for possible errors in the assumptions it is quite apparent that there is a considerable decrease in the aboveground activity, produced by severe weather.

A count of feces a year later on February 1, 1949, lends further information on the effect of temperature and other factors on the amount of aboveground activity. During the dawn hours of January 31, 1949, 4 inches of hard, ball-like snow fell. By mid-morning it began to rain; this froze upon falling and so formed a glaze of ice over the snow (see table 26).

Thus, with a comparable snow cover on the second date there was 10 times as many above ground feces per rat per day. The warmer nightly temperature certainly contributed to this greater aboveground activity. However, there is another condition which probably acted to negate the tendency of the rats to remain underground during cold weather. That factor was the increased social friction accompanying the fivefold increase in population density. In Area IV between boxes 33, 34, and 36 a group of box traps were piled during the February 1949 snows. At the beginning of activity in the early evening several rats from the same burrow or box would at short intervals

head for this pile of traps and begin fighting. This indicates that although the rats may aggregate together during the day hours for the conservation of body heat, there is sufficient antagonism between the members of the group to break off the close association during the night hours. The continuation of this situation should keep the rats above ground more continuously during the night.

TABLE 26.—*Feces above ground during two periods of comparable snow cover*

Date	Number of rats	Above ground feces per rat per day	Mean 5 p.m. to 7 a.m. temperature*
Jan. 26, 1948 to Jan. 31, 1948...	25	0.77	22.9
Jan. 31, 1949 to Feb. 1, 1949...	135	8.01	33.3

*Temperatures were probably lower than this in the hilly area north of Baltimore where the pen was located. (Baltimore City Weather Office.)

E. *Observed Activity of the Rats as it Relates to Periodicity.* Prior sections on periodicity of activity dealt mainly with quantitative records of the passages of rats in and out of the Food Pen. The interpretation of these activity records have in large part depended upon other observations or sources of data. Representative observations reveal the type of phenomena upon which the interpretations of the quantitative records of activity were based.

Fluctuations in intensity, type, and place of activity.

1. June 29, 1948
   6:25 p.m.   I have been in tower for an hour and yet have seen only two rats go to the food hopper, although many have been out.
   6:30 p.m.   The rats have certainly been doing a lot of wandering about and seem little interested in food. Several rats at a time may be active in Areas I or II with little sign of hostility.

2. July 7, 1948
   7:45 p.m.   Earlier in the evening the rats seemed little interested in eating, but explored about and showed markedly little antagonism. Now fights are occurring more frequently.

3. September 30, 1948
   5:33 p.m.   So far this afternoon very little activity centered about the food hopper, although many rats passed through the Food Pen. Even those who ate, also spent considerable time in spontaneous or wandering activity.

4. July 12, 1948 6:30 p.m.	The number of rats visible at any one time is greatly reduced from what it was an hour ago.
5. May 19, 1948 6:15 to 7:12 p.m.	Essentially no activity of young rats. There has been much more adult activity than I have been able to see or record.
6. October 7, 1948 7 p.m.	Although there is still considerable activity in the Food Pen, including eating and drinking, I believe, that there has been a shift in the past 15 minutes to other types of activity, as evidenced by an increase in activity around the South Alley Burrow, and the amount of gnawing heard.
7. January 21, 1948 10:30 to 11 p.m.	Only a few rats are active. They exhibit a wandering about not in evidence earlier in the evening. The rats which do go into the Food Pen mostly ignore the garbage.
8. June 1, 1948	
7:50 p.m.	Rats quite active.
8:55 p.m.	Only three to five rats were in Food Pen at a time. (7:55 to 8:55 p.m.— I was gone from observation tower.)
9:16 p.m.	Only one or two rats in Food Pen at a time. There were corresponding decreases in the other parts of the pen.
9:19 p.m.	Not a single rat to be seen.
9:20 p.m.	The lull began to break. Gradually rats began to emerge from the South Alley Burrow. Their caution parallels the usual late afternoon behavior.
9:30 p.m.	Rats fairly active.
9:50 p.m.	Rats nearly as active as at 7:50 p.m.
9. April 25, 1949 2:40 a.m.	Activity has nearly ceased. There has been considerable activity over the pen and in the Food Pen most of the prior part of the night. This must represent the characteristic slump of activity between midnight, and the predawn increase. I was out of the observation tower between 2:45 and 3:55 a.m. By the time I returned rats had again become quite active and this continued until shortly after 5:10 a.m.

A general summary of the situation is as follows: During the early dusk period rats gradually emerge with cautious hesitant behavior. Although rats frequently pass through the Food Pen in their intiial activity, they pay little attention to food, but rather engage in various investigatory and wandering behavior. There follows an intense period of activity related to the consumption and storage of food. This is again followed by a period of investigatory and other nonfood oriented behavior, although rats still pass through the Food Pen, before most of them again return to their burrows. Normally several additional such periods of activity and quiescence occur during the night with activity gradually ceasing shortly after dawn.

Time, space, and social stratification of activity.

1. May 18, 1948 7 p.m.	No rats active about the North Alley Burrow (although it contained at least female 42 and her seven 51-day-old young), while many rats were active about the South Alley Burrow.
2. June 1, 1948	Other than female 42 and two or three young the North Alley Burrow has been markedly deserted in comparison with the South Alley Burrow rats who have been quite active.
3. June 28, 1948 5:50 p.m.	The South Alley Burrow juveniles are quite active, as they have been since the rats first became active at 5:05 p.m. Most of the active rats are about the South Alley Burrow or over in the West Alley. No rats have been seen at the North Alley Burrow.
6:35 p.m.	Rats have been out 1½ hours, yet none have been seen at the North Alley Burrow, or in Areas II or III, except for one rat who came through Passage 3 and up Path 3.

An analysis of the observations made between 5:05 and 7:45 p.m. on this date provide the following table:

Number of individuals active during the early evening

Local affinity	Number of rats pelage marked	5:05–6:40 p.m. only	Both periods	6:40–7:45 p.m. only	Neither period
South half of pen.............................	18	8	2	5	3
Both sides of pen.............................	8	3	0	3	2
North half of pen.............................	15	0	0	3	12

Observations were terminated at 7:45 p.m. Presumably the majority of the rats living on the north half of the pen became active after the other rats became temporarily inactive.

4. July 8, 1948 6 p.m... I have seen only two rats at the North Alley Burrow. Although there have been many passages in and out of the South Alley Burrow.

5. July 9, 1948 5:50 p.m .. I just saw the first rat leave the North Alley Burrow, although a number have left or entered the South Alley Burrow.

6. April 19, 1949......... Although I have not recorded the presence or activities of all rats out during the past hour, there can be no doubt that females are much more active than males during these dawn hours. This is in striking contrast to the excess of males that were active at dusk.

7. April 25–26, 1949...... A portion of the population was pelage marked for distance recognition. There were two periods of observation. First: 10:45 p.m. to 2:30 a.m.; 2d: 4 to 5 a.m.

Period Active in Food Pen

	1st only	Both	2d only
Number of Males.........	8	7	6
Number of Females.......	1	4	1

At least for males this strongly suggests a time differentiation in the utilization of a common goal.

The terminal group of observations, Nos. 8 to 17, concern rats known to be at the very bottom of the social scale at the time the observations were made. They reveal how such socially low ranking rats avoid their more dominant associates by becoming active during the more unfavorable (daylight) portions of the day or during the night when the other rats are resting in their harborages.

8. Female 7   October 3, 1947; 2:19 to 2:44 p.m.; 324 days of age. Eating in Food Pen.

9. Female 7   October 24, 1947; 3 to 5:45 p.m.; 344 days of age. She was continuously active about Food Pen during this period when there were no other rats active.

10. Male 8   July 11, 1947; 267 days of age.
Although observations were made continuously from 6:15 to 7:54 p.m., Male 8 was only observed momentarily in the Food Pen at 7:28. Presumably this lack of appearance resulted from his avoidance of the other adult rats, most of whom were observed several times during this period.

11. Male 8   2:30 to 2:50 p.m.; October 9, 1947; 357 days of age. He made 11 trips from the Food Pen carrying garbage into Box 28. This storage of food will certainly aid him in avoiding the dominant male 12.

12. Male 8   3:40 p.m.; October 21, 1947; 369 days of age. He made several trips carrying garbage from the Food Pen to Box 28.

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13. Male 12   5:20 to 5:40 a.m. and 7:22 to 7:26 p.m.; May 17, 1948; 635 days of age Male 12 is now way down on the social scale. He was observed eating during these two periods when most other rats were inactive.

14. Male 12   2:00 to 2:15 p.m.; October 7, 1948; 778 days of age. With one other adult rat eating; few other rats active. This is another observation which shows that low ranking rats come out early to eat. After becoming senescent male 12 dropped from the top to nearly the bottom of the social scale.

15. Male 12   6:43 a.m.; October 8, 1948; 779 days of age. Now that all other rats have entered their burrows Male 12 has returned to the Food Pen. He was cautious even so and took the pellet of food to the northeast corner of the Food Pen to eat.

16. Females 17 and 20 (sibs)   May 17, 1948; 350 days of age. They ate in the Food Pen together after the dominant rats retired. They then returned to approximately the same place of harborage.

17. Females 20 and 25 (sibs)   5:05 to 6 a.m.; May 24, 1948; 357 days of age. Both rats are wandering about the Food Pen. This is further evidence that the social outcasts are forced to eat during times when other rats are inactive.

18. Spring of 1949   It has been a general observation that rats seen at the food source late in the morning or early in the evening were those with extensive wounds or poor pelage.

These and similar observations may be summarized as follows: All of the rats in the population were not simultaneously active. During the afternoon and early dusk a few of the socially lowest ranking rats visited the food source. As these retired to their harborages the socially high-ranking rats (in general those rats living in the south half of the pen) became active. It was usually not until these higher ranking rats had begun to decrease the frequency of their visits to the Food Pen that the majority of the lower ranking rats (in general those rats living in the north half of the pen emerged from their burrows and began visiting the food source. This social stratification of periodicity tended to be maintained through the night with the lower ranking rats seeking access to food during times of maximum quiescence of the remainder. Through such a process of social stratification of periodicity of activity strife between members of different groups was reduced but by no means eliminated. It seemed patent that the degree to which a rat had to modify its normal rhythms of activity and quiescence was a direct reflection of the degree of stress to which it was exposed. Since 20 rats appeared to be about the upper limit of numbers that were tolerated simultaneously in the Food Pen, it is apparent that as the population increased from one-half to nearly 10 times this limit, all individuals must have been exposed to increased stress through social action, because at the higher densities it would be nearly impossible for different groups of rats to time their activities so that there would not be considerable overlap.

THE NATURE AND CONSEQUENCE OF SOCIAL BEHAVIOR AND SOCIAL ORGANIZATION

Each rat in the course of its day-to-day activities comes into contact with other members of the population. Such contacts may be random as when two rats happen to arrive at the same point simultaneously. Where such a chance encounter results in an alteration in the behavior of one or both of the rats, this resultant behavior is considered as a social one. For example, the two rats may sniff each other or one may quite obviously turn and flee. On the other hand, some encounters embody an aura of purposeful intent as in the searching for estrous females by males or when a dominant male runs toward and attacks other males approaching his home burrow. From many such social behaviors there results spacially localized aggregates among each of which there exists mutual attraction among members and intolerance of members of other aggregates. This state of relationships is designated as social organization.

There can be little doubt that rats have some awareness of this social organization. However, I do not mean to imply that this awareness encompasses the particular ways in which I have attempted to formulate social organization. My endeavour shall simply be to describe the relationships which developed and their consequences for the individual or the group.

1. General Account of the Changes Occurring Throughout the History of the Colony.

A. *Introduction and Adjustment.* On February 4, 1947, seven male and seven female rats caught on Parsons Island in the Chesapeake Bay (see Introduction) were released into the Food Pen. These rats were confined there by plugging Passages 5 to 8.

Two tasks faced these rats. (a) They had to develop a social organization. Most of the rats had been trapped from different local colonies, therefore it was quite likely that they had few associations in common. (b) They had to learn a rather complexly structured environment.

Stage 1: February 4 to 12, 1947. The rats were introduced into the Food Pen at 4 p.m. with all exits sealed. Their initial reaction was to run around the periphery of the pen, climb the fence to the glass-screen overhang and jump to the ground. This indicated an inability to get over the barrier. At 5 p.m. five of the boxes similar to those used for artificial harborages in the areas were placed in the Food Pen. The one placed in the center had a 4-inch hole in one end and contained newspaper for nesting material. One each was placed halfway between the food box and the corners of the Food Pen with the entrance pointed toward the central-food box. By 6 p.m. only two rats had entered harborage boxes, while the rest still roamed about the periphery of the Food Pen. The boxes were then shifted to the edges of the pen and the rats herded in, after which the boxes were replaced in their former position. By 10 p.m. the rats were running between boxes. By that time the rats climbed no more than a foot up the fence.

Number of rats in the 4 boxes in following days:
February 5: 4, 2, 6, 0.
February 6: 0, 1, 2, 11.
February 9: 1, 0, 4, 4, 5 (in a newly dug burrow).
February 10: 1, 1, 0, 6, 6 (in the newly dug burrow).
February 12: 0, 0, 0, 6, 8 (in the newly dug burrow).

These give a distribution as follows:

Number of rats in a harborage box or burrow	Times observed
0	7
1	4
2	2
3	0
4	4
5	1
6	4
7	0
8	1
9	0
10	0
11	1

During this period considerable food was transported from the central food box to the four harborage boxes. Thus three behaviors; climbing fences, transporting food, and digging burrows, which involved manual ability, were known to be characteristics of the introduced rats. Furthermore, the tendency of the rats to occur in groups indicated social attraction.

Stage 2: February 13 to 17. Passages 5 to 8 into the Food Pen were opened. Other than for an occasional wandering out into the surrounding "Alley" the rats confined their activities entirely to the Food Pen. There was no evidence that the rats ever went into the "Areas". This indicated a strong tendency of rats introduced into a strange environment not to wander far from a known source of food and harborage.

Stage 3: February 18 to March 6. The food box was shifted to a position just below the observation tower between Passage 1 and the outside fence. This was done in an attempt to initiate explorations farther away from the centrally located Food Pen. On February 18 a trail of food was placed from the Food Pen to the new food source. During the next 2 nights the rats made the adjustment of going to the new location of food. Other wanderings, than that between the Food Pen, where the four harborage boxes were located, and the new source of food, were primarily confined to running back and forth along the southwest outside fence. On February 20 a burrow was dug in the loose soil by the fence opposite Box 36. This was in addition to three burrows then in the Food Pen. A blanket of snow covering the ground between February 23 and March 6 permitted an accurate determination of the rats' wanderings. Wander-

ings were primarily confined to those within the Food Pen, between the Food Pen and the food source opposite Passage 1 and between the food source and the burrow opposite Box 36. Rare wanderings occurred about the alley and through Area IV. There were rare wanderings into Areas I and II. No rats entered Area III. Along the heavily traveled routes the rats would make occasional short journeys of a few feet to one side before returning to the main route. The observations provide further support to the thesis that rats in a strange environment confine their activities to nearly the minimum imposed by the necessity of going back and forth between the sources of food and harborage. *No rats entered any of the 36 sunken harborage boxes.*

Marked competition, particularly in the form of fights and chases about the food source, occurred. In fact, the amount of fighting between the introduced members from this time through the summer of 1947 was greater than that among any comparable number of rats during the remaining history of the colony. Although this is a qualitative impression, I am convinced of its validity. It was this inability of rats which lacked a common prior history to develop a stable social structure with a minimum of fighting that probably accounts for the initial difficulty of this group of rats in reproducing and establishing itself.

Stage 4: March 7 to 14. The final stage in the adjustment of the rats to the pen was to induce them to go into the sunken harborage boxes and to utilize more equally the various parts of the pen. In order to accomplish this objective (a) the temporary harborage boxes were removed from the Food Pen, (b) garbage was placed in one box in each area (Boxes 3, 12, 21, and 30), (c) 30 Purina food pellets were placed in each of the other boxes.

Food was first removed from the boxes in Area IV near the burrow opposite Box 36. From here the removal of food on succeeding days indicated that the rats were gradually moving around the areas in a clockwise direction (table 27). The rats immediately began eating pellets in the boxes of Area I nearest Passage 1. However by March 14 only 22 of the 90 pellets in Boxes 4, 5, and 8 in Area I and only 4 of the 90 pellets in Boxes 10, 11, and 15 in Area II had been eaten. This indicated that the rats did not move in a counter-clockwise direction from Area I to II during this period.

TABLE 27.—*Accumulated total of food pellets eaten*

Location	Mean distance (feet) from prior food source [1]	Date		
		Mar. 9	Mar. 11	Mar. 14
Area IV......	38	47	174	240
Area III......	108	0	35	152
Area II......	178	0	25	56
Area I........	....	43	80	146

[1] Between Passage 1 and outside fence and calculated in a clockwise direction through the areas.

From these observations it must be concluded that exploration by rats in a new environment away from a discovered source of food is only sufficient to satisfy their current needs. However, as each new source is depleted, further peripheral exploration ensues.

B. *Regional Differentiation of Major Social Groups.* On March 15, 1947, the permanent food hopper was placed in the central Food Pen. During the next few days rats utilized all harborage boxes, passages through the barrier fences, areas, and alleys. In fact, once the 30-day period of "teaching and indoctrination," by the experimenter, had been completed, the rats exhibited a marked increase in ranging. Within the space of a few minutes a rat might cover fully half of the entire pen and from day to day it might shift its place of residence from one area to another.

By March 22, 4 of the 14 rats had died. One female was found in a state of poor motor coordination which lasted for several hours until she died. One rat was accidentally caught in a steel trap. Two others were accidentally sealed and suffocated in their burrow. The 10 surviving rats at the time of completion of the adjustment to the pen were designated as the original colonizers.

A summary of the history of these colonizers is given in table 28. They were arbitrarily divided into two groups, Southeast and Northwest rats, in accordance with which side of the pen the rat inhabited more frequently. This was done because the later history of the colony indicated a sharp division of the colony. Rats living on the Southeast side, Areas I and II and the South Alley Burrow, exhibited much more favorable characteristics of social status, growth rate, reproductive rate and survival. It was desired to determine if the initial history represented by the colonizers gave

any indication that this partition began immediately.

With regard to weight, the two heaviest males and the two heaviest females were members of the Southeast group. With regard to survival, four members of the Northwest group died before any of the Southeast group did, and four of the Southeast group lived 2 or more months after all of the Northeast group had died. With regard to pregnancies, each of the three Southeast females conceived three times; whereas only one of the Northwest females became pregnant, and it only twice. Both groups had poor survival of litters. Only 3 of the 11 litters survived. This is probably an indication of the marked tension and lack of a stabilized social structure characteristic to the colonizers.

With regard to social status, the most dominant female was southeast female No. 10, and the most dominant male was southeast male No. 6 (see pp. 179–203 for criteria utilized in judging dominance). Furthermore, following the death of this male (p. 198 and two of the other males, southeast male No. 12 was dominant to the surviving northwest male No. 8 The later history of male No. 12 exhibits his cognizance of this geographic relationship to social status. As may be seen in figure 107 there was a shift in place of residence corresponding to his reduction in social rank in 1948. The young born to the colonizing females also reflect this social stratification with reference to place of residence. Females 17, 20, and 25, the only surviving members of the litter (L–3) born on the northwest side of the pen showed a reduced growth rate (fig. 141, graph 31) and extremely low social status in relation to the 13 surviving members of the two litters born on the southeast side of the pen. Figure 141, graph 33 shows the more rapid growth exhibited by the females born on the southeast side.

Considering the marked fighting that did occur among the colonizers it is probable that the difference in distribution that developed was not a chance one, but rather resulted from social action. Although the number of individuals was small, the consistent trends favoring the Southeast rats with regard to size, survival, reproduction, and social status support the reality of this initial division.

Once the rats had become adjusted to their new environment there was a marked difference in the tendency to aggregate from that occurring when the rats were confined in the Food Pen between February 4 and 12. On 11 surveys of the harborage

TABLE 28.—*Summary of history of introduced rats*

Approximate age in days Feb. 1, 1947	Rat No.	Sex	1947 weights			Times and place captured March–October 1947		Date last recorded	
			Feb. 1	Mar. 27	May 17–30	Southeast	Northwest		
257.........	6	M	476	405	420	10	5	7–19–47	During part of time occupied South Alley Burrow with Female 10. Found dead with no wounds; head buried in shallow scratchings in soil.
112.........	12	M	316	378	350	19	6	10–28–48	Became dominant male during 1947 but dropped to very low social status in 1948.
357...	4	F	476	404	420	18	6	9–27–47	Became pregnant 3 times but raised no litters.
77..........	7	F	176	212	264	21	10	11–20–47	Became pregnant 3 times but raised no litters. Avoided contact with other rats. Death as for 6.
142.........	10	F	292	327	440	2	3	2–29–48	Died from exposure in trap at time of poor health and extensive infection of throat muscles. Was pregnant April, June, and August. Raised April (L–2) and August (L–5) litters. Mainly inhabited South Alley Burrow.
"Southeast rats" total.................						70	30		
109.........	5	M	312	353	336	2	4	5–17–47	On this last date it had many scars over pelvis, and one large and six small wounds.
104.........	8	M	296	327	291	8	18	5–17–48	He was quite definitely the most subordinate male.
104.........	9	M	300	345	370	4	5	6– 7–47	Death followed head injuries received in fight with Male 6.
162.........	2	F	316	316	337	3	13	5–30–47	Found eaten by other rats. Not pregnant to May 30.
97..........	11	F	224	264	324	4	22	7–30–47	Pregnant twice, April and May. Raised only second litter (L–3).
"Northwest rats" total..................						21	62		

boxes between March 27 and May 21 the following frequencies of size of aggregates were observed:

Size of aggregate in a
    harborage box..... 0   1   2   3   4   5
Number of aggregates
    of each size....... 332 49 12   1   1   2

The much lower temperature during the former period contributed in two ways to the greater frequency of larger aggregates. First, aggregating would favor conservation of body temperature. Second, it was cold enough to produce a retraction of the testes into the abdominal cavity and thus fighting among males was reduced.

The influence of this initial differentiation is reflected in the genealogical history of the colony (fig. 102). As a background for understanding this, it will be necessary to make further comment on the first surviving litter (L–2) and the fourth (and last) surviving litter (L–6) born during 1947. Litter 2 was born to the Southeast female 10 at the South Alley Burrow. Female 10 was apparently also the rat responsible for initiating the North

Alley Burrow. At any rate, her young after weaning seemed to utilize both of these burrow systems. One of these young, female 15, conceived as a young adult on the same date as her mother. Their litters were both born on the same date, August 16, 1947. Prior to this, when female 15 was 90 days of age, she was seen to be chased by female 10. Although this was the only observed aggressive encounter between these two females it is highly probable that the younger, smaller female 15 held a more subordinate status. In line with this subordinate status her litter (L–6) was born at the North Alley Burrow, whereas female 10 had her litter (L–5) at the South Alley Burrow.

With this introduction we may now return to the examination of the genealogical record (fig. 102). In the first place only one of the five colonizing females had descendants which produced surviving litters during 1949. Furthermore, this single female produced two line of descendents.

GENEALOGY

♀ 10   ♀ 11

L-3 A III 5-30-47
♂ 18,19,23,24
♀ 17,20,25

L-2 N&S AB 4-16-47
♂ 21,22,26,16
♀ 15,27

L-6 NAB 8-16-47
♂ 34,41,45,36
♀ 42,43

L-5 SAB 8-16-47
♂ 29,30,31,38,40
♀ 39,33,37,44,28

L-7 SAB 3-7-48
♂ 68,74,79,82,87,89,690
♀ 71

L-11 NAB 3-27-48
♂ 83,99,669,100,684
♀ 77,691
49 P NAB

L-22a SAB 6-1-48
♂ 725
♀ 767
49 L II

L-14 AI 4-17-48
♂ 95,97,84,85,94,665
♀ 78,92,96,93,86,652

L-9 A II 3-21-48
♂ 49,52,53,670,51
♀ 48,50
49 L T2B

L-8 A III 3-16-48
♂ 65,70,61,64
♀ 62,63
49 L SAB

L-16 NAB 5-16-48
♂ 651,696,667,672,673,687
♀ 674,686,694

L-22b NAB 7-8-48
♂ 668,869
♀ 792,894
49 P NAB

L-23C NAB 7-20-48
♂ 786
♀ 785,791,886

L-10 SAB 3-16-48
♂ 66,67,69,679,685,73,81,88,90,663,680
♀ 72,75,80,76
49 LP II   49 L SAB

L-30 A II 7-14-48
♂ 707,751,709
♀ 749,875,922,925
49 L AI

L 28 & 29 AI 8/16-20/48
♂ 735,737,757,799,852,873,874,872
♀ 734,851
49 L AI

L-13 A III 4-8-48
♂ 54,56,57,59
♀ 58,55,60

L-15 SAB 4-30-48
♂ 683
♀ 98,655
49 PL SAB   49 L III

L-25a AI 7-1-48
♂ 732
♀ 733
49 LP I

L-18 A III 6-1-48
♂ 657,660,662
♀ 658,659,661
49 P NAB

L 23b A IV 7-20-48
♂ 742,863,721,743,768
♀ 766,740,769,911
49 PL III   49 L III

L 27a AI 8-10-48
♂ 736,739,760,798
♀ 758

L25b SAB 7-15-48
♂ 376,775,777,862,880,879
♀ 778

♀ 43   ?   ♂ 37

3 LITTERS A IV 9-19-48
♂ 429,434,436,462,464,460,918
♀ 352,354,370,915,797,854
49 L? IV   49 P III

L 17 & 19 SAB 5-18-48
♂ 675,677,678,681,693,698,699,703,897,909
♀ 676,688,689,697,700,702,704,705
49 L T1B   49 L T1B   49 L WA   49 L T1B   49 L SAB   49 L SAB

L 32,37a &b SAB SEPT '48
♂ 498,385,479,427
♀ 383,378,475,477,1075
49 L WA   49 L II

49 L III

Figure 102.—Geneology of colony. The lines of descent are based entirely on mothers, since fathers could not be determined with any degree of assurance. Litter number, place, and date of birth is given above the row of numbers designating the eartags of the weaned members of the litter. Lines extend upward from the litter to the mother. Where two or more litters were born on about the same date of the same place, it was possible only to designate which females were involved as mothers, but not which females were the mother of which members of the composite litter. Rats whose eartag numbers are enclosed in rectangles died before 150 days of age. See table 66 for growth rates of rats living less or more than 150 days. All others lived longer than this. Those whose numbers are underlined were still alive May 17, 1949, when the process of killing of the colony began. I, II, III, and IV refer to birth in one of the four triangular areas. NAB and SAB refer to birth at the North or South Alley Burrow. T1B = passage 1 extension of the South Alley Burrow (see fig. 21). WA = West Alley. L & P refer to state of lactation and pregnancy at time rats were killed in May 1949. Males 384 and 773 referred to in figure 112 are not included on the genealogy chart.

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However, of the 21 litters born during the spring of 1949 and surviving to the time of termination of the colony in May 1949, 20 of these were born to females of the line having the closest affinities to the Southeast side of the pen. It is also interesting to note that the one remaining litter was born to the only female of the second line who, herself, was born on the Southeast side of the pen. The importance of these observations and those which immediately follows, is that among these Norway rats only a segment of the population successfully reproduced. Thus there should result a more rapid development of genetic homozygosity than would be anticipated purely on the basis of random breeding. Dispersal of males from their place of birth (pp. 170–171; table 30), particularly the dispersion of males from the Southeast group to the Northwest group, might be considered as preventing the more rapid development of homozygosity. This situation does not vitiate the former conclusion since the females with which these displaced males came into association, produced essentially no surviving progeny.

By taking into consideration the genealogical record and certain other data regarding reproduction, survival, and migration, it is possible to gain a picture of the fate of the colony with reference to its two main lines of descent. These data are shown in tables 29, 30, and 31.

TABLE 29.—*Survival of rats weaned during 1948*

	Survived less than 150 days	Survived more than 150 days	Total
Southeast born:			105
Died before May 1949.	20	20	
Alive May 1949......	....	65	
Northwest born:			66
Died before May 1949.	14	21	
Alive May 1949......	....	31	

TABLE 30.—*Relationship between place of birth and place of later residence (i.e. migration)*

Place found May 1949	Place born (1948)						Total born in 1948		
	Southeast half of pen			Northwest half of pen					
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Southeast half of pen......	11(a)	18(a)	29(b)	0	0	0(b)	11	18	29(c)
Northwest half of pen......	26(a)	10(a)	36(b)	15	16	31(b)	41	26	67(c)
Total.............	37	28	65(c)	15	16	31(c)	52	44	96

	Tests of significance	
Comparison	Chi Square	p
a. Sex difference in place of residence during May 1949 of rats born in Southeast side of Pen......	6. 348	0. 02
b. Tendency to leave home in relation to Place of Birth...................................	23. 215	. 01
c. Redistribution of the population between 1948 and 1949...............................	25. 531	. 01

TABLE 31.—*Reproduction during spring of 1949 in relation to place of birth in 1948 and place of residence in May 1949*

Place born, 1948	Place residing, May 1949	With litters	Without litters	Chi Square	p
Southeast side of pen...................	Southeast..................	14	4	6. 518	0. 01
	Northwest.................	5	5	. 021	. 80
Northwest side of pen.................	Southeast..................	0	0		
	Northwest.................	2	14	7. 941	. 01
Total...........................	....	21	23		
Expected ratio...................	....	. 477	. 523		

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On the grounds that equal facilities were available on the northwest and southeast side of the pen for reproduction, and therefore, there should have been an equal reproduction on the two sides of the pen, there was a significantly (Chi square, 8.89, p > 0.01) greater number of rats weaned on the southeast side of the pen (table 29). However, there were no significant differences in mortality with references to place of birth.

Even so, the proportionately greater mortality before May 1949 of the northwest born rats, who lived over 150 days, provides additional support to the belief that the northwest half of the pen developed into a less favorable place of living (middle column, table 29, Chi Square 3.60, p circa 0.06).

Shifts in places of residence from the time of birth in 1948 to the places where the rats were found in May 1949 (table 30) succinctly reflect the sociological forces in operation. Of those rats born on the southeast side of the pen, twice as many males migrated to the socially more unfavorable northwest side of the pen as remained near their place of birth; whereas only half as many females made this shift as remained at their place of birth. This significant sexual difference in frequency of migration by members of the socially higher ranking groups of rats indicates the greater social pressure experienced by males. In contrast to this situation where over half of the members of the socially higher ranking groups of rats established themselves in the half of the pen inhabited by lower ranking rats, *none* of these lower ranking rats of the northwest side of the pen established themselves in the southeast side (comparison b, table 30). Thus, the separate phenomena of (a) the greater number weaned on the southeast side of the pen, (b) the greater survival rate of southeast rats, (c) the marked invasion of the northwest half of the pen by the southeast rats, and (d) the failure of any northwest rats to invade the southeast half of the pen, all contribute to a significant redistribution (comparison c, table 30) of the members of the population.

One of the consequences of the social stratification and redistribution of the population was a differentiation in reproductive rates. At the time of the termination of the colony there were 21 surviving litters. Many other litters conceived during the spring of 1949 (see later section on stress and reproduction, pp. 214–216) were either resorbed or lost shortly following parturition.

Therefore, when consideration is made of the marked strife that was existing within and between members of different groups of rats, it is unlikely that many more litters would have survived in the absence of a marked drop in the adult population. In fact any such survival of rats after May 1949 would probably have increased the discrepancy in reproductive rate between rats born in the southeast and northwest halves of the pen during 1948 (see table 31). For the 44 surviving adult females born during 1948, 21 had surviving litters and 23 were without surviving litters. If the ratio of 0.477 with litters to 0.523 without litters is taken as the expected ratio, it may be seen that the females born on the southeast side of the pen, and who remained there, exhibited a significantly better survival of their litters. On the other hand the northwest females had a significantly poorer survival of their litters. The survival of litters born to southeast females, who migrated to the northwest half of the pen was poorer than those which did not migrate, but was better than that of the northwest females. This is a reflection of the more favorable conditions surrounding the early life of the southeast born females.

This differential in reproductive performance, as fully shown in table 31, is particularly striking if we consider only those females who remained in the same half of the pen in which they were born. The ratio of successfully reproducing to unsuccessfully reproducing rats was 14:4 for southeast females and 2:14 for northeast females. The chi square for this difference is 14.335 with a probability of chance occurrence of less than 0.001.

Mention has already been made of the inference that such differential reproduction should lead to a greater degree of genetic homozygosity than one would anticipate for the same number of randomly breeding rats. Such a trend toward greater homozygosity should be further enhanced by the differential sex ratio. In 1949 the ratio of males to females was 11:18 for the southeast rats and 41:26 for the northwest rats. The chi square for this difference is 4.397 with a probability of chance occurrence between 0.05 and 0.02. The effective breeding population may be roughly approximated by 0.5 of the total females and 0.25 of the total males, and furthermore, these breeding individuals tend to be more closely related than do their non-breeding associates. However, any trend toward more rapid development of genetic homogeneity produced by this restriction of the actual breeding

population must be in part cancelled by the tendency of males and females of a local colony to have different origins (see p. 203).

In the preceding brief history of the colony it is shown that there was considerable difficulty in getting the introduced rats adjusted to their new environment. An accompaniment of the difficulty of adjustment to the new environment was a marked social antagonism in the form of frequent fighting. There was also poor survival of litters during this first season as well as a social stratification with the higher ranking rats inhabiting the southeast half of the pen. This regional social stratification was maintained through the remaining history of the colony, with the southeast rats characterizing a more favorable social status, more progeny, and better survival. The most rapid rate of population increase occurred during the second of the 3 years. By the third breeding season the population density, and the accompanying strife between rats, had so increased as to produce a marked inhibition of reproduction.

2. *Observations Concerning Young Rats From Birth to Sexual Maturity*

A. *Death of Litters Shortly Following Parturition.* The number of pregnancies determined by palpation of embryos far exceeded the known number of litters which survived through weaning. Probably most losses occurred during the first 2 days after birth. The following data will bring out the salient circumstances surrounding litter loss.

On April 5, 1947, one of the colonizing females, No. 4, who was circa 426 days old, was observed in Box 25 with two to three newborn young. The lid of the box was opened only momentarily for this observation. On the next day she was found in a large new nest in Box 7, but the young were not with her, nor were further traces of them found. On September 10, 1947, she was found in Box 2 with 12 young born the previous night. Sometime between then and September 13, when she was found alone in Box 8, her litter disappeared. Between these two dates two additional litters must have met similar fates since embryos were palpated on two intervening occasions. Although the minimum stimulus of momentarily opening the harborage boxes may have been the precipitating situation which led to the destruction of the litters, it must be noted that other females who were similarly disturbed reared their litters successfully.

Female 4 was known to exhibit a subordinate status to the two original females, Nos. 10 and 11, who did successfully rear litters. It is therefore concluded that the emotional state characteristic of more subordinate females predisposes them to be poor mothers (also see p. 260). Emotional state is here equated with the incidence of disturbing situations.

Such poor maternal care is particularly well exemplified in the histories of the three Litter 3 females, Nos. 17, 20, and 25. These three females were characterized by slow growth, small mature size, and many wounds received in chases by other rats. Details of their history and that of their sibs are given on pages 145–147. On the basis of palpation of embryos these females had 3, 4, and 5 pregnancies respectively, yet only one litter was reared, L–25b by female 17. As with female 4 the actual fate of the lost litters was unknown. Females 17 and 20 were autopsied and found to have 38 and 32 placental scars respectively, thus verifying the relative frequency of pregnancy of these females.

One of the characteristics of these and similar socially low-ranking females, who failed to rear litters, was that the increased tendency to construct nests during the first 4 days following parturition frequently continued even after the litter disappeared. Thus, even though both nest construction and that maternal behavior concerned with manipulation and nursing of young are normally accentuated by the physiological state of the rat following parturition, the above observation points to the fact that these two types of behavior may be independently modified. Failure to exhibit proper maternal care represents a failure of interacting with other individuals, their young. The subordinate status of these same females reflects their inability to develop favorable interaction adjustments with their adult associates.

There may occur an incidental death of a litter shortly following parturition even though the mother may be one which evinces good maternal care. One case of this was observed. Normally hooded nests are constructed immediately preceding parturition. Such a nest was constructed in a burrow adjoining Box 29 by female 37. She had a litter here on the night of June 19–20 or 20–21, 1948. This was during a period when I was trapping rats and excavating some of the burrows. At such times there is considerable shifting about of rats as a result of this disturbance.

Presumably this was the cause of the invasion of this burrow by six 63- to 105-day-old subadults. Upon excavation of this burrow on June 21 the hooded nest was found collapsed upon the young by the six rats then occupying the burrow. The mother was not in the burrow. Presumably she was away from the burrow being sexually pursued by a pack of males while this happened. Although the young were not quite dead they were not accepted later by their mother. Under more normal conditions this mother exhibited good maternal care as evinced by her successful rearing of several litters.

The stage of maturation of the mother, including prior experience in handling and caring for young, appears to be an important factor in the success of the mother in rearing her young. A case in point is that of 187-day-old primiparous female 48. She was found on September 18, 1948, with several newborn young on a simple pallet nest in Box 14. Her litter disappeared so soon after birth that little or no nursing had occurred, since 3 days later her teats were in the one-plus nonuse state.

It will be noted that both the behaviors of nest building and maternal care were poorly expressed. During the spring of 1949 she successfully reared a litter. Upon autopsy in June 1949 she had only 16 placental scars. This indicates she had only these two litters. A somewhat similar history was that of female 378 described earlier in the section (p. 27) titled "History of a Typical Burrow during its First Week."

There were nine females born during 1948 for whom the fate of the first litter was known (see table 32). All of these females conceived and reared a second litter except female 92. She did not again conceive. Those rats which reared their first litter exhibited a more favorable pattern of growth, as indicated by their maturity index rating. They also were born earlier in the breeding season, when their was less opportunity for stress resulting from competition with more associates. This provides further evidence that the degree of maternal care is negatively correlated with the intensity of social interaction.

TABLE 32.—*Characteristics of 9 females born during 1948 for whom the fate of the first litter was known*

	Rat No.	Mean maturity index	Date of birth (1948)	Place of birth
Reared first litter.....................	92	I. 36	April 17..............	Area I.
	96	I. 17	....do..............	Area I.
	75	I. 00	March 16.............	South Alley Burrow.
	80	I. 07	....do..............	South Alley Burrow.
Did not rear first litter................	48	I. 19	March 21.............	Area II.
	378	II. 17	Sept..................	South Alley Burrow.
	697	I. 50	May 18..............	South Alley Burrow.
	702	II. 00	....do..............	South Alley Burrow.
	733	I. 50	July 1...............	Area I.

B. *Some Case Histories of Mother to Young Relationships.* Litters were most frequently born in burrows or were transported there from an adjoining harborage box shortly after birth. Few observations were possible under such circumstances. However, there are three groups of data which are sufficiently detailed to present a better comprehension of the life of the young rat than is gained from the presentation of more isolated records.

a. *Litter 2.* This litter was born on April 16, 1947, at the recently constructed South Alley Burrow, and represented the first successful litter born

in the pen to the introduced rats. On the night of April 30–May 1 there occurred a rainstorm which innundated the burrow, and forced the mother, No. 10, to transport her young to a drier location, Box 36, in which there was already a nest. My first awareness of this incident was during the morning of May 1 after the sun was well up. The mother was observed in the process of transporting the first of the six well-furred young, with eyes still closed, back to the home burrow. After a quick examination of the remaining five young in Box 36, I left the pen in order not to further disturb the mother in this process of transportation.

They were not observed again until they were 40 days of age on May 26. Just before sunset, while I was inside the pen, four of these young rats were observed. In contrast to the older rats they really scampered about. Their pelage was in the soft gray stage. One was seen to drag an orange rind from within the Food Pen into the drain tile then serving as Passage 7. These young rats seemed to be mostly utilizing the North Alley Burrow.

Two days later (age 42 days) more detailed observations were made from the tower. The young travelled back and forth between the North and South Alley Burrows by crossing through the Food Pen and utilizing Passages 5 and 7. More time was spent about the North Alley Burrow. One was seen on the mound of the South Alley Burrow sitting on its haunches cleaning itself. Several times these young transported food into the drain tile of Passage 7, where they sat and consumed it. The failure of rats of this age to transport food all the way to their burrows—the distance to the North Alley Burrow from the center of the Food Pen was about 25 feet—is a characteristic of rats of this age. Old males 8 and 12 came into the Food Pen and ate garbage. These old males (circa 223 and 281 days of age respectively) loped along with their backs arched, whereas the young rats darted back and forth. It took these males quite a while to adjust to these youngsters. Every time the old males would settle down to eat, a young rat would make a rapid movement into or out of the Food Pen, at which time the adults would run aside a few feet. This was repeated several times until the adults finally quit exhibiting avoidances every time the young moved rapidly. There seemed to be no antagonism between these two adult males and the juveniles. In fact they adjusted to eating side by side. Finally all six young of Litter 2 came in and were simultaneously eating at a pile of corn meal and the two adult males departed.

Other pertinent notes listed chronologically:

May 30 (44 days old): Males 21 and 22 caught in same trap.

May 31 (45 days old): Nursing had apparently ceased since the teats of the mother had regressed to the one-plus stage characteristic of non-lactating adults. Therefore, weaning must have occurred probably a week or 10 days earlier, at least. No further dependency relationships were observed after this although the four surviving members of this litter, males 16, 21, and 22, and

female 15 spent part of their time, until sexual maturity began to set in at about 85 days of age, about the South Alley Burrow where their mother, female 10, remained.

b. *Litter 3.* The seven young of this litter were born to female 11 the night of May 30–31, 1947, in Box 22, in Area III. When I opened this box on the morning of May 31, I could hear faint squeaks of the newborn young, but they could not be observed because the nest was roofed with foot-long, green, leafy stalks of goldenrod. The box was closed immediately because I did not wish to disturb the mother further. The places where eight of the goldenrod stalks had been clipped were found within 2 feet of Box 22.

June 5, 1947 (6 days old): The young are no longer in Box 22, although during the previous 3 days the entrance tile was noted to be plugged with soil and grass. It is presumed that this behavior of plugging entrances to burrows or boxes by lactating females is one associated with the exclusion of other adults from the young. The neighboring Box 25 contained the largest nest I have yet observed in a harborage box. This nest was a hooded mass of green vegetation filling the entire front half of the box. The young were not heard nor was the nest disturbed sufficiently to determine the presence of the litter.

June 8 (9 days old): The nest in Box 25 had been sufficiently compacted to reveal the seven young. Black pigment of erupting hair covered their dorsal side although the ventral side remained pink. They did not emit any sound. Two pieces of bread and a piece of meat carried from the Food Pen, presumably by the mother, were in the box.

June 10 (11 days old): When I opened the lid to Box 25, the mother was in the opposite end from the young. She immediately went to the young and crouched over them, but as I continued to look she became somewhat agitated and ran out and into Box 21. The young were just about covered with fine hair.

June 12, 1947 (13 days old): The young were in Box 20. They were well covered with hair but their eyes were still closed.

June 14 (15 days old): Female 11 was crouched over her young. Although Box 20 was filled with freshly cut honeysuckle shoots, the nest proper was at the very rear. Practically the only vegetation immediately neighboring this box was honeysuckle vine. Similarly the last two nests were

primarily of goldenrod, the vegetation immediately surrounding Boxes 22 and 25.

June 15 (16 days old): Three inches of rain fell during the previous 48 hours. Female 11 and her young were no longer in Box 20. A large new hooded nest of goldenrod was in Box 28, and although I could not see in it, I suspected that they were there.

June 18 (19 days old): The overhead covering of the nest in Box 28 was now sufficiently trampled that the young could be seen. The mother was not in the box at 5:30 p.m. when these observations were made. During the 5 minutes they were watched no sound was emitted. They walked unsteadily about the box, apparently paying no attention to me, and finally they clumped together in the nest depression. The poor locomotor ability of the rats to this age indicated that the prior three transfers of residence were accomplished by their being transported by their mother.

June 19 (20 days old): At 7 a.m. they were huddled together in the depression of the nest in Box 28. They were still in this position at 10 a.m. when they were handled for the first time and marked. The mother, female 11, was caught in a trap by Box 27. Upon release she wobbled unsteadily to Passage 3 where I lost sight of her. However, an hour later she was in Box 28 nursing her young. Numbers assigned: Males, 18, 19, 23 and 24; Females, 17, 20 and 25.

June 21 (22 days old): Young seen in Box 28 nursing their mother.

June 28 (29 days old): The seven young, but not the mother, were seen in Box 28. Upon this disturbance of opening the lid to Box 28 three of the young rats ran along the trail and into Box 33. I then chased them out and back into Box 28. The mother was in Box 6 in Area I.

June 30 (31 days old): Female 11, the mother, was in Box 7 alone.

July 3 (34 days old): Position of capture in traps or harborage boxes: male 23 in trap by Box 21; male 19 in trap by Box 28; male 24 and female 17 in same trap by Box 30; male 18 in trap by Box 31; females 20 and 25 in Box 36. It will be noted that there were two pairs among these captures of the young. This indicated a continued social bond among the sibs. All the young were released in the West Alley. Two hours after this the mother, female 11, was found in Box 28 with one of her young, although earlier she must have been in a burrow since she was not in any of the 36 harborage boxes. She must still be nursing her young for her teats are in the well worn three-plus condition.

July 4 (35 days old): Position of rats: Male 18 in trap by Box 3 in Area I; males 19 and 24 in same trap by Passage 3. While trying to read their eartags by looking through the wire roof of the trap without handling them, they engaged in several fights. This behavior of engaging in combat by two rats captured together in the same trap upon the observer making a close approach to them was commonly exhibited by rats of all ages. I have interpreted this situation as evidence that aggressive action is initiated more readily when other circumstances increase their anxiety state. The mother and three of the young were in Box 19, and the remaining young were in Box 25.

July 13 (44 days old): The mother made several trips carrying food from the Food Pen into Area III. This continued food storage in the general region inhabited by her young must reduce the number of their excursions to the Food Pen where increased competitive action with other adults would occur.

July 18 (49 days old): Female 11 and six of her young in Box 21, while the remaining one was in Box 19.

July 25 (56 days old): The mother and three of the young were in Box 19, while another was nearby in a trap at Passage 3. Two other of these young were trapped; one by Box 28 and the other by Box 31. One was not captured. The condition of the teats of the mother was the two-plus stage indicating cessation of lactation.

July 30 (61 days old): One of the young was seen running between Areas I and IV, while another was seen running between Boxes 30 and 31. They keep to trails previously worn smooth by adults. The development of trails by adults produces a sociological-biological conditioning of the environment which makes it more habitable by juveniles.

July 31 (62 days old): The mother and all seven of her Litter 3 young were in Box 26. Thus despite the cessation of lactation the bond of association between the mother and young continued. The four males of this litter disappeared shortly after this date as a result of unknown events.

September 10 (103 days old): Females 17 and 25 together in Box 35. There was no new nesting material. No wounds on either rat.

September 15 (108 days old): Females 17, 20, and 25 together in Box 23. They had built a small nest of green herbs.

The above events show that at least up until the 20th day rats do not of their own action depart from the home harborage, although they may be transferred by the mother from one place of residence to another. During the next 9 days they develop the ability to make short excursions from the home harborage. Between the 35th day and 56th day after birth extensive independent excursions take place. Even so, close association with the mother, insofar as place of harborage was concerned, was maintained until 2 months of age. Beyond this time there was continued close association among the three surviving female sibs. On February 4, 1948, all three (250 days of age) were in Box 9 in Area I. During this period of midwinter they were the only rats inhabiting Area I.

c. *Three litters of female 43.* The first three litters, L–8, L–13, and L–18, which this female had during 1948 reveal additional information about mother-and-young relationships as well as the competitive relationships which may develop between members of consecutive litters. Figure 102 may be examined to determine the membership of these litters. The later sections on growth and on social behavior should be examined for further data concerning the fate of these litters.

The six members of her first litter, L–8 were born in Box 20 on March 16, 1948. By the time they were 17 days old she had transported several hundred Purina food pellets from the Food Pen into this box with her young. They were not further disturbed until April 16 (31 days old) when they were observed in Box 28. On this date the mother was in a nest cavity in the ground beside Box 28. A hole gnawed through the side of the box connected the two nests. With her were the seven 8-day-old members of her second litter, L–13. One hundred forty food pellets carried from the Food Pen the previous night were in Box 28. Litter 13 was born 23 days after Litter 8. This indicates that the mother conceived during the day following the birth of her first litter. This is the only case where such conception was known to occur, although on several occasions females were noted to be followed by males engaging in sexual advances on the day following parturition.

On April 23 (L–8, 38 days old; L–13, 15 days old) all 13 young of the 2 litters were still with the mother in Box 28. The three-plus condition of all

14 of her teats suggests that all members of both litters were still nursing. Certainly it was highly probable that nursing competition existed during the first 10 days of life of L–13 and perhaps a week or more longer. Following this disturbance by the observer examining the rats, the mother moved her 15-day-old young to Box 21, where on April 24, they were found nursing. The six 38-day old L–8 rats had followed her here, and though they were not nursing at the time of the momentary observation they were huddled up against their mother.

April 28 (L–8, 43 days old; L–13, 20 days old): The L–13 young were nursing their mother in Box 21, where she had brought at least 100 food pellets during the past 4 days. The L–8 young were not in any of the boxes in Areas II and III. Presumably they had just moved to the harborage where they were noted 15 days later on May 13. By this date, when the L–8 young were 58 days old, and for the previous few days of trapping, they were mainly concentrated about the burrow along the northeast outside fence in Area II opposite Box 17. Here they joined Litter 9, which was a few days younger. At this time the mother of L–9, female 44 was in the terminal stages of lactation, and had not conceived a second litter. This female transported food into this burrow and its vicinity until these litters were between 60 and 70 days of age. Following this she shifted her range slightly over into the burrow by the fence opposite Box 10 in Area II, although most of the members of both L–8 and L–9 remained about the burrow opposite Box 17 until about 100 days of age. Other instances of juveniles initiating their adoption into other litters will be cited later.

May 13 (L–13, 35 days old): Female 43 was in Box 29 with three of this litter. The condition of teats indicates that she was still lactating despite being in the fourth day of pregnancy.

May 14 (L–13, 36 days old): Female 43 was in Box 26 with one of her L–13 young. Three others were in Box 22 10 feet away. These observations of May 13 and 14 indicate that there was still considerable attachment between the L–13 young and their mother, and that perhaps she was still nursing them.

On the night of June 1–2, 1948, 12 young of L–18 were born to female 43 in Box 19. During the following night she must have been away from the young most of the night, since she was observed over long periods to be followed by a pack of males attempting to copulate with her.

June 4 (L–18, 3 days old): After a little over 48 hours there were only six young left in Box 19. The fate of the six which disappeared is unknown. Two possibilities exist. They may have been eaten by males invading Box 19 while trailing the estrous scent of female 43. If this were the case, the question arises as to why all were not destroyed. The second possibility is that they were destroyed by their mother. Whatever the cause of the infanticide it must result in the surviving young securing a more abundant food supply while nursing. The six young were in one corner of the harborage box in a nest. There was another accessory nest in another corner and a small food cache in another.

June 8 (L–18, 7 days old): Eyes were closed. Five hundred food pellets in Box 19 with the young. An extensive burrow system joined Box 19 through a hole in its wall.

June 12 (L–18, 11 days old): Eyes still closed, and their dorsal sides at least are covered with a fine brown hair. Still six young.

June 24 (L–18, 23 days old): Female 43 in Box 19 with all six of her young. Later two of these young rats followed her to Box 24. This is probably the earliest age that rats engage in independent locomotion outside the home harborage. Since the L–13 rats were 53 days old when L–18 was born, they produced no nursing competition for the younger rats. An occasional older rat other than female 43 was seen extending its head out into Box 19 from the burrow which adjoined it. Although the identity of these rats was not known, it indicates that the L–18 rats must have had some noncompetitive associations with older rats during the time of their dependence upon their mother.

June 10–25 (L–13, 63 to 78 days old): There was a total of 25 captures of the seven members of this litter. Twelve were about the North Alley Burrow, six in Area III and seven in Area II. Since all members of L–13 appeared to be ranging over this section of the pen, it means that they were making associations with members of L–9 and L–11 as well as their sibs of L–8. This development of interrelationships with many other rats is probably the most important phase of this period preceding sexual maturation.

July 13 (L–18, 42 days old): They remained mostly about Box 19 although their mother has been noted storing food in Area IV.

October 7: Female 43 in Box 21 with 180 day old L–13 male 54.

October 25: Female 43 in Box 21 with 198 day old L–13 females 58 and 60. These are the only two surviving females of this litter. These records of 3 of the surviving 6-month-old young of L–13 being associated with their mother during this time, while none of the 10 surviving members of L–8 and L–18 were, may be purely coincidental. However, it suggests a relationship between the nursing competition encountered by the L–13 rats and the degree of their dependency attachment to their mother. The reason for suspecting this is that the deprivation with respect to total quantity of food or frequency of feeding exerted upon the L–13 rats by their older L–8 sibs should have enhanced the reward value symbolized by the mother in her nursing capacity.

The records for February 1949, when all members of these three litters of female 43 were 7 or more months old, provide further data on their interrelationships. Female 43 was in Box 20 with 10 other rats. Two of these were again females 58 and 60 of L–13 along with male 70 of L–8. The other seven members of this aggregation had their origin from scattered places and litters. Of the 12 remaining surviving members of Female 43's first 3 litters, records of their places of habitation are available for 8. Seven of these eight were centered in the small region between Box 20 and the burrow at Passage 3. This concentration of mother and adult progeny in a small area is without a doubt in part due to the competitive action of more dominant rats elsewhere in the pen which prevented their expansion of range. However, there were at least two other important factors which were probably in operation. These were the attachment to the physical structure of the environment about their place of birth and the attachment to other individuals with whom they had early associations.

C. *The Social Conditioning of Juveniles by Adults.* Beginning at about 30 days of age young rats begin to wander alone away from the site of their birth. These excursions bring them into contact with adults with whom they have had little or no prior association. These contacts may occur along trails, at passages through the barrier fences, in or about other places of harborage, or at the source of food and water. Along trails adults usually ignore the juveniles. They either walk right over them or crowd them off the trail. About harborages, other than the juveniles' own home, overt antagonism was rarely observed until the period

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of attaining sexual maturity, 86 to 115 days of age.

One of the most potent social forces affecting juveniles and tending to reduce the likelihood of them remaining at home was the action by their mothers. Between the ages of 60 and 85 days the young were frequently chased away from the vicinity of the home burrow by their mother. The juvenile might be caught up with, knocked and rolled over, whereupon it squealed, but the rarity of wounds on rats of this age indicates that they were rarely bitten in the process. This action by the mother may occur whether or not she is lactating or pregnant.

However, lactating females sometimes become particularly antagonistic to all juveniles over 46 days of age. I have not observed this increased antagonism against juveniles under this age. If this absence of aggression by lactating females toward juveniles between the ages of 25 and 45 days is actually true, it will certainly have survival value for the young, in that following that age they will be better developed physically to meet the exigencies of the environment.

Adults of both sexes show antagonism toward the juveniles at the source of food when the latter make too frequent incursions upon their feeding activities. During its first few trips to the food source, a 30–45-day-old rat will dash among and over adults who are feeding. This dashing activity by the juvenile in itself is sometimes disturbing to an adult feeding aggregate, because they have come to associate rapid motion (p. 179) with the occurrence of interadult strife. Furthermore, the juveniles will push right in and take away food from the adults. Although this action may be initially ignored, it is usually followed by the adult pushing the juvenile away with its fore or hind feet. If the intrusion of the juvenile continues, as it usually does at this stage, the adult will turn on it more vigorously. In this process the adult may knock the juvenile over and give it a thorough trouncing with all four feet.

Up until 50 days of age (see fig. 122) the juveniles are never bitten by the adults. In fact, it is extremely rare that the juveniles are ever bitten by adults under any circumstances, even up to the age of 86 days when sexual maturity begins to develop, despite the apparent severity of the thrashing or fight which develops. Because of the usual absence of wounds received by juveniles in this process of social conditioning by adults, I have

termed this category of actions as "psychological drubbing". That this action is effective soon becomes apparent. Even as early as 45 days of age a young rat will run and sometimes squeal as an adult wheels toward it. Certainly during the period between 86 and 115 days, when the juvenile is rapidly developing sexual maturity, this avoidance behavior toward the threats of adults is apparent in all rats. The juveniles not only learn to avoid the threats of adults, but they also learn to avoid expressing those behaviors which would elicit the antagonism of adults, such as attempting to take priority over a particular morsel of food, or in pushing an adult away from a passage through the barrier fences.

The social conditioning of the young encompasses considerably more than the adjustment to the priority rights of older rats as a result of the psychological drubbings. These other aspects of social conditioning, whereby the young rat comes to express adult behaviors and becomes integrated into the adult society, mostly stem from a gradual transition of the mother-to-young relationships into those of adult-to-adult relationships. As soon as young rats engage in movements outside of the burrow, independent of being transported from place to place by its mother, they may be seen closely trailing their mother. An example is as follows:

On June 1, 1948, female 37 who had conceived 2 days previously was observed transporting food up Path 1 and over into Area IV near Box 29, where she had recently shifted her place of residence from the South Alley Burrow. Two of her 30-day-old young were seen trailing her in an apparent attempt to grasp a teat.

There are two important behaviors here. First, there is trailing. Second, there is the oral inspection of the posterior ventral region of the mother.

Whereas trailing is most commonly observed with reference to the mother, it may also be observed very early with respect to other animals. The manner in which this shift may be made is exemplified by the instance in which one of female 37's 31-day-old young was following her from the Food Pen toward Area IV. Along the way adult male 22 crossed between them, whereupon the young rat followed him for a few feet. I strongly suspect that it is such accidental following of mother substitutes which leads to the occasional harboring of a 35- to 40-day-old juvenile rat with some other adult than its mother at the time the mother is

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terminating lactation. This trailing behavior is most strikingly exhibited in the behavior of adult males following estrous females. In fact, it is impossible to make any clear break in the behavior of the young trailing the mother to that of rats, 85 days or older, who trail estrous females. Both trailing and oral inspection of the posterior ventral region of adult females by juveniles of both sexes continues from before weaning right through to sexual maturity. Although the trailing behavior is gradually lost by sexually maturing females, they maintain the behavior of oral inspection of the posterior ventral region of other estrous females.

Close trailing of one adult by other adults is rarely observed, in other than sexual behavior, when it cannot as well be attributed to chance simultaneous movement in the same direction along the same trail. Despite the absence of close trailing by adult rats of the type observed in sheep, I suspect that juvenile trailing behavior and the attendant duplication of the action of the adult is influential in establishing the general characteristic of simultaneity of action so frequently observed. One of the common examples of this simultaneity of action is that of the periodicity of activity and rest by a local group of rats.

Mutual grooming and oral inspection is early exhibited among juveniles and adults other than with their mother. An example of this is as follows:

The participants were 236-day-old male 8 and a 55-day-old juvenile. The action occurred on the mound of the South Alley Burrow. Male 8 walked over to the juvenile and pushed his head under it in an apparent genital inspection. Then several times for 2 to 3 minute intervals they stood up facing each other while propped up by the multiple bases of a small tree. At these times they worked over each other with forefeet and mouth. There was no sign of antagonism between them. There is another behavior which is closely allied to these oral behaviors. This is the approach of two rats to the point of touching noses momentarily (p 179). This recognition behavior occurs between juveniles, between adults, and between juveniles and adults. Following this nose touching the two individuals may ignore each other or may engage in various types of interactions. Although the origin of this behavior is unknown, its frequent occurrence between juveniles and adults indicates its importance in the early formation of social bonds.

Interactions between young sibs or between juveniles who are of a similar age, although not sibs, are a maturational phenomenon which further prepares them for integration into an adult society. In addition to the behaviors previously mentioned, one of the most common is that which may be placed under the general category of play. With the exception of those terminal phases of fighting, which include biting and loud vocalization, juveniles engage in pseudofighting play behavior with most of the motor actions characteristic of the adult sequence of behaviors from approach with nose touching, standing on hindlegs and sparring with forefeet, and tumbling fighting in which the participants roll over and over while grasping each other with legs and teeth, and finally the termination of the sequence with a short chase. The lack of serious antagonistic relations in these activities is shown by the fact that the sequence of activities may suddenly be terminated at any point with the participants then ignoring each other while remaining in close proximity. In fact it is rather doubtful that rats under 85 days of age are capable of injuring each other in a fight. On several occasions juveniles of the same or near the same age were captured in the same trap. Usually upon the approach of the investigator these trapped juveniles would engage in what to all appearances was a very severe combat. However, upon removing the rats from the traps they were never found to be injured from this fighting, despite the fact that they most certainly did grasp each other with their teeth. Juvenile rats also exhibit the adult behavior of passage guarding, but in a quite strikingly more playful manner. While in a play chase, one juvenile may arrive at one of the tile passages through the barrier fence. It will remain in the tile and block the passages through it of the other rat. From time to time the rat occuping the tile will kick out with its hindlegs at the other rat trying to push through the passage. This differs from the similar adult behavior in that the adult which blocks a passage with its body will actively chase away most approaching rats.

This playful aggression of juvenile rats prepares them more effectively to participate in aggressive action with older rats. As may be seen from table 33 there was infrequent aggressive interaction between rats of the same age until they were quite mature, in contrast to the amount of aggression existing between subadult rats (to the age of 150

days) and rats which were considerably older than they.

TABLE 33.—*Number of paired aggressions in relation to age*

Difference in age	Age of the younger rat		
	Under 150 days	150 to 300 days	Over 300 days
Less than 50 days of age between combatants (including sibs)............	3	15	19
Over 50 days between combatants................	30	36	24

The young-to-mother bond serves another function in the socialization of the young rat. When a female is in the terminal stages of lactation—this might be designated as the 25th to 38th day following parturition—she is less antagonistic toward other rats including the young of other females. Where there are such females in the vicinity of other litters whose mothers have recently ceased lactation or who are nursing younger sibs, they attract such recently weaned rats. This leads to the formation of multilitter aggregations of juveniles. One such case has already been mentioned in the history of the litters born to female 43. This case referred to the joining of female 44's Litter 9 by female 43's Litter 8. Another case was observed on May 23, 1949. Female 734 was in Box 9 with her six 33-day-old young. She was still lactating. With them were eight 56-day-old rats and one 70-day-old rat. The mothers of both of these invading litters had ceased to lactate. These close associations between members of litters which were born in the same general locality must facilitate the formation of more harmonious aggregations as adults.

D. *Period of Initial Sexual Behavior of Sub-Adult Rats.* The age of rats at which definite sexual behavior first makes its appearance is about 80 days. The terminal age of this initial period has arbitrarily been set at 115 days. By that time much of the full pattern of sexual behavior has been established. Although females of this age have not been seen in copulation, this must at times be accomplished since both females 15 and 75 were known to have conceived at the age of 94 days. Males of this age show nearly the complete sexual

behavior, including smelling and pawing of the genital region of the estrous female, following the female, rolling at burrow entrances and passages through fences where the estrous females have left their scent, and even occasional attempts to mount. It is my impression that the sexual rolling is not nearly so well developed as among adult males; at least it is only fleetingly exhibited among subadults of this age, whereas fully adult males engage in rolling for periods of 10 to 30 minutes with hardly a pause. The 21 cases of sexual behavior observed for this age group of subadults fall into four categories (table 34).

TABLE 34.—*Early sexual experience*

Participants	Number of cases
Two subadults...................................	2
Subadult male and adult female [1]...................	15
Subadult female and adult female [1]...............	1
Subadult female and adult male...................	3

[1] All these adult females on the basis of their interactions with adult males were known to be sexually attractive at the times of these observations.

One of the interesting things about this tabulation is that only 6 of the cases involve subadult females whereas 17 involve subadult males. Actually only five cases involve subadult females since one observation of a subadult female being chased simultaneously by adults as well as a subadult was placed in both the first and last category. The age structure of the population during June and July 1948, when the 1948 observations on sexual behavior were made, was interesting with reference to the frequency of sexual behavior. During this time there were 11 males and 10 females over 300 days of age as well as 23 males and 11 females in the 80 to 115 day old range. Only two of the subadult females were noted in sexual activity and one of these advances was upon an estrous adult female in a similar fashion to a male. Considering the fact that there was a nearly equal number of adult and subadult females, and that 7 of the 10 adults were judged to have come into estrous during this time, as judged by their behavior, it is concluded that up until the age of 115 days most females are insufficiently matured to be sexually attractive to males.

The initial sexual experiences observed for female 15 form an interesting set. At the age of 81 days she was observed to be followed to the South Alley Burrow by 320-day-old male 12. After she entered the burrow, he engaged in a series of sexual rolls at the burrow entrance. As male 12 began to

depart, the female came out of the burrow and smelled the earth where male 12 had been rolling. As she was doing this he returned and they touched noses. The activity was terminated when all the rats in the pen became startled from some unknown cause. At the age of 94 days she was seen to engage in extensive wanderings through the East Alley and Area II. Upon leaving Area II by way of Passage 2 she apparently heard adult male 8 who was grooming himself about 15 feet away against the outside barrier fence. She turned around and went over to him, whereupon he inspected her genital region and there ensued a sexual chase. She was known to have conceived that night. Nine days later one of her brothers kept attempting to mount her as she was departing from the Food Pen. These attempted mounts were made while she was in motion. Intermittently she stopped and pawed him away with her forefeet. This is a typical behavior of a female who though still sexually attractive to males, is herself not receptive.

The general impression that I have gotten from these observations is that subadults between the ages of 80 and 115 days engage in sexual behavior less frequently than do adults; that sexual behavior which they do engage in is less complete or less intense; and thay they are more likely to engage in sexual behavior with an adult than with another subadult. This latter is quite similar to the situation in which subadults rarely fight effectively among themselves, but rather experience aggressive social conditioning by interacting with adults.

The time sequence of some of the maturational phenomena are diagrammatically shown in figure 103.

3. Sexual Behavior and Reproduction

A. *Sexual Behavior.* There are certain behaviors, which, though not necessarily of sexual implication, form the background for the full expression of sexual behavior. One of these is the habit of one rat closely following another. Its origin may

AGE IN DAYS FROM BIRTH

SQUEAK WHEN DISTURBED

ERUPTION OF DORSAL HAIR FOLLICLES

TRANSPORTATION BY MOTHER

EYES BEGIN TO OPEN

EXPLORATIONS OUT OF NEST – BUT WITHIN BURROW

INITIAL EXPLORATIONS ON SURFACE – BUT NEAR HOME BURROW

FIRST EXTENSIVE WANDERING – INCOMPLETE FOOD TRANSPORT

TERMINATION OF NURSING MOTHER

FIRST HARBORING AWAY FROM SIBS OR MOTHER

CLOSE BOND WITH MOTHER – THEY FOLLOW HER

SIBS HARBOR TOGETHER – AWAY FROM HOME BURROW – MOST OF TIME

SOCIAL ADJUSTMENTS WITH ADULTS – IN WHICH ADULTS ARE RELATIVELY TOLERANT

1. BEGINNING ADULT SEXUAL BEHAVIOR

2. LOSS OF JUVENILE PELAGE

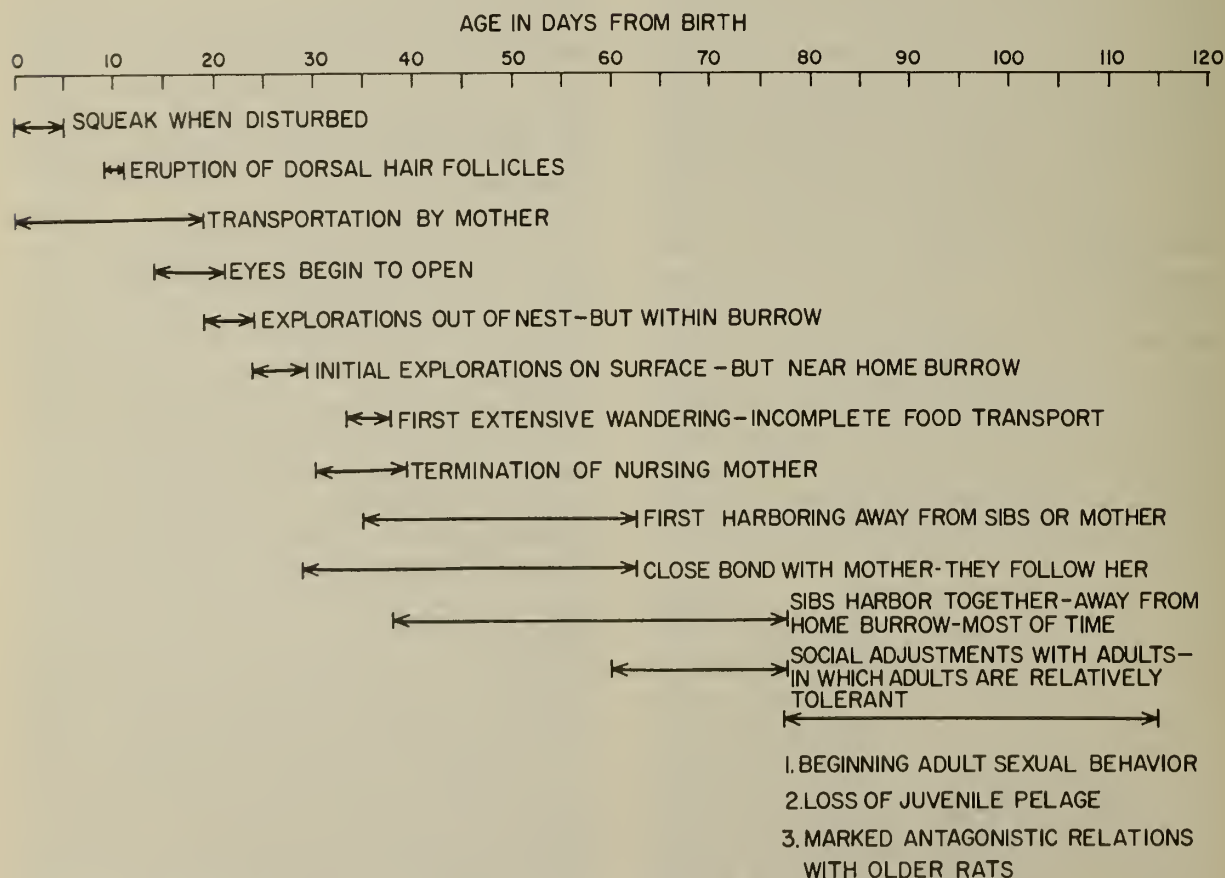3. MARKED ANTAGONISTIC RELATIONS WITH OLDER RATS

Figure 103.—The time sequence of some maturational phenomena from birth to the beginning of adult sexual behavior.

be traced to the habit of still nursing juveniles, who trail their mother from the home burrow. This situation has previously been discussed in more detail with reference to the socialization of juveniles. A second behavior is the one involved in recognition, in which approaching rats touch noses. This is frequently followed by genital inspection. As the rats begin to pass each other after nose touching, one or both extend their heads under the other's belly just in front of the hindleg. This inspection may also take the form of extending the head under the other rats tail until the nose apparently is in contact with the anal region. A third behavior is that of the formation of signposts associated with urination and defecation. Urination and defecation normally occur at those points where forward locomotion is temporarily halted. Passages through barrier fences, intersections of trails, and proximity to a vertical structure are the most frequent locations. Rats also urinated on sticks and over rocks. Genital inspection and signpost formation normally elicit no further behaviors of sexual implication. There is only momentary inspection of a signpost or of another rat, before the rat continues with nonsexual behaviors.

On or near the date when females are capable of conception, the behavior of both sexes becomes altered. There is a precopulatory phase. This lasts for at least part of 1 night, and in some instances apparently for the entire night before copulation occurs. The female wanders more than normal beyond the limits of her customary home range. She actively seeks males; they touch noses, exchange genital inspections; and as the female moves away the male may follow her for a few feet, before returning to his prior activities. There then develops a change in the attractiveness of the female to males. Involved in this change is an alteration of the scent of the female and her behavior in dispersing it. As she wanders about she rubs her sides and anal region against the tiles through fences, or into harborage boxes, or the sides of entries into burrows, at the entries of the activity recorders, or against trees or posts. At these times she frequently drags her genital-anal region over the soil at these points. The ventral part of the body is kept flat against the ground as the rat wriggles back and forth and pulls itself along. Within seconds or a few minutes after the female has left such a point a male frequently arrives. He repeats her performance, and trails

her from point to point until he locates her in a burrow or harborage box. Rarely did the male enter, although he frequently extended the forepart of his body down into the entry, while at the same time rubbing his genital region against the arc of earth surrounding the entry. After a few minutes the male usually desisted in these activities and went away. When the female left she continued in her signpost activity. During this phase she might also actively seek a male. When a male was located she sometimes chased him for a short way, as if in a mock aggression; then she would turn around and he would pursue and closely trail after her for quite some distance before she again entered a burrow or harborage box, where he would repeat his rubbing and rolling.

Other sexually oriented behaviors accompany this precopulatory phase. Upon approach and nose touching the female may back up. The male follows keeping his nose close to hers. Then he rolls over, gets up, turns around with his anal region toward her, and she inspects it. While they are close together he may throw his hips against her. This same behavior is utilized as an aggressive threat between males (p. 180). The female may also lick the nape of the male's neck as he extends his head under her belly. There is also a dancing, pebble-rolling routine. This was noted twice on the night of October 7–8 1948, but by two different rats. This was on a night during which at least one female was leaving scent attractive to males. At 5:45 p.m. there were two unidentified rats in the Food Pen. Their sex was not determined. The larger rat was probably over a year old, and the smaller one 4 to 6 months of age. The larger of the two kept rubbing against one of the posts supporting the food hopper. The smaller rat kept approaching the larger one with a stamping gait, but would retreat as the larger turned toward it. This stamping gait is one in which the back is slightly arched. The legs are maintained somewhat extended and rigid as rapid steps are taken. Three times the smaller rat included in this routine the rolling of a pebble or ball of mud. Just before dawn male 30, who was over a year old, was seen rubbing and throwing his hips against the inside entry to one of the activity recorders. He then went 2 feet toward the food hopper before turning around. In the return toward the recorder tunnel he exhibited the stamping gait and the rolling of a pebble with his forefeet. I suspect that a female, capable of conception, was in the recorder tunnel.

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The rubbing, rolling, and dragging of the body by males at places where females leave their scent, particularly around burrow entries, demands further note. These are by far the most frequently noted sexual behaviors. They occur primarily about the burrow into which the female has retreated. Such retreats by the female may follow mutual courtship activities, but precede mountings by the male, or they may be interspersed between mountings, once this phase has begun. Typically the male extends the forehalf of his body down into the tunnel. The posterior half of the body is swung slowly back and forth in an arc with the penis and testes dragging over the ground. After a few seconds or minutes of this the male backs out. At this time, just as his head emerges, the head of the female can be seen with her nose in near contact with his. She immediately withdraws back into the tunnel. At this time he may scratch the soil at the burrow entrance, and occasionally he eats it. There ensues a more elaborate rolling in which there is considerable extension and twisting of the body. The forefeet are maintained in close contact with the entry, and are moved back and forth in much the same fashion as in the stamping gait, noted above. The hindquarters are swung back and forth across the funnel of the burrow mound, which leads down to the entry. As this is done the hindquarters rotate so that first one side and then the other is against the ground. One hind leg extends into the air, while the other, nearly fully extended, presses against the sloping sides of the funnel. This whole routine may last for as long as 15 minutes and may be repeated several times in succession. The impression one gets after watching this type of behavior in relation to the whole sequence of sexual activity, is that it heightens the sex drive of the male and facilitates later successful copulation. On one occasion, after a male had just completed a sequence of rubbing, dragging, and rolling, he was noted to bend over and clean his penis in the fashion that usually immediately follows mounting and the exhibition of lordosis by the female. Between such sequences at burrow entries the male may engage in other behaviors of erotic implication. He may drag his penis and testes over small rocks or clods of dirt, 1 or 2 inches in diameter. When the rocks or clods approach the size of a rat, the male will arch his body over the object and slowly rock the body back and forth across it with the ventral portion of the body in contact with the object. Rats drag

sticks of one-half to three-quarters inch in diameter on to the burrow surface. This is done prior to initiation of sexual activity. The male will crawl under these sticks, so that they rub against the fur of his back, or he will drag his penis and testes over them or along them. He may also eat the bark of such sticks or the grass near the burrow entry (if it is a bolt hole). All of these objects are saturated with the scent of the female.

Mounting, and perhaps intromission, is the next phase of sexual activity. This normally does not occur until during the second night of sexual activity by the female. When the female has just given birth to young, males attempt to mount as soon as she goes out and begins leaving her scent. By the time a female is receptive to being mounted, there is usually more than one male about the surface of the burrow. At such times a male is occasionally attracted out of his accustomed range. The following is the typical sequence of behavior when the female is fully receptive:

The female emerges and proceeds away from the burrow at a pace between a fast walk and a run. One or more males follow her. Just before the nearest male makes contact with her, she abruptly stops and settles with her belly nearly touching the ground. He initially grasps her with his forelegs just in front of her hindlegs. At this time he grasps her in the midback with his teeth. He gradually slides forward until he has grasped her by the nape of the neck with his teeth. By this time her stance is one of chest on the ground, neck arched backward with head held high, hindlegs extended and back arched upward (lordosis) so that the male is lifted clear off the ground. At this time, when intromission apparently occurs, her tail may be arched above the body. There is a sudden eruptive pulling away of the female from under the male. Total contact time is slightly over 3 seconds. She wheels around toward him and they may rear up momentarily facing each other. He bends over, holds his penis with his forefeet and licks it. He may fall over backward during this process. The female crouches and watches him without moving until he ceases. Actually, he may begin bending over as soon as the female begins to pull out from under him, so that by the time she has wheeled around he has already grasped his penis. She either moves away or engages in a mild boxing with another male before moving away. In this initial receptive period there seemed to be no aggressive implication to this

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boxing. The same male or another male would then follow and mount. Even when the female was in this receptive phase, successful copulation did not necessarily occur. At least the female might break away without exhibiting lordosis. Occasionally the signal for the stopping by the female is the stepping on her tail by the male. When the male was still standing on her tail as she pulled from under him, he was likely to be upset as he bent over to grasp his penis.

Two to twelve males might pursue the female in a relatively compact pack. As soon as one male mounted, the others merely stood around and watched, or wandered off to roll at a burrow entrance. There was never any attempt by one of these males to interfere with the male who had mounted. Yet they frequently fought when two males simultaneously attempted to roll at a burrow entry, where the female was hiding.

Where a single male dominates a burrow system, he is able to keep away most other males. An occasional male from surrounding colonies is able to avoid the dominant male and copulate with the receptive female. However, the actions of the dominant male both reduce the number of mountings while she is receptive, and effectively preclude other males bothering her after she is no longer receptive. When there are relatively few adult rats, as was the case during the 1948 breeding season, a female who is sexually attractive to males is not unduly bothered by them, even though there is no dominant male residing near to her place of harborage. The female can either avoid the few males or repulse their advances.

However, when there is no clearly dominant male at the burrow inhabited by a sexually attractive female, and when many males live in the vicinity, the fate of the female is quite otherwise. For the rest of the night, at the beginning of which the female is first receptive to being mounted, a pack of 2 to 12 males will be in continuous pursuit. This pursuit continues after she has ceased being receptive. That receptivity does decline is indicated by the fact that after a number of consecutive mountings she begins aggressive action toward the males. She will not only pull out from under a male, who has begun to mount her, but she will wheel around, box, and even attack and bite the male. Even so, many males succeed in mounting; although the frequency with which she exhibits lordosis declines. Between each mount or small group of mounts or attempted mounts she retreats

into the burrow. As soon as she enters, the pack of males who were in close pursuit, immediately scatter to adjacent entries. In this way nearly every possible route of escape by the female is covered by at least one male. It is at such times that fights most frequently occur between males as two vie for the right to exhibit sexual rolls at the same burrow entry. As mentioned elsewhere (pp. 183–148) this aggressiveness becomes transferred to other places in the pen. Males who are not involved in direct competition over the female, nor who have even exhibited sexual activity of any sort, receive the brunt of the aggression of males, whose sexual activity and aggressiveness have been heightened as a result of the presence of a female who is sexually attractive. Thus, young males and adult males not involved in the sexual activity were frequently attacked in the Food Pen. Among those males in the sexual pack there was frequently clear-cut differentials in the ability to win combat, yet territoriality was absent. This situation, when compared to that where there is a dominant male exhibiting territorial defense, suggests that hierarchical organization without territorial defense may actually be detrimental.

When the female emerges she is immediately covered by a male, and the rest of the pack join the pursuit, until she again enters the burrow. Often the male at a burrow entrance may be seen to bounce up into the air as the female sticks her head out and nips him. The exact number of mountings or attempted mountings per night is unknown, but it must approach a thousand. Normally the males in a pack do not enter the burrow, but if the female stays in too long one will venture in and force her out. Practically all of this activity occurs in the immediate vicinity of the female's home burrow. Only rarely does she get the opportunity to go to the Food Pen, and even then, males who paw and inspect her genital region or attempt to mount, give her little opportunity to eat or drink. There can be little doubt that this sequence of events produces a marked stress on the female's physiology. Under the topic, "Stress and Reproduction" (p. 214) it is pointed out that females exposed to such intense action by males have a slightly reduced number of conceptions, and practically none of the young conceived are raised.

The description of most of the sexual behavior described above was facilitated by the frame by frame examination of several thousand feet of film taken by the U.S. Army Signal Corps.

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The events described to this point cover the first 2 days of the female's attractiveness to males. The wandering, mutual courtship, and lower attractiveness of females, which comprise the first day, are either omitted or highly abbreviated in time for females who have just given birth to a litter. These individuals nearly immediately fall into the category of receptiveness and high attractiveness to males, which characterize other females on the second day.

On the third day for most females, or on the second day for females who have just given birth to a litter, they are still quite attractive to males, but no longer receptive. They are still followed by males who exhibit sexual rolls and rubs at signposts. Attempts at mounting are reduced, but inspection of the female is continued. Attempts at mounting or genital inspection is repulsed. The female pushes the male away with her forefeet, boxes them, may actually fight and chase them, or kicks them away with her hindfeet. The attractiveness of the female gradually declines during the 7 to 9 days following maximum receptivity until by the 8th to 10th day males no longer pay any attention to her of a sexual nature other than that of the casual genital inspection, which may characterize rats of either sex upon meeting and passing. During this period of declining sexual attractiveness the females may still exhibit the rubbing at signposts of the fashion characteristic of the first 2 days. Stimulation of the male to roll and rub at signposts was not observed after the day following the female's receptiveness. Females who are lactating also exhibit this declining phase of sexual behavior for the week following parturition. On the day following maximum receptivity there is a tendency for the females to be quite retiring, particularly if they have a new litter. For comparable periods of observation the female may never be seen, although on the previous day she was frequently out and pursued by males.

A number of females failed to produce litters, even though mountings had occurred, and intromission seemed to have occurred. If conception was effected, resorption must have set in rapidly since the embryos were not carried long enough to reach the size where they could be detected by palpating the female's abdomen. Lack of conception, or possible early resorption of embryos, materially reduced the reproductive potential.

The length of the estrous cycle, that is the number of days elapsing between one period of receptivity to another, is inadeuqately known for these free-ranging rats. One period of observed receptivity frequently followed a month or more after the previously observed receptivity. Intervening dates of receptiveness may well have fallen on days when no observations were made. Three periods of receptiveness for one female were separated by 7 and 11 days, and conception was known to occur on the third date. Another female was known to conceive on the ninth day following the loss of a litter on the day following parturition. These observations coupled with the fact that the attractiveness of females declines for a week following receptiveness, suggests that the cycle must, at a minimum, be slightly longer than a week. I am inclined to believe that in many cases it is considerably longer than this. Were it not on the average longer than a week many more signs of sexual activity, such as that of rolling and rubbing by males, should have been observed. Yet there were many days on which no such sexual behavior was noted even though there were a minimum of 5 to 10 females who were not lactating or pregnant. In four instances conception occurred on what was probably the first period of receptivity at the terminal phase of lactation. These were at 26, 27, 30, and 31 days following the birth of a previous litter, which was raised successfully. Another female was sexually attractive at 28 days.

There appears to be an erotic implication to aggressive action. On several occasions a male, who had just attacked another male, exhibited sexual rolls or rubs. The reason for believing that this sexual behavior was not just coincidental to aggression was that the male might have been resting for several minutes at a signpost, particularly at a passage through the median barrier fence, without exhibiting any sexual behavior, but immediately following the attack he would return and roll, rub, or dig in the earth. One female at the termination of three consecutive aggressions toward other females immediately engaged in dragging of the genital region over the ground in front of one of the activity recorder tunnels. She was in the ninth day of lactation.

Four instances were noted of behavior that might best be categorized as homosexual. The one case involving males was between two individuals, who were members of socially outcast all male aggregates inhabiting Area IV (see discussion of colonies

h and k, pp. 212 to 213). On Apirl 21, 1949, the date of observation, one was 297 and the other 324 days of age. Both had similar histories of many wounds received from their associates. On this date each had an open purulent wound over the sacrum approximating 2 square inches. During the previous winter one had an open purulent wound over the scrotum. This was healed by April and the testes descended in a normal manner. The other rat had received much more damage to the genital region. During the previous fall it received a warble infestation of the scrotum. Following emergence of the adult fly the penis was left protruding posteriorly outside of the sheath; one testis was destroyed. The other testis was reduced in size, and even during the warm spring weather it rarely descended into the healed scrotum. The behavior noted was close following, of the type associated with a receptive female, mild boxing, hip-bumping, and momentary mounts.

The other three cases of homosexual behavior involve females. On June 30, 1948, my notes record the fact that a 113-day-old female was courting 318-day-old female 33. No details of the behavior were recorded. On April 25, 1949, 403-day-old female 63 was seen to smell and paw the genital region of 297-day-old female 733 for several seconds. This was the only observed instance of such a marked genital inspection of one female by another, in the fashion normally exhibited by males. The third instance was between two 284-day-old sisters. On May 26, 1948, the date of the behavior, female 42 was in her 10th day of lactation, while female 43 was in the terminal stage of pregnancy—she delivered 5 days later. Ten minutes before the beginning of their relationship, female 42 had chased senescent (circa 644 days of age) male 12 out of the Food Pen, across the alley, and into Area III. The behavior between the two females occurred in the Food Pen just in front of the activity recorder at Passage 7. Each dragged her genital region over the ground, across a stick, and rubbed her sides against the sides of the recorder. They also kept sidling up against each other. Female 42 kept throwing her rear against and occasionally on top of female 43. Occasionally one would paw or nudge the other's body, but mainly the sidling and nudging activity was most conspicuous. Occasionally female 43 would jump away from female 42, as if not too sure she could court her. This activity lasted for about 10 minutes. Adult male 22 came in the Food Pen

shortly after they broke up. He smelled where they had been, but otherwise paid no attention to them. There was no evidence in the observations of this and the following day these females were attractive to males.

Females, who are themselves not attractive to males, do inspect signposts left by females who are attractive to males; however, none exhibit any of the rolling, rubbing, dragging, etc., which is characteristic of males. Initial attempts to correlate behavior with known states of the estrous cycle, as indicated by vaginal smears, had to be discontinued. Avoidance of traps, which precluded recapture, was a practical problem. A more serious reason for discontinuing vaginal smears was the obvious disturbance to the rats as a result of capture and handling. I was fearful that excessive trapping would disturb the physiology of the rhythm. Trapping definitely did alter maternal behavior in relation to new-born young.

An attempt was made to ascertain the relation of the behavior of males to known states in the estrous cycle of a female. Scent was obtained from a hooded laboratory rat, No. 44, whose estrous cycle was being followed by vaginal smears in Dr. Curt P. Richter's laboratory. Each morning a clean metal pan was inserted under the cage. On the following morning 50 cc. of a 50 percent alcohol-water solution was sloshed around in the pan for several minutes over the urine and feces deposited during the previous 24 hours. Each day's solution was kept in a separate jar. Samples were obtained from June 2 to 11, 1948. This female was in estrous on June 5 and 10.

Four irregularly oval rocks, about the size of an adult rat's body were placed in a line down Path 1 on June 29, 1948. The rocks were at 2-foot intervals. The contents of the jars for June 2, 4, 5 (estrous), and 6, were poured over separate rocks at 5:15 p.m. During the next 45 minutes four males approached. Each smelled one or all of the rocks before proceeding away. During this time the rocks were still obviously wet. The evaporating alcohol probably served as a repellent. Male 22 was the first male to be excited by the rocks. This was 80 minutes after the solution had been poured on them. He smelled at each and walked over each dragging his genital region. There was no differential response. Male 47 approached a few minutes later and responded likewise—with the exception that he twice drug over the rock for June 4 (the day before estrous). He immediately

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proceeded to the South Alley Burrow and rolled at a burrow entry where a receptive female had recently been. The third male, No. 46, which approached, smelled all four rocks, but stayed longest on the rock for June 4. Female 33 then approached; smelled the rock for June 2; then went to that for June 4 and drug over it before running away as though startled by something. The fifth rat, male 69, smelled all four rocks, but drug over only those for June 4 and 5. Observations were discontinued at this point at about 7 p.m. The scent of this domesticated rat attracted males regardless of her stage in the estrous cycle; however, that of day of estrous and the day preceding it seemed more stimulating. By the next morning all four rocks were greasy and dirty from rats dragging over them. The dirt about the base of each, where the solution had soaked, was scratched up and apparently had been eaten. There was no detectable difference in the usage of these four rocks.

These observations were repeated on the night of June 30. Dates of scent samples: June 7, 8, 10 (estrous), 11. During the day small samples were repeatedly poured over four clean rocks, so that by dusk each was dry, but had an odor which I could detect. Five rats were noted to respond to these rocks. Although each rat responded somewhat differently I could detect no difference in the degree to which the four rocks elicited response. The only conclusions warranted by these observations is that the scent of this female, regardless of the stage of her cycle, was markedly stimulating. In fact, it looks as though there had been a chance selection toward an enhanced stimulating value of the scent of this domesticated female. Samples preserved for 9 months from this female elicited the full response of rubbing, and rolling by males, when placed at points where such behavior had been observed on other dates.

B. *Seasonal and Maturational Aspects of Reproduction.* Domesticated rats are known to conceive as young as 60 days of age. Furthermore, litters are regularly reared by domesticated rats to 450 days of age. With duration of pregnancy taken as 23 days, and a minimum interval between pregnancies of either 23 or 53 days, depending upon whether reconception accompanies parturition or the terminal phase of lactation, it is possible for 7 to 17 litters to be conceived and possibly reared during the 390 day span prior to senescence

setting in. And yet the reproductive performance of the wild Norway rats in the pen never reached this level. In this section we shall consider some of the seasonal and maturational aspects of reproduction associated with lowered performance.

TABLE 35.—*Physical signs of sexual maturation*

Age in days	Males [1]		Females	
	Number of observations	Proportion with scrotal testes	Number of observations	Proportion with perforate vagina
25.......	15	0	10	0
35.......	24	0	19	0
45.......	17	.12	14	.29
55.......	24	.13	23	.83
65.......	30	.40	16	.94
75.......	20	.65	73	1.00
85.......	14	.79	12	1.00
95.......	15	1.00		
105......	17	1.00		

[1] March to September observations only.

The vaginal orifice of young females is sealed by a membrane, while the testes of young males are confined to the abdominal cavity. Perforation of the vaginal orifice or descent of the testes into the scrotum is the first overt sign of approaching sexual maturity (table 35). Not until after weaning do any members of either sex exhibit these conditions. All females have perforated vaginas by 75 days of age. This is before any females were observed exhibiting sexual behavior. Males do not attain a comparable state until 20 days older. By this time (95 days) a few individuals of both sexes exhibit some sexual behavior. At this age neither sex is fully sexually mature from a behavioral viewpoint. See "Period of Initial Sexual Behavior of Subadult Rats" (p. 151).

Further confirmation of the slowness of sexual maturation was revealed through the condition of the teats of females. Four stages were recognized. These stages were represented by symbols: 0, +, ++, +++ (fig. 104). 0 is the stage in which the teat is flat. It is often difficult to locate such teats, even by blowing aside the covering hair. + is the stage when the teat is slightly enlarged and convex. The hair still has to be blown aside to see the teat. ++ is the stage when the teat is elongated and cylindrical, but the body hair still closely surrounds

Figure 104.—Seasonal variation in the condition of the teats.

it. Nevertheless the teat can usually be seen without resorting to blowing aside the surrounding hair. Milk can frequently be expressed. This stage develops near the time of parturition. It also characterizes the period of 1 to 4 weeks following weaning. +++ is the stage of lactation. The teats are as in the previous ++ stage of elongation but the hair is matted down around the teat by the nursing of the young and milk can always be expressed. This system was adopted from that already in use by Drs. Emlen and Davis of the Rodent Ecology Project. ++ and +++ thus characterize those rats which are or recently have been lactating.

From table 36 it may be seen that none of the females between the ages of 83 and 115 days, which were handled during the breeding season, had attained the state of lactation. Furthermore, only 22 percent of the females between the ages of 116 and 196 days were in this lactating phase. Between 6 and 12 months, around 43 percent were lactating, but it was not until the age of 12 to 15 months that over 50 percent of the females were lactating. Judging from the fact that laboratory breeds of the Norway rat regularly begin breeding between 3 and 4 months of age, this slower attainment of sexual maturity is probably attributable to the slower attainment of the full pattern of sexual behavior, which is requisite for successful copulation in an open society (For a detailed review of the maturation of reproduction see pp. 264 to 273).

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Table 36.—*Age and seasonal aspects of lactation*

Age in days	March to September		October to February	
	Number of observations	Proportion lactating or recently lactating [1]	Number of observations	Proportion lactating or recently lactating
83–115..	24	0	23	0
116–196..	28	.22	86	0
197–277..	21	.41	71	0
278–363..	27	.45	60	0
364–450..	39	.54	....	....

[1] Rats for whom the teats were marked: $++$ or $+++$.

Table 36 also reveals that October to February was a period when young were not raised. Further seasonal aspects of the reproductive state of females may be seen in figure 104. Since all of these females were between 6½ and 15 months old, they probably were capable of reproduction, except for seasonal effects upon their physiology. By January, the teats of most females had regressed to the most inactive stage. From this time until June and July, when the teats of practically all females were no longer completely inactive, there was a gradual increase in the number of individuals evincing some hormonal stimulation of the teats. Conceptions of weaned rats (table 37) also reveal the effect of season. One litter was known to have been conceived during November, but it did not survive longer than 2 days. If any other litters

Table 37.—*Temperature and season of conception*

Month	Known conceptions of weaned rats (1947 and 1948)	Mean minimum nightly temperature (° F., 1948)
January........	0	22
February............	36	27
March....	26	37
April........... ...	30	45
May....	15	56
June...	33	64
July..... ... - .	29	70
August...	22	67
September...	0	60
October. -	0	49
November.. . - .	0	45
December.....	0	33

were conceived between September and January, no evidence of this was observed. Three of the four litters conceived during February were during the last week. Temperature was not the primary inhibiting agent. The temperatures in March, April, and May, when 71 rats conceived, was lower than the corresponding months of November, October, and September, when no conceptions occurred. It is possible that initiation and termination of conceptions was under photoperiodic control. Conceptions did not begin until there were 11 hours between sunrise and sunset, and conceptions ceased as soon as this period was less than 13 hours.

There was also a seasonal cycle in the number of males whose testes were scrotal or abdominal (fig. 105). During December and January the testes of many males were retracted into the abdomen. When brought into a warm room, descent into the scrotum occurred within 30 minutes. Despite this immediate effect by temperature, the annual cycle showed no close correlation with temperature. For example all males had scrotal testes in April but less than 50 percent did in October and November, when the temperatures were comparable to April (table 37). Here again photoperiodic control is indicated. During April there was 12.5 or more hours between sunrise and sunset, but less than 12 during October and November.

In addition to age and season, factors affecting growth and physical maturation influence reproductive success, if not also sexual maturation. This is discussed in part under the topic of "Stress and reproduction" (pp. 214 to 216). Further pertinent data is presented in table 38. It is quite apparent from this table that those conditions which inhibit growth also reduce the likelihood of conceiving or the success of rearing young. My observations are of little help in delineating the extent to which altered physiology, behavioral immaturity, or the development of abnormal behavior contribute to the lowered reproductive success of these slower growing females.

4. *Utilization of Space*

A. *Home Range.* Home range refers to the total space occupied by the individual as it engages in its various activities from day to day. Certain aspects of this problem have already been covered in the earlier sections on orientation (pp. 71 to 82). In these sections emphasis was placed upon the fact

that all portions of the home range are not equally utilized. There was evidence that from a center of orientation there was a regularly decreasing frequency of visitation to places of greater distance. Furthermore, activity was considerably channelized by the habit of rats running along trails between such centers of orientation as harborage, the food supply, or passages through barrier fences.

TABLE 38.—*The relationship between growth and reproduction*

A. 35 adult females examined for placental scars in June 1949

Placental scars	Surviving progeny	Mean maturity index	Number of females
Yes..........	Yes........	I.63	15
Yes..........	No........	II.21	16
No...........	No........	II.46	4

B. Females born in 1948 who lived to May 1949

Surviving progeny	Number of females in each maturity index range		
	I.00–I.66	I.67–II.33	II.34–III.0
Yes..........	13	8	1
No..........	7	13	11

Chi square = 10.043; *p* less than .01

In the present section, we shall be particularly concerned with the restriction of activities to particular sections of the pen by most individual rats. In addition, we shall deal with the shifts in place of residence exhibited by some rats and not by others.

Even the 10 introduced rats (table 28 and figs. 106–108) showed marked evidence of restriction of place of activity during the first 7 months of residence in the pen. Since there was equal access to the Food Pen from all portions of the pen, it might be anticipated that each rat would have been found as frequently in the southeast and northwest halves of the pen, had they formed no attachments to a particular portion of the pen. The observed distribution for each rat may be tested for its approximation to the 50:50 ratio by the Chi Square test, $\frac{(x-y)^2}{x-y}$, recommended to me by Dr. Ardie Lubin

for this particular data. The sum of the Chi Squares for the 10 animals is 40.86, which with 10 degrees of freedom is significant at well below the 0.01 level of confidence. Therefore, it may be concluded that the original colonizers did not wander about at random, but rather confined their activities to particular portions of the pen.

All animals born in the pen differed from the colonizers in that their places of later residence might be influenced by the place of birth. That place of birth was an important variable is amply demonstrated in table 39A. For rats born in the south quarter of the pen, there were 290 captures in the south quarter, but only 68 in the opposite north quarter. Likewise, for rats born in the north quarter of the pen, there were 294 captures in the north quarter, but only 44 captures in the south quarter. The Chi Square of the difference in these two distributions is 295.3, which is significant far below the 0.01 level of confidence. It is therefore quite clear that place of birth affects the place of later residence.

A more precise appreciation of the degree to which rats confine their activities to those portions of the pen adjacent to the place of their birth may be seen by examining figures 111 to 116. It must be recalled that the positions shown in these figures denote actual places of harborage or places where the rats were trapped. These trapping records primarily indicate proximity to place of harborage, since rats were regularly observed to enter those traps closest to the place where they were at that time harboring. Even so, the density of records of places of capture depicts quite well the actual intensity with which various parts of the environment were utilized. A case in point is that of the home range of male 22, figure 109. Only on one occasion was he observed outside the line demarcating his adult home range. This occasion was when he was attracted over into Area III by the presence of estrous female 43.

The comparisons between these figures permit the formulation of certain conclusions concerning home range and the shifts in place of residence:

1. There was a marked tendency for the socially more dominant rats born in the south quarter of the pen to exhibit shifts in place of residence such that there was an encroachment upon the home range of the socially lower ranking rats born in the north quarter of the pen. This is particularly well demonstrated by figures 114 and 115.

SEASONAL VARIATION IN THE DESCENT OF THE TESTES
126 TO 450 DAYS OF AGE
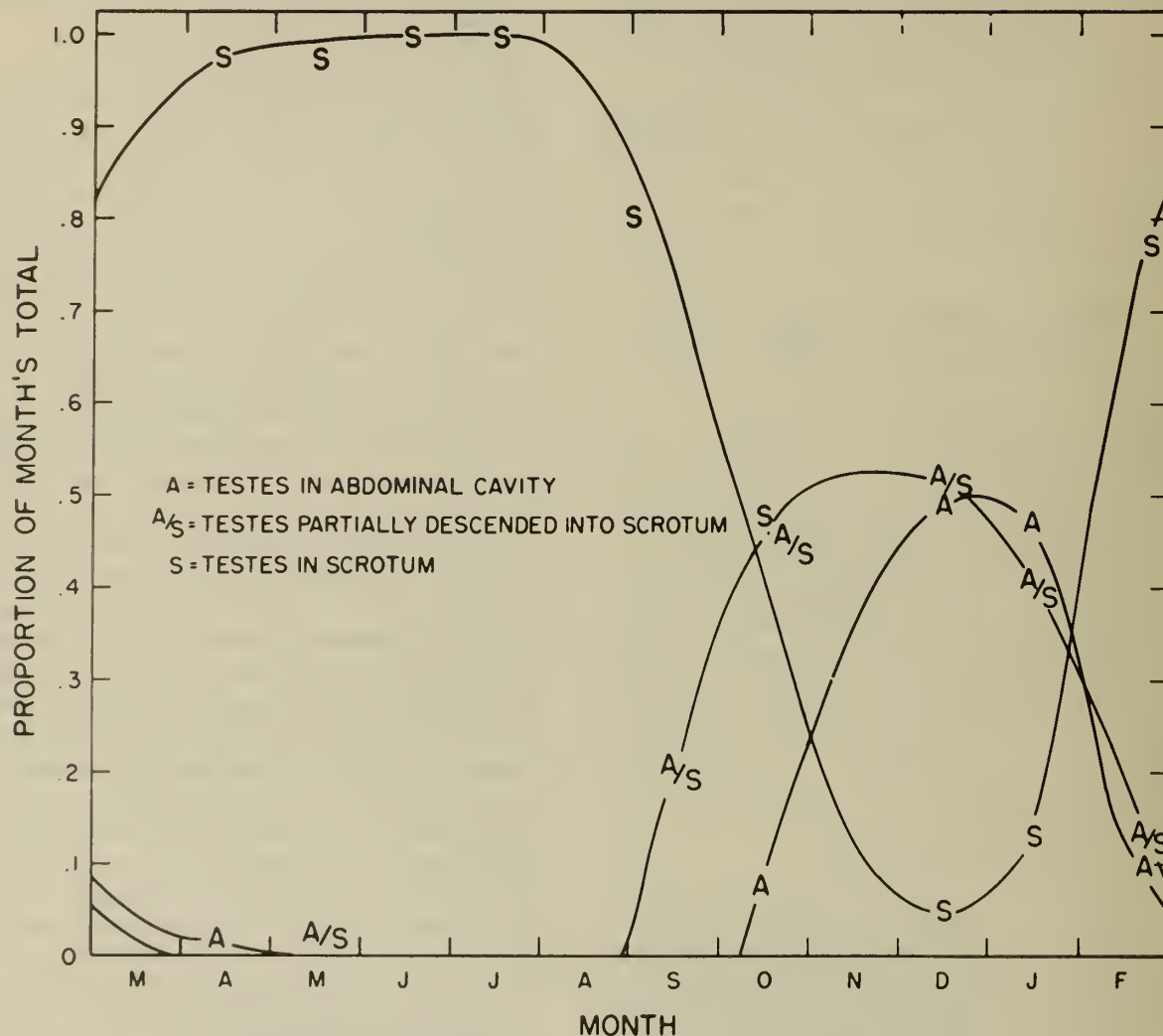
Figure 105.—Seasonal variation in the descent of the testes.

TABLE 39A.—*Places of capture of rats born during 1948*

Place of birth	Sex	Total captures	Proportion of total captures by place of capture					
			South Alley Burrow	Area I	Area II	North Alley Burrow	Area III	Area IV
South Alley Burrow and Area I	Male.............	328	0. 32	0. 16	0. 05	0. 09	0. 05	0. 32
	Female..........	204	. 41	. 24	. 06	. 04	. 07	. 18
North Alley Burrow and Area III .	Male............	192	. 07	. 02	. 08	. 40	. 33	. 10
	Female..........	270	. 04	. 06	. 16	. 23	. 34	. 17

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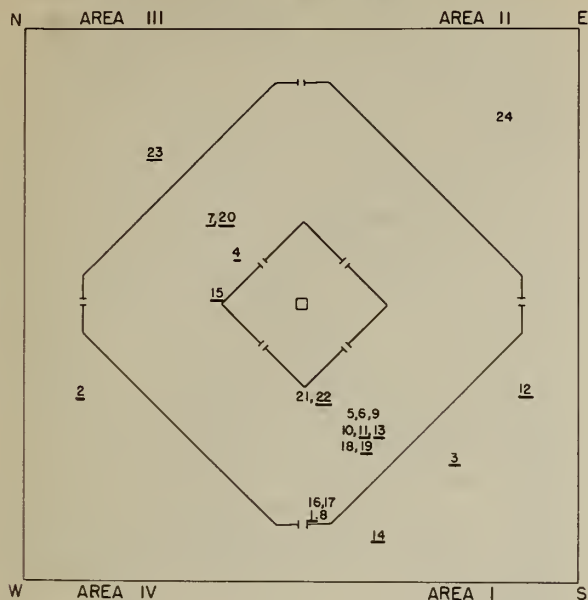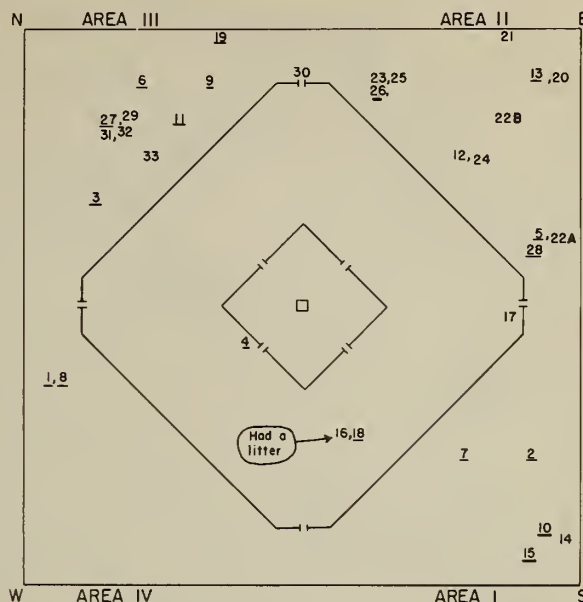
Figure 106.—Places of capture or observation of two of the introduced females. The numbers indicate the chronological order of the places observed. Each underlined number indicates that this position of observation is in a different locality (i.e. different alley or area) from the next observation. Female 7 was socially lower ranking, whereas female 10 was higher ranking. Sixty-eight percent of the observations for female 7 were in areas II and III, but only the last two records for female 10 were here. This was at a time when she was a senescent nonaggressive individual. It is also interesting that 5 out of the 9 records when female 7 invaded the range of the dominant female 10 came at a time when she was pregnant and delivered a litter, even though she did not rear it.
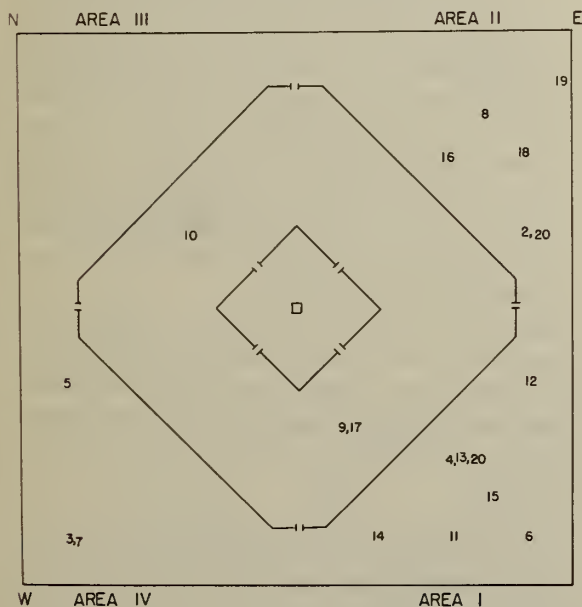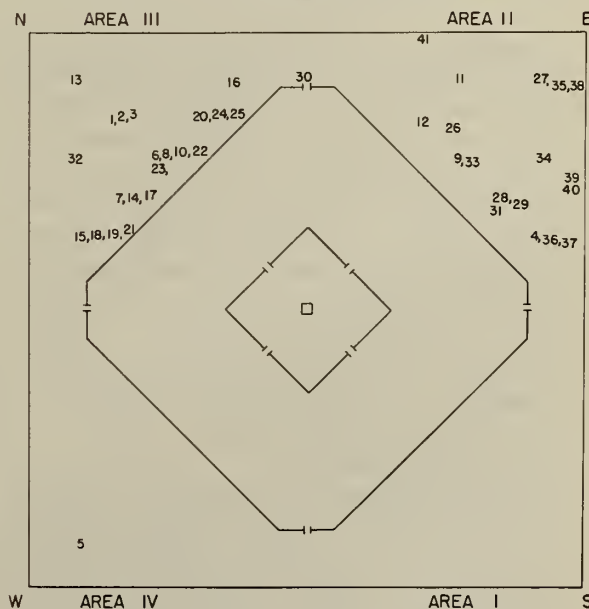
Figure 107.—Range of the introduced male 12. Note the shift of region of habitation accompanying different periods of life. During the earlier half of his life, when he was becoming the dominant rat of the pen, he was in the southeast quadrant of the pen half the time. All later data indicated that this was the most favored quadrant of the pen. After he became senescent and reduced in social rank, he completely avoided this most favored region.

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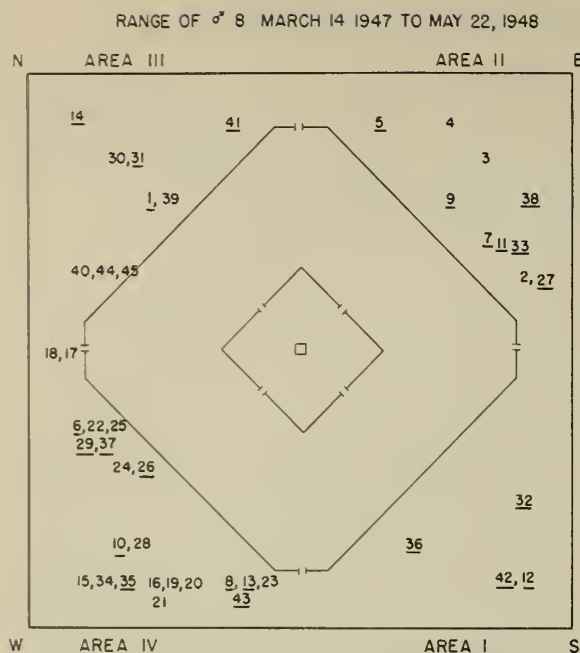
Figure 108.—Range of the introduced male 8. The numbers refer to the chronological order of capture. It will be noted that he continually shifted his place of residence. Each underlined record indicates that he moved to same other locality in the pen. He held a very low social status. Other rats continually forced him to change his place of residence. Furthermore, he seemed particularly susceptible to shifting his residence as an immediate result of handling by the observer.

2. Females tend to remain closer to their places of birth than do males. This is shown in figures 112 to 115. An exception to this is shown in figure 111. Here the females became as widely dispersed as the males: This resulted from the fact that both sexes were excluded from their place of birth by more dominant invading rats. See particularly the later discussion of the formation of Colony e in 1949 in Area III (pp. 207 to 209). Further aspects of the differential shifts in place of residence with respect to social rank and sex have been previously treated in table 30 and the accompanying text.

3. In their dispersion from their places of birth, which results in shifts in location of home range, young rats avoid neighboring areas occupied by socially high-ranking adults. The clearest situation pertains to the rats born at the South Alley Burrow during 1948 (figs. 113, 114, 116) with respect to Area I. From the spring of 1948 until May 1949,

Area I was dominated by male 22, female 28, and their progeny (figs. 109 to 111). In extending the area or shifting the position of their home range, rats born at the South Alley had equal opportunity to invade Area I or Area IV. The latter area in contrast to Area I was not occupied by adults, which defended the area or were raising young, until late in the summer and fall of 1948. There were only 25 captures in Area I of rats born at the South Alley Burrow, whereas there were 129 in Area IV. Furthermore, 24 of these 25 records in Area I were for rats born at least a month before female 28 had her first litter in Area I. The degree of exclusion is further reflected by the fact that only 2 rats born at the South Alley Burrow occurred in Area I after sexual maturity, and these 2 rats, which were accepted into the local colony being developed there, accounted for 17 of these 24 records.

4. The condition of restriction of home range by each rat to only portions of the pen reduced the frequency of contact between individuals. Examples of this are shown in figures 109 and 110. It is apparent from these that such individuals have essentially no contact with each other, except at the food source. It will be recalled from the earlier section on periodicity of activity that rats living in different portions of the pen tended to become active at different times, thus further decreasing the probability of rats living in different localities having associations. This role of restricted home range in limiting the frequency of paired associations is discussed in detail in the later section on "The Function of Group Structure in Altering the Frequency of Contact Between Rats" (pp. 172 to 175).

This latter section will further emphasize that a home range is not an exclusive portion of the environment, but rather is one which is shared with a number of other associates. The territorial aspects of home range are discussed on pages 184 to 188.

A cursory examination of the figures (Nos. 111 to 116) on places of capture indicated that there was a decreasing frequency of captures after weaning at increasing distances from the place of birth. This distance may be considered in two ways: 1. The shortest distance between the place of birth and the place of later capture irrespective

RANGE OF ♂ 22 MAY 30, 1947 (44 DAYS OLD)
TO DEC. 7, 1948 (602 DAYS OLD)

RANGE OF ♂ 59, MAY 26, 1948 (48 DAYS OLD) TO JUNE
1, 1949 (419 DAYS OLD)

N   AREA III   AREA II   E

32

RANGE
JUVENILE
ADULT

7, 10
2, 3

1

14

6

5, 8
PLACE OF
BIRTH
39, 40

4,
13

34

16, 30, 3
33 42

19, 35
37

20, 23
36, 38

25

27, 28   18, 41

17, 21, 25

24, 26
43

9, 11, 12, 1
22, 29

W   AREA IV   AREA I   S

N   AREA III   AREA II   E

PLACE OF BIRTH

15

26   14 16 11, 12, 13   8, 9
22   31
7, 10   5 23
27

1, 2

3, 4, 6, 18
19, 21, 29
30, 31, 32

28

17
24

33

20
25

W   AREA IV   AREA I   S

Figure 109.—Localization of home range of males 22 and 59. Numerals in each figure represent chronological order of points of capture. Each restricted its activity to a portion of the pen near its place of birth. Male 22 was a fairly high ranking rat socially, while male 59 held extremely low rank.

RANGE ♀ 28, OCT. 14, 1947 TO APRIL 10, 1949
(59 TO 603 DAYS OF AGE)

RANGE ♀ 43, NOV. 12, 1947 TO MAY 26, 1949
(89 TO 649 DAYS OF AGE)

N   AREA III   AREA II   E

2

7

5

3

PLACE OF
BIRTH

1, 17
21, 25
27

14 15
28
23 24
20
29

4, 6, 9   36

30 37

31   34

13, 18, 19   16, 33   10, 11, 12
22   32   35   26

W   AREA IV   AREA I   'S

N   AREA III   AREA II   E

23, 24
LITTER   20, 21, 22
HERE   → 27
14, 15, 16
17, 18, 19

25

5

10   7, 8, 12
28, 29

PLACE OF BIRTH

30   3

6

9, 26

2   1

31

13

4

11

W   AREA IV   AREA I   S

Figure 110.—Home ranges of females 28 and 43. Numerals indicate chronological order of points of capture. It will be noted that these two females, each of which had several litters, had very little association.

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Figure 111.—Points of capture of the young of female 43. The points circled indicate terminal records. Note that there was absolutely no invasion of area I, which was on the opposite side of the pen from which these rats were born. All the females but 55 survived to May 17, 1949. Only males 54, 56, 59, 660, and 662 survived this long. The interesting thing about the terminal records of these longer surviving rats was that all were forced from their place of birth into area IV or the North Alley, to become members of colonies g, j, and k (see pages 385–390). These rats were born in what at the time was the least desirable portion of the pen, and they were later displaced into other localities which had become even less desirable by the time they became adults.
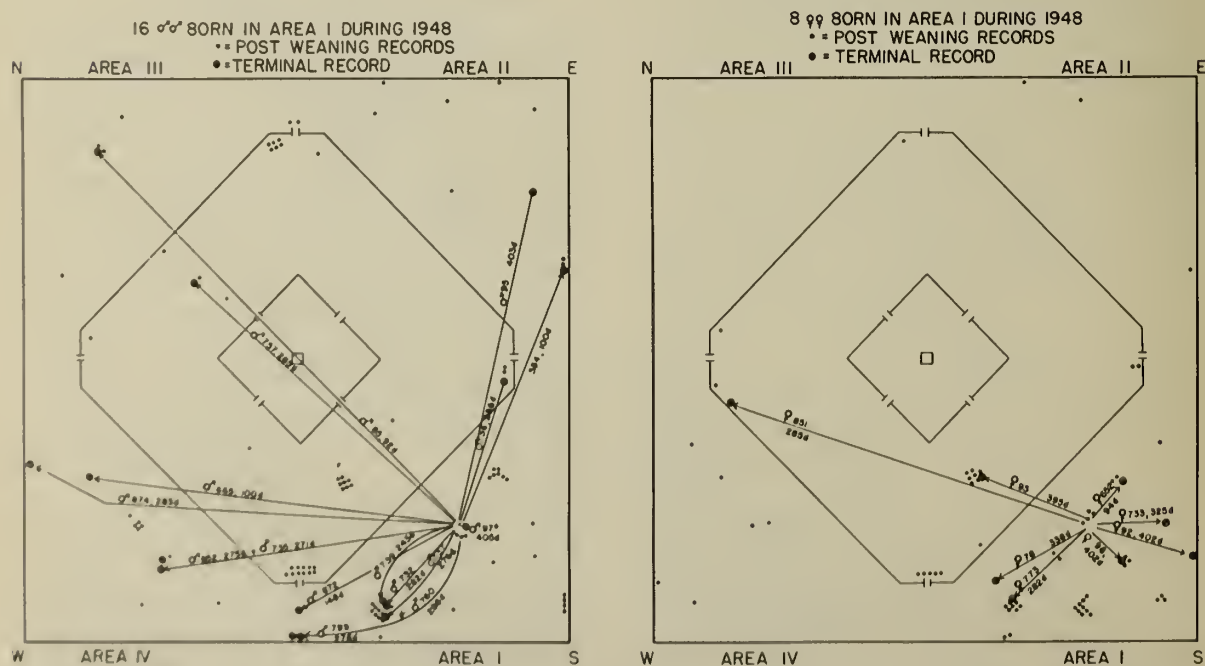
Figure 112.—The points of capture of rats born in area I during 1948. Arrows point to terminal captures. Note how the females tended to remain near their place of birth, whereas the males became distributed more widely through the pen.

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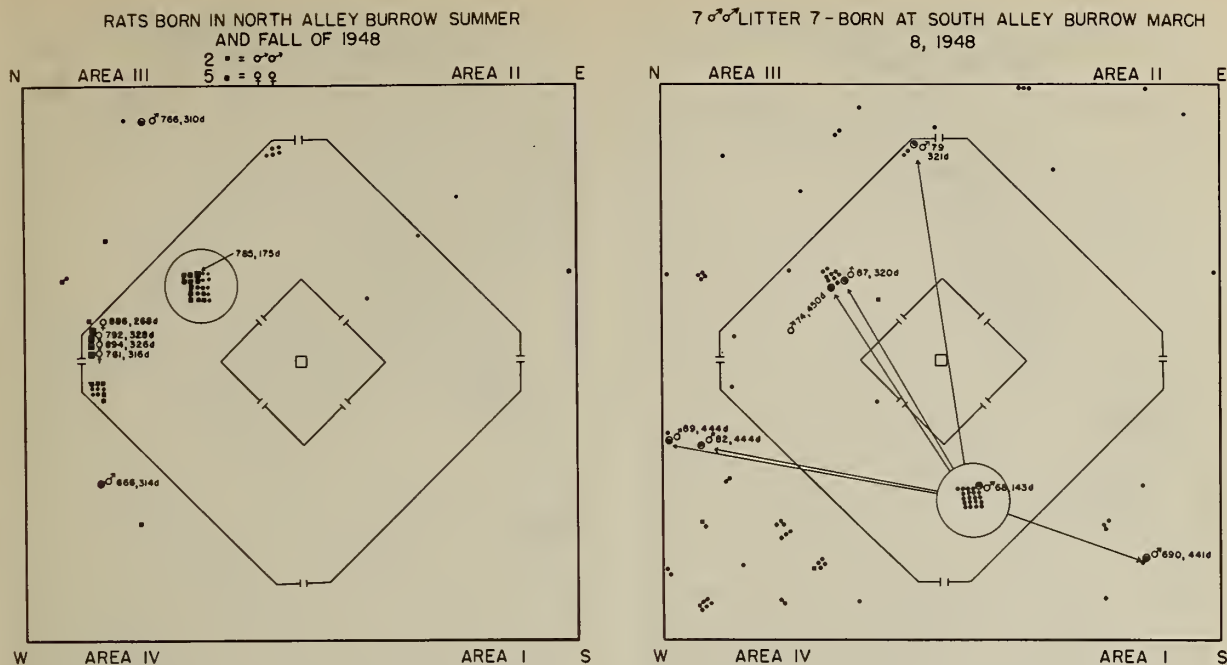
Figure 113.—Differences in the distribution of captures of two groups of rats. The South Alley Burrow was a place which fostered the development of high social rank in comparison with conditions about the North Alley Burrow. Note how the males born at the South Alley Burrow become widely dispersed, whereas rats of both sexes born at the North Alley Burrow remained near their place of birth. In part, these records exemplify the inverse relationship between social status and the ability to invade other areas already inhabited by rats.

♂♂ BORN AT SOUTH ALLEY BURROW, 1948
6 ▪ = BORN MARCH 16, 1948
8 ▪ = BORN MAY 18, 1948

♀♀ BORN AT SOUTH ALLEY BURROW, 1948
5 ▪ = BORN MARCH 16, 1948
8 ▪ = BORN MAY 18, 1948
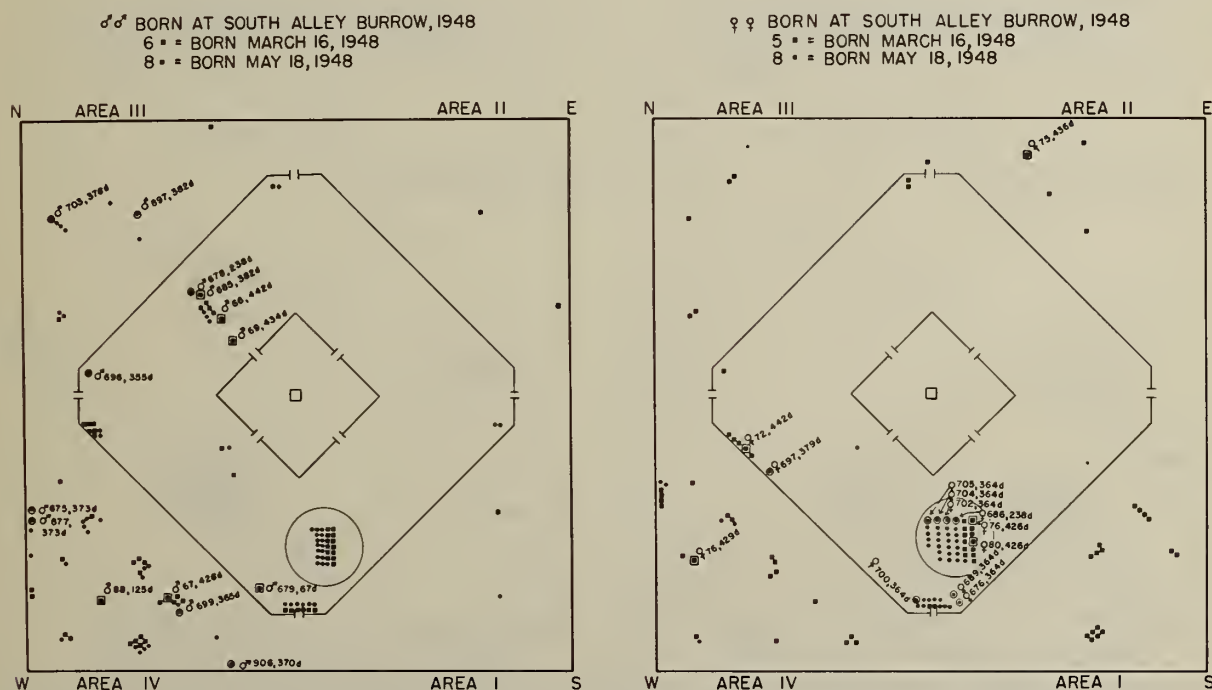
Figure 114.—The distribution of captures of rats born on March 16 and May 18, 1948, at the South Alley Burrow. Enclosed dots or squares represent terminal records. These records exemplify the general tendency of females to remain near their home burrows, whereas males become more widely dispersed.

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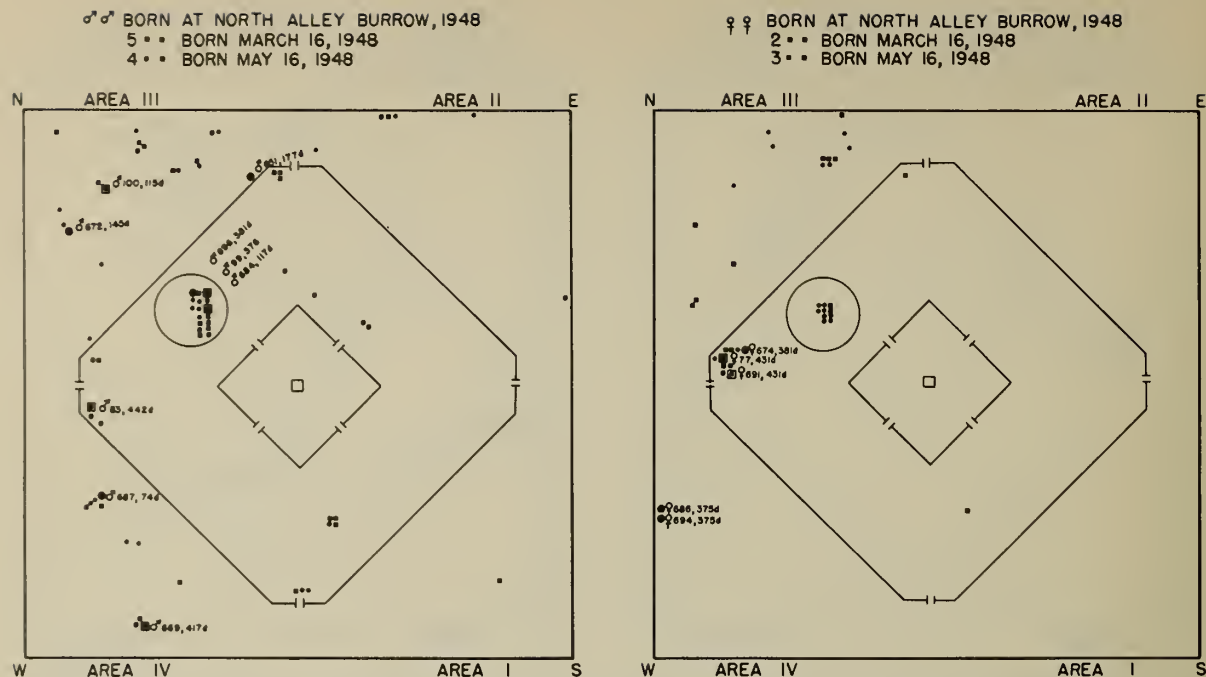
Figure 115.—The distribution of captures of rats born on March 16 and May 16, 1948, at the North Alley Burrow. Enclosed dots or squares represent terminal captures. These records exemplify two principles of distribution following birth. The first of these is that males become more widely distributed than do females. Secondly, individuals of both sexes of these socially lower ranking rats showed considerably less tendency to invade areas away from their place of birth, than did rats born in a more favorable location such as at the South Alley Burrow as shown in figure 114.
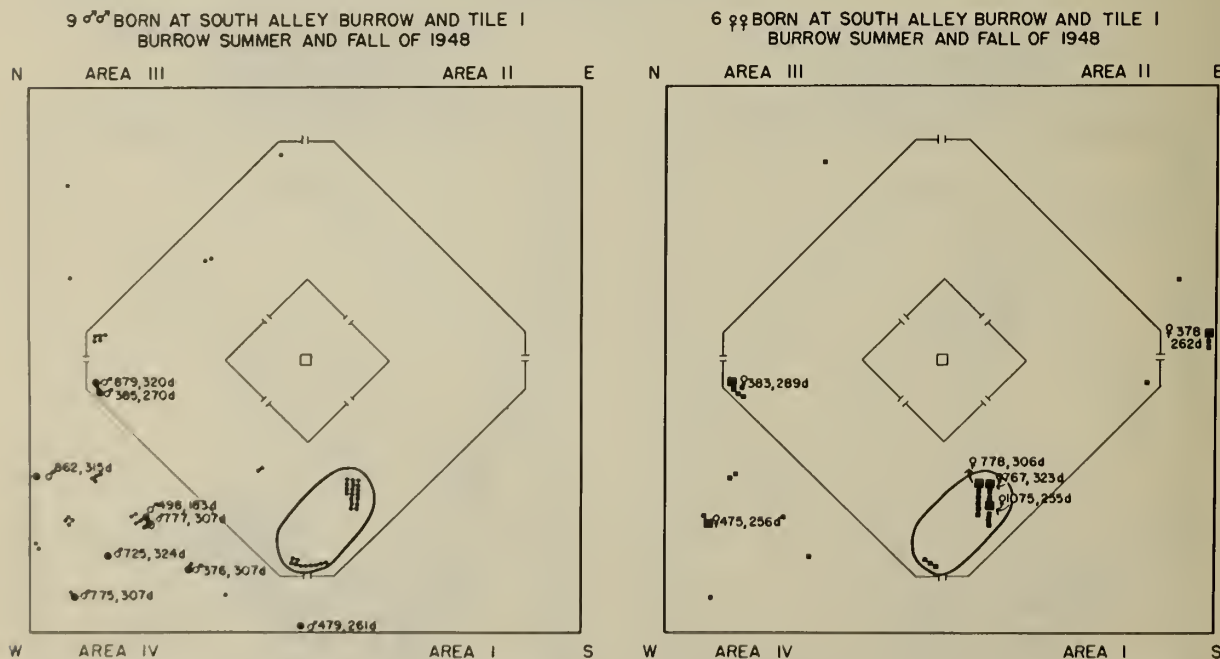
Figure 116.—The distribution of captures of rats born at the South Alley Burrow during the summer and fall of 1948. Enclosed dots or squares represent terminal captures. These rats born at the South Alley Burrow late in the breeding season experienced more stress from social interactions than characterized rats born here earlier. As a consequence these later born rats, particularly the males, became less widely dispersed, and more confined to area IV, which became a place where social outcasts aggregated. Compare with figure 114.

of intervening barrier fences; 2. The shortest distance between the place of birth and the place of later capture with respect to the distance which the rat must actually travel around barriers between the two points. Both of these two ways of examining the distribution are shown in figure 117. For both plottings, the general conclusion of decreased frequency of captures at increased distances remains valid. However, only the distribution of distances across barriers (table 39B) presents a consistent pattern of decrease. The conclusion is therefore drawn that the rats maintain their orientation to the site of birth with reference to actual, rather than to "locomotor" distance.

If this is really a valid conclusion, and the data indicate that it is, the question then arises as to how such orientation is maintained. In the first place, we may exclude the contention that the orientation is a spurious one resulting from the chance dispersion of the rats, for were this so, we might have anticipated a consistent decrease in the frequencies of distances around barriers. Therefore, we must conclude that the orientation is real, and furthermore, that the place of birth holds a permanent attraction for the rat. Since the places of capture represent for the most part actual or approximate places of residence, the rat must be able to detect both the direction toward and the distance from the place of birth. The

observations were not amenable to offering any definite proof of the means of perception of the site of birth from points removed from it. However, the existing conditions suggest possible means. In the first place, the barrier fences, though barriers to locomotion, were not barriers to vision. Even so, considering the fact that most orientation occurred during hours of low light intensity, and that intervening vegetation must have precluded visual observation by the rat for any appreciable distance, it is concluded that vision was not the primary means of perception of the site of birth. I am inclined to suspect that the perception involved is that of hearing the vocalizations of those rats which are residing at the site of birth. It is quite certain that a rat in one portion of the pen can respond to the vocalization of a rat in another part. The fact that a rat as an adult is not residing at its place of birth is mainly attributable to social action from other rats which produced its exclusion. Therefore, the final postulate is that a rat is able to recognize the particular vocalizations of one group of rats in contrast to that of all others.

The extent of the home range of the introduced rats was in general much greater than that of rats born in the pen. There were three major contributing conditions to this greater extent of home range. 1. The initial training period, February 13 to March 14, 1947, was such as to force all the rats

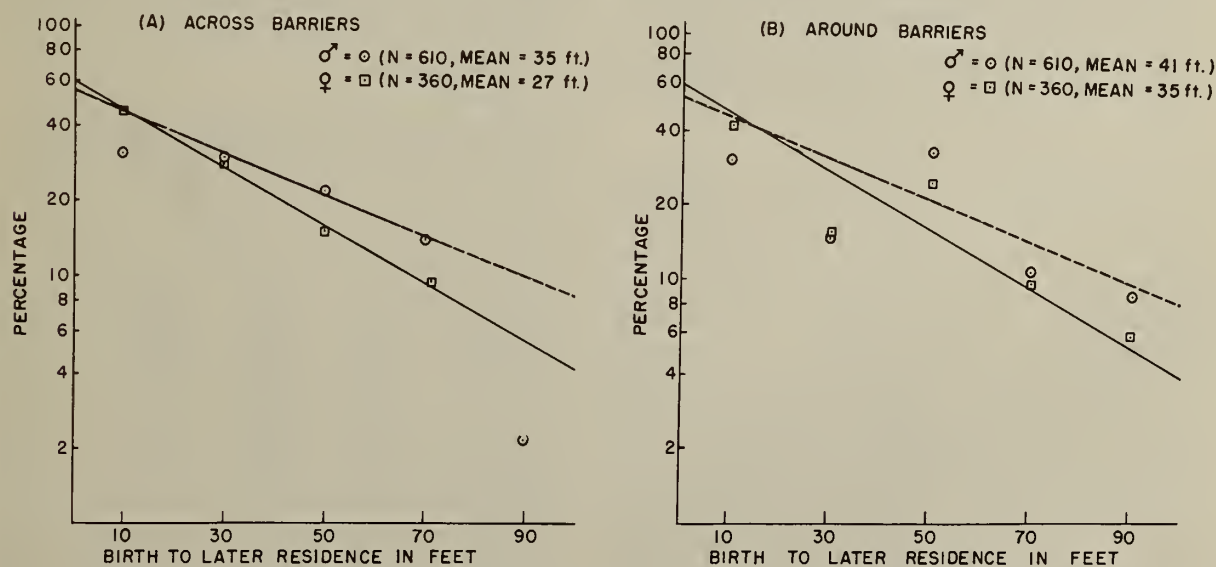Figure 117.—Distance of place of birth to places of later capture. The distance to each place of capture was measured in two ways. 1. across barriers such as fences in a straight line from the place of birth; 2. around barriers along the shortest route a rat would have to travel from its place of birth. In (A) straight lines have been fitted empirically to the points. These same lines were reproduced in (B) for comparison.

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to learn all portions of the pen. 2. The population density was lower. This condition provided a minimum restriction due to social action. 3. The handling of the introduced rats at each capture was frequently a sufficiently disturbing experience to induce a shift in place of residence from the proximity of the place of capture.

This latter point is amply documented in figures 106 to 108. In these figures, it may be seen that there is a marked tendency for a capture to be in a different area or portion of the alley from the preceding one. This continual shifting about was quite in contrast to the greater localization of home range exhibited by rats born in the pen such as shown in figures 109 and 110.

B. *Dispersal With Reference to Age.* Until 30 days of age the rat remains very close to its home burrow. In fact, there is practically no emergence from the burrow until about 25 days of age. I have never seen a 25–30-day-old rat go more than 10 to 15 feet away from its home burrow. Although rats of this age may play among themselves about the surface of the burrow, as well as follow their mother about while nudging under her as if to try to nurse, their attachment to the home burrow is sufficient to prevent farther wanderings. However, with the onset of weaning there begins a gradual process of extension of the area encompassed by wanderings from the home burrow. Coupled with this there is frequently a shift in place of harboring.

A measure of the dispersal was obtained from the records of place of capture in traps or from the burrow or harborage box in which the rats were removed. Since traps were most frequently placed near burrows, and since rats were usually observed to enter traps nearest to the burrows from which they initially emerged following the setting of traps, these records primarily reflect proximity to the current place of residence. These records (table 39B) were tabulated with reference to their distance in a straight line across barriers from the place of birth of the rats (see pp. 164 to 170).

During the juvenile period of 30 to 55 days of age rats were found more frequently (0.65) within 20 feet of the place of birth than at any later age. There is one peculiarity of dispersal at this age that requires further comment. It will be noted in table 39B that these young rats occurred more frequently at a distance of 50 feet from their place of birth than at 30 feet. An examination of the individual records indicated that the major reason for this increase at the 50-foot distance (i.e., 49–59 feet) was the habit of the young of this age of changing their place of harborage to that which was the same or close to that occupied by their mother. Thus, when she exhibited a change in place of residence, her young at this age tended to make a similar change. This was discussed in more detail in the section on "mother and young interrelationships" (pp. 144 to 148).

Through the next two periods of subadult life, 56–85 days and 86–115 days, there was a marked alteration of the dispersal pattern such that an increasing proportion of the records occurred at

TABLE 39B.—*Dispersal of rats with reference to their age*

Age in days	Sex	Total captures	Proportion of total captures with respect to distance across barriers from the place of birth to the point of later capture.				
			10 ft.	30 ft.	50 ft.	70 ft.	80 ft.
30–55 (juvenile)...	M + F*........	138	0.645	0.116	0.145	0.087	0.007
56–85	M + F*........	208	.510	.250	.144	.091	.005
86–115 (adolescent)..	M + F*........	197	.411	.279	.213	.081	.015
Total subadult.	M............	345	.496	.226	.183	.084	.012
	F............	198	.530	.227	.146	.091	.005
Over 116 (adult)	M............	262	.076	.405	.271	.214	.034
	F............	185	.330	.314	.135	.086	.000
Total	M............	607	.315	.303	.221	.140	.021
	F............	358	.464	.288	.151	.095	.003

*Males and females showed such similar results within each of the subadult age groups that they warranted grouping together.

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more distant points from the place of birth. Through these subadult periods both sexes exhibited similar patterns of dispersal. However, there developed a marked sexual difference in dispersal as adults. Adult females exhibited no increase in dispersal from the time of maturing sexuality (85–115 days). Adult males, on the other hand, exhibited a marked shift away from their place of birth. The character and causation of this latter shift by males will become more apparent in the discussion of "male dominance" (pp. 198 to 202).

Four choices of dispersal were open to the maturing rat: (1) It might remain about its place of birth; (2) It might invade an area inhabited by adults whose social rank was higher than that of the adults near its place of birth. Such dispersal, which required development of subordinate status, was rarely observed. (3) It might invade an area inhabited by adults who had subordinate status with reference to the adults about its own place of birth. Such a situation favored the development of favorable social status by the invading rat in its new home. This was a regular phenomenon involved in the invasion of the northwest half of the pen by rats born in the southeast half. (4) It might invade an uninhabited area.

Thus, dispersal from region of birth is a function of inability of certain individuals to compete successfully with their associates. Furthermore, dispersal occurs in those directions which result in either a reduced frequency of social contacts or in which the invading rat is more likely to dominate resident ones.

C. *Intercolony Affiliations.* As discussed in the previous section on home range, each individual tends to remain near the place of its birth. Here it becomes a member of a local colony formed by its mother, its sibs, and a few other adults along with their progeny. Later some individuals may be forced to emigrate, and a few others emigrate by choice in seeking more favorable localities for living (see discussion of female 44 and her sibs pp. 173 and 199 to 200). Although such shift from the place of birth do occur, as do shifts during later life, they are still of infrequent occurrence. For the most part each individual belongs to a local colony whose membership is stable over periods of weeks or months. This stability of aggregations particularly applies to the period of rest within the place of harborage.

At some times and places intermingling between members of different colonies occurs. This intermingling occurs particularly where there is some common goal to which they are attracted. In the pen, the single central Food Pen formed such a place of frequent associations. Yet, despite their membership in different colonies, there was much less antagonism expressed among them, so long as the supply of food and water was available, than there was when rats from one colony approached the place of harborage of another colony.

Each local colony habitually developed a single route of travel to the Food Pen which was used more than alternate routes. Finally these routes were such that there would be the least opportunity of encountering members of other colonies. An example of this is shown in figure 118. On April 3, 1948, a 3-foot wide strip was hoed bare of vegetation around the outside of the Food Pen, from the corners of the Food Pen to the passages through the median barrier fence opposite to each corner, and for a 10-foot strip from each of these passages to the outside limiting fence (fig. 3). Over this hoed earth trails were reestablished. The relative intensity of their usage was determined by such criteria as the amount of compaction of the earth, and the amount of feces and urine deposited along them.

From time to time the pattern of the most used routes changed as a consequence of changes in the location and membership of local colonies. There was, however, an overall symmetry to these routes with respect to the rats inhabiting the corner areas. Area I rats most frequently used Passage 1; Area II rats, Passage 2; Area III rats, Passage 3; and Area IV rats, Passage 4 (fig. 118). In each area the harborage boxes nearest this most used passage were more frequently used than were those nearer the lesser used passage at the opposite corner of the area (see table 18 and fig. 74). This pattern of movement reduced to a minimum the number of contacts between rats inhabiting different areas, while on their way to and from the Food Pen (see discussion on pp. 83 to 85).

On the positive side, affiliations between colonies were enhanced by the tendency of a few adult females to visit their place of birth. The most striking instance of this was for female 28. She was born at the South Alley Burrow during August 1947, but during the following winter settled in the adjoining Area I, where she was the dominant female. During the spring and summer of 1948
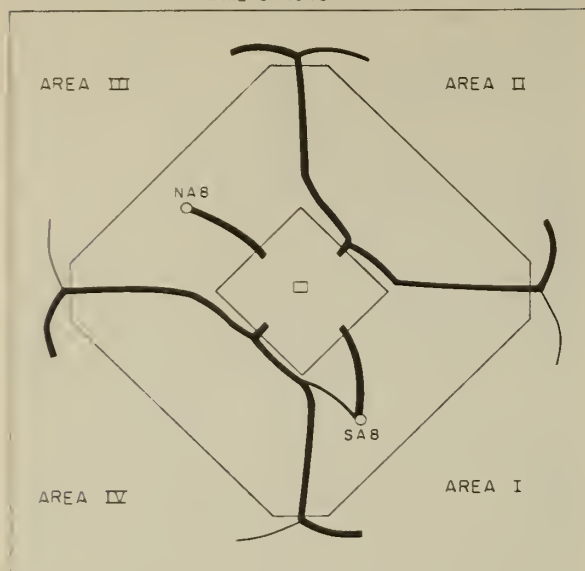
Figure 118.—Most used routes of travel to the Food Pen on April 8, 1948. Thickness of lines is roughly proportional to the intensity of usage of each route. At this time there were six aggregates of rats. There was one in each of the areas, and one each in the large burrows in the North and South Alleys. Note that the routes of travel from the areas were such that there was a reduced opportunity of rats from the aggregate in one area contacting those from another in passing through the passages of the median barrier fence. Those rats living in the alleys selected the shortest route to and from the Food Pen. These alley inhabiting rats were at that time of higher social rank than their nearest neighbors in the areas. Near the Food Pen these area inhabiting rats diverged away from the higher ranking alley rats, and entered the Food Pen by passages which reduced the probability of their contacting these alley inhabiting rats.

she frequently utilized the South Alley Burrow as a way station, while on her way between Area I and the Food Pen. Occasionally her sisters, who had young at the South Alley Burrow, would chase her away. However, for the most part their relations were amicable. Between 35 and 65 days of age female 28's young of litter 14 spent as much time residing at the South Alley Burrow as they did closer home in Area I. Visitations by adults to neighboring colonies was less frequently observed during the breeding season for rats living elsewhere in the pen.

However, during the winter, when sexual activity was inhibited, there was a more marked intermingling of members of local colonies. This took two forms: (a) There was a reduced constancy of membership in local colonies. That is any particular rat would shift its place of residence between several of the places of harborage available to it within the region of the pen it was then inhabiting. Thus, there was a moderate amount of flux of the composition of a group harboring at a particular place. (b) There was a marked attraction between members of different local colonies. The following record typifies this situation:

1. January 23, 1948; snow on ground; observations were begun before any rats were active above ground.

 First exchange: 5:48 p.m. A rat, which resided in Area III or in the burrow opposite Box 14, came through Passage 3, and ran over the runway through the North Alley to the North Alley Burrow, which it entered.

 Second exchange: 6:07 p.m. A rat left the South Alley Burrow and proceeded through the Food Pen without stopping, and went to and entered the North Alley Burrow.

 Third, 4th and 5th exchanges: 6:08, 6:13, and 6:20 p.m. Three rats as for first exchange.

 Sixth and 7th exchanges: Just before 6:25 p.m. Two rats as for second exchange.

Similar behavior was observed on a number of occasions during the winter of 1948–49. Thus, the North Alley Burrow served as a way station or assembly point for rats during the period just preceding the first intensive period of feeding in the Food Pen. This temporary association included members of colonies of both lower and higher social rank than that of the North Alley Burrow itself. Whatever the cause of this intermingling at the North Alley Burrow, such a situation certainly contributed to the disorganization of the social structure of the North Alley Burrow, so apparent by the spring of 1949.

D. *The Function of Group Structure in Altering the Frequency of Contact Between Rats.* A number of observations lead to the belief that adult rats assemble in groups, and that these maintained their identity through as much as several months time despite shifts in place of harborage. Such assemblies have been designated as "ingroups". If such ingroups have any reality other than that which may be produced occasionally, even in a population whose members are moving at random, it might be anticipated that the members of the ingroup have more contacts with other members of the same ingroup than would have been the case had there been no ingroup organization.

In order to investigate in more detail the nature of the contacts of members of the population with members of ingroups, it was decided to examine a few groups of rats, with respect to which there was particular reason to believe that they each formed a real ingroup. These four groups were as follows:

Group 1: East Alley Ladder Association of males. On March 4, 1949, six males, Nos. 54, 56, 657, 662, 669, and 873 were captured under the paint-bucket stand of a small stepladder, which had been laid on the ground in the East Alley during the previous January. This was certainly a low-ranking group of males (see p. 214 and tables 55 and 57). This harborage site was continuously used until the study was terminated in May 1949. On April 25 three marked rats, males 57, 873, and 662 were noted using this harborage. On May 17, 1949, males 56, 83, 662, 868, and 873 were captured at this location. Thus nine of the rats, which later analysis (table 39C) showed to be members of this ingroup, were actually observed using this particular harborage. However, the analysis of the group stemmed directly from the initial six members.

Group 2: Rats associated with female 44 on January 6, 1949. On this date females 44, 62, 58, 48, 922, and males 29, 49, and 670 were caught in Harborage Box 12. Each of these rats was at least 6 months old. Four, 48, 49, 670, and 922 were young of female 44, and one, 29, was her sib. Following my disturbance of them, four shifted to a new and very unusual harborage location. These four rats, numbers 44, 48, 29, and 670, built a nest in the recorder shelter at one of the four entrances into the Food Pen. Until I disturbed them 2 days later, they maintained a clean nest here which indicated that they had prevented other rats from utilizing this passage into the Food Pen. The entire eight rats were utilized as the presumed ingroup.

Group 3: The five females living in the burrow adjoining harborage box 25 on February 17, 1949. The nine rats living here on this date were: males 742, 909, 918, and 87, and females 37, 915, 71, 75, and 352. Four of these five females were still here in May 1949 (see table 48). Only the five females in this group were utilized as the members of an ingroup, with which the paired associations of the population were analyzed. This was done to keep the members of the ingroup as near six as possible.

Group 4: The six lactating females taken from the central (SW) portion of the South Alley Burrow on May 17, 1949 (see fig 21). All of these six females were born in this burrow in the spring and summer of 1948. During 1949 they formed part of the harem of 13 females associated with the most dominant male, No. 49.

These four groups were assumed to be representative of the organization of the population. In order to assess the reality and function of group organization it is necessary to know how this contrasts with a population whose members move about at random, and assemble in groups purely by chance. An approximation of this situation was made by selecting at random six rats and designating them as a "random group." Four such groups were selected.

A tabulation was prepared of the number of paired associations which each member of the population had with each member of these groups. The capturing of two rats on the same date at the same place was defined as a paired association. Contacts between rats were assumed to be proportional to such paired associations. For example, a rat might have three paired associations with one member of a group, two with another, one with a third, and none with the other three. This rat was then said to have six contacts with the group. In these tabulations, the population was limited to the 155 rats who were born in the pen and who lived over 150 days. Contacts were only counted when the youngest rat of the pair was over 60 days of age. Results are shown in figure 119. These curves are for the average of the four random groups and for the average of the four ingroups. The curves for the separate groups closely approximated that for the respective averages.

Even with groups of random membership, some rats had more contacts with the members than did others. There is an approximate exponential decline in the number of rats which have fewer and fewer contacts with the groups of random membership. Organized groups show a similar relationship of frequency of contacts with the members of the population, who are not members of their ingroup. However, members of the ingroup exhibit a marked increase in the number of contacts they have with each other. Even here there is an approximate exponential decrease in the number of rats which have fewer and fewer contacts or paired associations with the other members of the ingroup. Because of the difference in the rate of decline of the exponential curves of association by the ingroup with itself in contrast to that with other
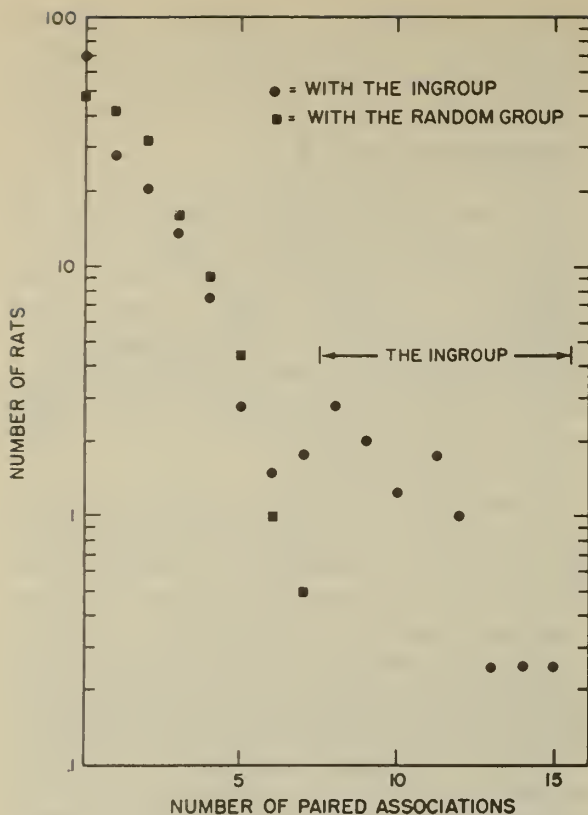
Figure 119.—Average pattern of frequency of association by all individuals in the population with members of ingroups and randomly composed groups. Each set of points is the average of four groups of six rats each. No individual rat had more than seven recorded paired associations with the members of a random group. All rats with more than seven paired associations with the six selected members of an ingroup are apparently members of that ingroup. By this method of analysis rats form ingroups of from 10 to 15 individuals.

members of the population, it is possible to approximate the real size of the ingroup. On the basis of the figured average results, the size of the ingroups must have been between 10 and 15 rats, although only 5 to 8 members of the ingroup were selected for the purpose of the tabulation.

Seven was the greatest number of associations any of the 155 rats had with a random group. Therefore, any rat having over seven paired associations with one of the four suspected ingroups was assigned as a member of it. On this basis the addition of new members was: eight for the East Alley Ladder ingroup; four for the Female 44 Lead ingroup; four for the Box 25 Burrow ingroup; and three for the South Alley Burrow ingroup. This latter group lost one member. Thus the total sizes of the ingroups were 14, 12, 10 and 8.

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Figure 119 permits a generalization regarding the structure of the ingroup. It is logical to equate affinity to the group with the number of associations a rat has with its members. Thus, there is a single rat with greatest affinity and an increasing number with lesser and lesser affinity. No sharp demarcation can be made between marginal members of the group and nonmembers, who by chance have an increased number of contacts with the members of the group. The rat with the greatest affinity to the group may be considered a leader, primarily in the sense that by its more frequent membership, it has a greatest opportunity to exert an influence upon the other members of the group.

TABLE 39C.—*Number of paired associations with the East Alley Ladder ingroup* [1]

Rat number	Sex	Paired associations of successive analyses			
		A	B	C	Total
54......	M	8	6	5	19
56......	M	12	11	11	34
59......	M	9	11	15	35
57......	M	7	9	7	23
60......	F	*11*	*14*	16	41
83......	M	6	8	6	20
99......	M	8	*21*	15	44
657......	M	10	12	9	31
659......	F	8	10	12	30
662......	M	*11*	*15*	17	43
669......	M	12	*13*	10	35
749......	F	7	*14*	11	32
868......	M	*11*	*12*	11	34
873......	M	10	10	6	26

[1] Italicized figures indicate the rats assigned as the ingroup for the purpose of successive analyses.

A more detailed analysis was prepared for one of the presumed ingroups, the East Alley Ladder Association (table 39C). The 14 rats with the most associations with these 6 rats are shown in Column A. Utilizing the six rats with the most associations as the central members of the group, another tabulation was prepared of the associations with them by the population. This process was repeated again, and the rats with the most associations are shown in Columns B and C. By this stepwise procedure, it was possible, to more accurately delineate the membership and size of the group. Two rats, Nos. 60 and 99, not noted in the original group, proved to have the greatest affinity to the group;

while two others, Nos. 54 and 873, who were original members, proved to have only marginal association. This analysis corroborates other lines of evidence, that group size among rats rarely exceeds 10 or 12 individuals.

The 10 rats with the greatest accumulated total of associations in Columns A to C were considered as the real members of this group, and a tabulation of the associations of the population with them was prepared. Forty-five rats were never observed to have any associations with these 10 rats; 100 had an average of 3.9 paired associations each; while the 10 members of the group had an average of 11.5 associations with the other members.

Organization of the population into relatively discrete groups increases the number of associations that the members of a group have with each other. It also increases the number of rats with whom the members of the group have no association.

E. *Contacts between Groups.* Rats do organize into fairly discrete groups with stability through time. However, any individual may transfer membership from one group to another, or it may simultaneously have varying degrees of association with, or affinity to, two or more groups. When any individual has contacts with members of two groups there exists the possibility of transfer of information between the two groups. Such individuals may be designated as potential messengers. Information is here broadly defined as any state or condition characterizing one or more rats. Disease organisms, or behavioral traits are such types of information, which appeared to be transferred from one individual to another. This raises the question: How does the organization of the population into ingroups alter the possible effectiveness of messengers?

In order to approximate an answer to this question, a further study was made of the four suspected ingroups, and the four groups whose members were selected at random. This study was of the number of contacts or paired associations which each member of the population (the 155 rats as designated on p. 173) had with two groups. A sample of such an analysis is shown in figure 120. Six such analysis were made for the four ingroups and six for the random groups. These analyses provided data on 930 contacts with 2 ingroups, and 930 with 2 random groups. These analyses are summarized in table 40.

Messengers may be classified into three categories on the basis of the number of contacts each has with two groups: 1. Few or no contacts with
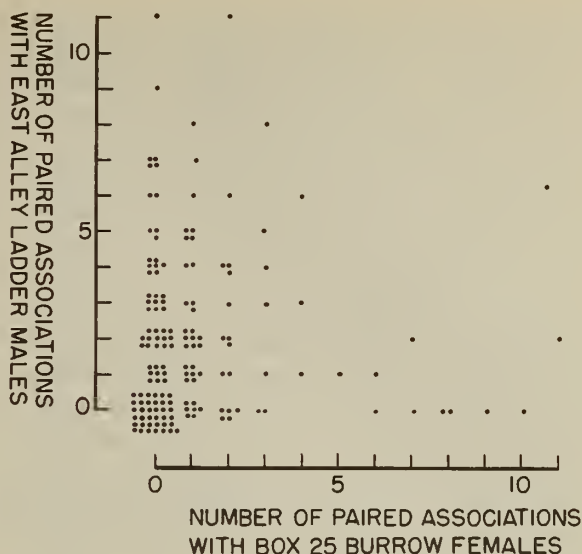
Figure 120.—The number of paired associations each of the 155 rats in the population had with members of two different ingroups. Each dot represents a rat.

TABLE 40.—*Proportion of population (155 rats) having contacts with 2 groups*

Frequency of contact	With two ingroups	With two random groups
Contact with neither or only 1 group....................	0.684	0.477
Moderate (1 to 5) contacts with each group.................	.263	.504
Many contacts (6 or more) with 1 group and moderate (1 or more) with the other.........	.053	.018

either group; 2. A moderate number of contacts with both groups; 3. Many contacts with one group and a moderate number with the other. Effectiveness as messengers should increase in the order listed. Organization of the population into ingroups increases the number of individuals who have little contact with either of two groups. In other words there is a decrease in the number of messengers. With regard to the latter two categories we will consider the effectiveness of rats as messengers. Effectiveness of transmission of a message should be dependent upon the frequency with which two rats make contact. This should be true whether we are considering

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disease organisms or learned behaviors as the bits of information. In either case one might anticipate a threshold for frequency of contacts necessary to insure transmission of a message. Below the effective threshold of contact frequency each contact represents noise as conceptualized by information theorists. Contacts by rats, who have only a moderate number with each of two groups, may be classified as noise. Since this category of rats is reduced by nearly half in a population organized into ingroups, such organization effectively reduces noise. Those rats with a moderate number of contacts with one group but many with another should be the most effective messengers. Although this category of rats remains a small proportion of the total, the organization of the population into ingroups produces a threefold increase of this category.

These interpretations of table 40 are patently quite hypothetical insofar as transmission of information is concerned. However, the logic of this analysis clearly shows that where a certain threshold of contacts does result in the transmission of information, advantages accrue to populations organized into ingroups because: (1) The amount of noise is reduced and, (2) the number of effective messengers is increased.

5. Sociality

A. *Social Rank and Social Stress.* Membership in an ingroup assures that the individual will most likely share in the advantages or disadvantages experienced by the other members of that group. Even the most cursory observations of local groups soon revealed much similarity among members as to physical characteristics, past history, behavioral traits, and types of experiences. Despite similarity within groups, marked differences existed between groups with regard to these variables. This stratification of groups indicated a class structure of the population. To understand what I imply by social classes requires an examination of my delineation of social rank of individuals, since social class is in essence the mean social rank of the component members. Social rank is considered as equivalent to the likelihood of a rat satisfying its drives. Its associates may facilitate or interfere with this satisfaction of drives. It is difficult to measure such satisfaction directly. Practically one must rely on observable characteristics or conditions which presumably reflect the degree to which rats satisfy their drives. Some of these criteria represent causes and others consequences of evolving social rank. When a rat experiences much difficulty from its associates in satisfying its drives it is considered as being in a high state of social stress. Thus social rank and social stress are negatively correlated abstractions. In this section and those that follow I shall attempt to define criteria for arriving at conclusions of social rank and stress, and will then document how these are exhibited by the rats. In these discussions it will be impossible to separate clearly cause and effect.

B. *Criteria for Judging Social Rank* include the following:

a. *Proximity to goals:* If a rat lives nearer to a goal than do some of its associates, it will be possible for it to reach that goal and make a satisfactory response, without so frequently encountering a rat which is not a member of its own local colony. The term goal is used in the sense of an object (this may be another rat) with respect to which a response may be made that satisfies some need felt by the organism. Assume that there are two individuals A and B, of which B lives farther away from a goal than does A, and also that B has to pass near A's place of residence en route to the goal. In this situation A can more easily detect whether there is another individual at the goal—even before it has left the immediate vicinity of its burrow. However, the critical point is that B must pass near A's place of residence. At this time any interaction between A and B will interfere with the time sequence of B's reaching the goal and satisfying a particular need. After repeated experience with such a situation one might anticipate that B would attempt to avoid A regardless of what the nature of their interaction had been. Once this avoidance behavior had been initiated it is easy to see how A might then attack B, and thus there is developed territorial defense in which the rat living farther from the goal is at a disadvantage. As the relationship between A and B is developing, it must be remembered that there is a greater probability that A will be satiated with respect to the reward arising from responding to the goal. This formulation offers the most logical explanation of the observed situation which existed in the pen with reference to the source of food and water as goals. The social system was soon structured so that rats living nearer the Food Pen, that is in the alleys, exhibited dominant behavior over rats

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inhabiting the more distant areas. Inexperienced young rats inhabiting the areas were at a particular disadvantage when they had to pass near the place of residence of adults in the alleys, who had already developed a dominant status. Rats living farther from a goal were also forced to expend more effort in satisfying their needs. This greater demand on the individual's physiology presumably places it at a disadvantage.

b. *Size and age:* Larger and older individuals regularly win when open conflicts develop between two rats. Furthermore, the smaller individuals, regardless of age differentials, most frequently exhibit avoidance of other rats.

c. *Social genealogy:* Rats born in colonies, whose adult members more frequently exhibit submissive behavior to members of other colonies, in later life also tend to exhibit submissive behavior. Thus, even in the absence of observed status-revealing interactions, the origin of a rat is taken as a criterion of social rank.

d. *Place of residence and associates:* Rats frequently depart from their place of residence and take up residence elsewhere. The past history of the inhabitants of the area in which they become established serves as a criterion of social rank. This is a particularly good criterion with respect to whether the invading rats displace the residents or are amalgamated into the resident group. In any case an invading rat develops new associations, which may include those with rats which have arrived from several places of birth. The more unfavorable are the places of origin represented by the members of a group, the lower is its assigned social rank. Furthermore, the more places of origin that are represented by the members of a group, the lower is the assigned social rank. See the discussion of the homogeneity index (p. 214). It was certainly apparent that when there were several places of origin represented in a group its members were less successful in satisfying their needs.

e. *Competition during early life and rate of growth:* Young rats which are exposed to contacts with other young and adults have their growth rate inhibited in proportion to the frequency of contacts with their associates. Growth rate is particularly inhibited if these associations are with older unweaned sibs of a prior litter who are not yet weaned, or if the associations occur between the time of weaning at about 35 days and attainment of sexual maturity between 85 and 100 days—that

is during the postweaning juvenile period. This latter also is the period when "psychological drubbings" of juveniles by adults occurs. Thus, the relative frequency and type of associations is taken as an indication of later social rank, particularly with reference to the degree of inhibition of growth.

f. *Observed outcome of combat:* Adult males, particularly those born in colonies under favorable conditions, fought for the right to remain at the place of birth, or at some other place which was still favorable in relation to other existing locations. It is patent that few of these adult males could attain the dominant status. Thus, despite their large size and potential ability to win over smaller males inhabiting less favorable localities, many of these males eventually were forced to reside with smaller males, which were characterized by less favorable early history. Despite their larger size and more favorable early history, these males which were excluded from the more favorable places of residence, never seemed to be able to develop a clear-cut dominant status over their smaller associates. It was because of this sequence of events that size alone is not a valid criterion of social rank. These events apply similarly, but less frequently to females.

g. *Sex ratio of the colony:* The fewer males there are in a colony in proportion to females, the greater is the likelihood that (a) the individuals will on the average be larger, (b) the reproductive success will be better, (c) the individuals will have had a more favorable earlier history, and (d) in the case of combat with members of other colonies the members of such colonies will win. In some cases the past history of a group, which now has a favorable sex ratio, will have lead to its higher social rank, even though it lives farther from the food source For example, refer to the discussion of. colony c in Area III in comparison with colonies g, j, and k in the North and East Alleys as they existed in the spring of 1949 (pp. 206 to 213). This is a case where the criterion of proximity to the food source is overridden by other conditions in the past history of the groups.

h. *Reproductive success:* The conception rate and the ability of females to rear young to weaning both reflect social rank. However, this may be judged only by the average performance of the females in a colony. When the average performance is high, this is taken as a criterion for all the rats in the colony, both males and females.

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I do not believe it is possible to completely separate cause and effect for most of these criteria for judging social rank. For example, an animal may have a slow growth rate and a low adult weight as a result of intense competition from other juveniles or from frequently receiving psychological drubbings from adults while it was a juvenile, then because of its small size as an adult it will more frequently lose in combats and thus exhibit a low priority of action with reference to reaching and satisfactorily responding with goals. In other words, as a result of developing low social rank, a rat grows slowly, and then, because it is small, as an adult it is unable to develop higher social rank. Likewise, a rat may develop low social rank because it lives far from the food source, and because it has developed low social rank it is unable to shift its place of residence to a more favorable situation nearer the source of food. The social structure of a society of rats develops through the interaction of several variables such that cause and effect of rank within the structure are inextricably interwoven. Furthermore, the relative effect of any one variable changes with time. When these circumstances are recognized, it is possible to take the facts at hand and assign relative social rank for any particular time in the history of the population.

C. *Culture.* Through time the physical structure of the environment is modified by the rats which inhabit it. Much of this modification, such as the pattern of trails or the presence and position of burrows, alters the way of life of later generations. Through time the social structure of the population changes. These changes modify the social structure of later generations, and in a general way predetermines the fate of particular individuals.

The characteristics which describe the rats' society at any particular time can largely be described in quantitative terms, or in terms of rates of change. They include: (1) growth of trailway communications systems (pp. 54 to 63); (2) growth and disintegration of burrow (pp. 15 to 54); (3) denuding of vegetation; (4) density of the population (pp. 244 to 246); (5) individual rates of growth (pp. 216 to 236); (6) mortality (pp. 237 to 244); (7) reproduction (pp. 214 to 216); (8) migration (pp. 170 to 171, 214); (9) group structure (i.e.: sex ratio (tables 56 and 57); places of birth (pp. 196 to 198); dominance of members in combative situations (pp. 179 to 195) etc.). One may designate these character-

istics at any time as representing the state of the culture of the group.

This raises the question of levels of these states with reference to desirable or undesirable states of the culture. Two criteria may be taken for judging the level of culture. In the direction of higher levels these criteria are: 1. The characteristics pertaining to the group or its component members should enable them to compete more effectively when they come in contact with members of other groups. 2. The cultural state should permit the most efficient utilization of available energy supplies compatible with maintaining a stable population density. Thus, I consider the levels of culture existing through time as having much of the same type of variation as does social class among the local colonies of a population during a particular time of its history. Social class and cultural level refers to the standard of living; that is to the ease of satisfying the needs felt by the individual. Thus, the average individual in a group having high social class or the average individual of a population having a high level of culture, will, in either case, have a high standard of living.

One can judge social rank and cultural level, as I have defined them by two specific conditions: 1. Growth rate of the individual with respect to the attainment of its genetically determined maximum weight or size. 2. Reproductive success. By this latter I mean that conceptions attempted will be effected, and that the progeny conceived will be born and reared to weaning.

All other characteristics by which social rank or cultural level may be assigned should be either causative or dependent variables to these two or should arise from the same set of independent variables. By so phrasing sociality and culture, these manifestations of life may be treated from a comparative biological viewpoint.

Reproductive success was defined in the above-limited sense, since it is quite obvious that the reproductive potential of any species in the absence of limiting factors will permit the population to increase in numbers beyond the available energy supplies to support them. A very rapid rate of increase in density may indicate relatively high social class for the groups composing the population, but this criterion cannot be used to indicate a high cultural level, unless the system embodies some method whereby density will be checked at a level compatible with available energy sources, without reducing the individual growth rate.

D. *The Role of Aggressive Behavior in Social Organization.* Social organization among rats has its primary expression in the close association of several individuals in the same burrow or in a group of neighboring burrows. All types of interactions between individuals which foster the formation or maintenance of such a group comprise facets of the social organization. These include (1) maternal care, (2) contacts among juveniles living in the same locality, (3) assembly in winter for the purpose of conserving body heat, and (4) aggressive behavior which maintains exclusion of nonmembers. A number of other conditions facilitate the molding of the population into local groups. They include (1) attachment to place of birth, (2) similarity of past history, (3) presence of barriers to locomotion, and (4) attraction to a common goal.

The members of a group frequently engaged in similar activities at about the same time and place, but there was no evidence of rats engaging in cooperative behavior of the kind requiring joint effort to accomplish a task incapable of attainment by a single rat just taking a longer time. Even so, aggressive behavior, whether actual or threatened, frequently lead to the formation of more closely knit groups. The following description of aggressive behaviors, and the conditions under which they were expressed, will delineate the role of aggressive behavior in social organization.

a. *Nose-touching.* The behavior of nose-touching, of itself, is not an aggressive behavior. It merely involves two individuals approaching to the point that the tips of their noses actually or apparently come in contact. This is an act of recognition which is by far the most common interaction. It becomes an aggressive interaction to the extent that one of the participants interprets the recognition as portending a threat. Most frequently each rat proceeds with its prior course of action following the nose-touching. Occasionally some positive interaction such as sexual behavior develops. On the other hand one of the members may immediately and rapidly flee even though the other member of the pair does not pursue it. This reaction has been interpreted as indicating a more subordinate status for the rat which flees. More infrequently both individuals run in opposite directions following nose-touching.

b. *Avoidance behavior.* By avoidance behavior is meant the change in the route toward a goal or the departure from a goal upon perceiving another rat.

The term avoidance behavior will also be used to include similar actions by one rat in the absence of any other rat but at a place where frequent interactions with other rats have previously occurred.

There are two circumstances, at least one of which always operates, in the avoidance of one rat by another. The first of these is that there shall have been a marked difference is social rank previously established. When such a differential exists the subordinate rat runs aside or away from its dominate associate, whenever and wherever they encounter. Even when the subordinate rat detects its dominate associate, when the latter is not aware of the former's presence, the subordinate rat will turn and run away. This raises the question: Can one rat detect the identity of another at a distance? The only sure statement that can be made is that a subordinate rat can recognize the social rank of another at distances of 10 to 20 feet during the dawn and dusk hours. The avoidance may occur whether the dominant rat is facing toward or away from the subordinate one. Even though it may be true that there is no recognition of individual rats as individuals, there are actions or postures characteristic of extremes of social rank that identify them as such.

The major aspects of these socially differentiating behaviors will be mentioned here. The dominant rat more frequently stops at those intersections of paths or passages through fences where they are likely to be perceived or encountered by other rats. Here they groom or pace back and forth. In contrast to this the stopping of more subordinate rats at such points is one of momentary hesitation, while they look and listen before proceeding on in a hurried fashion. There is also the wheeling around by the dominant rat to face the approaching subordinate rat, but in so turning it does not give ground. Upon a continued approach by the subordinate rat the dominant one then begins a deliberate prance toward it. This prance is one of body raised by extending the limbs, while at the same time raising high the forepaws during the forward steps. If the subordinate rat flees soon enough, the dominant one may not give chase. When the dominant rat, which has been detected by the subordinate one, is located along the route between the goal which the subordinate has left and the one toward which it is proceeding, there is elicited a peculiar vacillating movement characterized by an alternation of approaches toward and withdrawal from the dominant rat. This may also take the form of movements back and forth in an

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arc in front of the dominant rat. These gross behavioral differences must make it rather easy for one rat to detect the rank of another.

The second circumstance eliciting avoidance behavior is the rapid approach of one rat toward another. This situation is one in which one rat, which is eating, or drinking, or is engaged in some other stationary activity, is approached from the rear or from one side by another rat in rapid motion. The rat which is being approached frequently dashes away for at least a short distance, regardless of whether it is lower or higher in rank in comparison with the approaching rat. This holds true for all but the very highest ranking rats. The critical point to note here is that the rat which does the avoiding does not have the opportunity to make any discrimination regarding either the individuality or rank of the approaching rat. By running to one side it gains the opportunity to examine the situation and decide whether to return or continue in fleeing.

The avoidance behavior of the first type discussed above appears to become elaborated to the extent that the presence of the dominant rat is not required. After a rat has experienced many threats, chases, or losses in combat at a particular place the same vacillating, and hesitant approach and withdrawal is elicited even in the absence of any other rat. This sort of behavior with reference to entering the Food Pen, as well as that of carrying food from the hopper over into a corner of the Food Pen to eat, probably have their origin in the avoidance of a dominant by a subordinate rat. Each of these behaviors comprise aspects of the syndrome of the social outcast (pp. 195 to 196). Male 8 exhibited these behaviors in 1947 as a result of his experience with the then dominant male 12. The latter in 1948 after having become subordinate to some of the younger, more vigorous adult males also exhibited it.

c. *The combat.* Juvenile rats at least up until the initiation of sexual maturity, 85–115 days of age, engage in what may be termed "mock-combat." They exhibit nearly the full repertoire of actions including preliminary periods of boxing in which, while standing on their hind legs and bracing themselves with their tails, they knock at each other with their forefeet. This is frequently followed by a brief episode of rolling and tumbling over each other in which the participants apparently hold on to each other, although this apparent holding may simply be the act of one rat closely

following the escape movements of the other. The reason that such encounters are thought to represent "mock-combat" or play is that terminating the action each goes about its own activities without any show of aggression or avoidance. In fact they may even sit near each other and groom. Furthermore, although two juveniles who have been caught in the same trap together may fight viciously upon the observer's approach, there is rarely any evidence that wounds are received in such encounters. Thus, there may be both lack of ability as well as lack of intent to injure among young rats. The low prevalence of wounds among young rats is shown in figure 122.

This "mock-combat" behavior gradually is transformed into real combat through the interaction with older rats. A typical case is as follows: On July 6, 1947, 370-gram, 320-day-old, dominant male 12 was seen at the North Alley Burrow boxing with 293-gram, 81-day-old male 21. At first, they stood up facing each other while boxing without moving out of their tracks. Finally male 12 forced male 21 over on his back and the boxing continued such that male 21 kept pushing away male 12 who was leaning over. Male 21 was held on his back for 15 seconds. Finally, one of the rats must have taken a bite at the other for there was a squeal followed by 21 running away, while 12 remained and groomed for several minutes. Although male 21 may have experienced some punitive action in this encounter, the mild character of the combat may be judged by comparing it with the following account of a combat between two adult males.

A frame-by-frame examination of the filmed sequences of combat taken by the U.S. Army Signal Corps at the Towson plot enabled a very accurate description of the sequence of events occurring in combat. The following is the best such account available. The action occurred at the North Alley Burrow, during April 1949 in the presence of an estrous female: The scene begins with two adult males peering down into a burrow entrance through which an estrous female had just escaped their advances. The rat on the right just slightly throws his hip at the left male, which at first moves slightly away and then several feet away. Although the remaining male examines the entrance intently he does not engage in any sexual rolling. All of a sudden this male jumps up in the air, apparently as a result of being nipped by the estrous female, whose head can be seen for two frames while the male is in the air. At this time the other

male reapproaches the hole. He is very close by the time the nipped male lands on the ground. They extend their necks and bodies until their noses are about an inch apart (their vibrissae seem to touch). Then the male with apparent priority again sticks his head down the entrance, while the other male gradually approaches and does likewise. Upon this crowding the dominant male swings his head toward the other male, who begins to rear up on its hind legs, while he uses his right forefoot to fend off the dominant male. Then both rear nearly straight up. The right forefoot of the left rat (the submissive one) fends off the left forefoot of the right rat (the dominant one). Their heads then approach until their teeth appear to be in contact (this lasts for not quite two frames). The power exerted by the hindlegs seem to be critical at this point. The greater force exerted by the dominant rat throws the other rat over. As the submissive rat lands partially on its forefeet and partially on its side, the dominant rat appears to be biting it on the midback. Whereupon the submissive rat whirls his head back to the right at the head of the dominant rat, but the dominant rat pushes him flat on his back with his forefeet, and then strikes at the submissive rat's genital region with his teeth. At this point the submissive rat begins to roll over and the dominant rat continues his biting on the posterior sacral area. The submissive rat completes his roll, breaks, and runs away. The total elapsed time of this action, from the dominant rat swinging his head toward the submissive one to the breaking away of the latter, was 1.5 seconds. This shows the value of moving pictures in describing and interpreting behavior. The dominant male then turned back to the burrow entrance from which the estrous female was beginning to extend her head. The scene closed with the dominant male just initiating a true sexual roll.

Observation without the aid of the camera supports the belief that this account is exceedingly typical. There is nearly always an initial threat. This threat may include any one or all of the following:

1. Whirling of the head and/or body toward the other rat;
2. The prancing approach toward the other rat; or
3. Sidewise motion toward the other rat, against whom a hip is thrown.

These threats are followed by a momentary or prolonged (in terms of seconds) period of boxing.

Although contact, or impending contact, may be broken off at any point with the more submissive rat running away, the interaction is frequently terminated by the rolling over of the two rats while still in contact, the emission of a squeal, and the fleeing of one of the rats. It is at this breaking away period, when the posterior region of the submissive rat is exposed to the dominant one, that most wounds must be received. Most of the several hundreds of records actually state that the wounds were on the lumbar-sacral region. In fact it was the V-shaped area from the mid-back posteriorly over the sacrum and hips which in many mature males was characterized by much scar tissue. Fewer wounds occurred over the shoulders, and there was only an occasional wound about the head. Wounds on any portion of the ventral aspect of the head, body, or legs were extremely rare.

d. *The Chase.* One rat giving chase to another may precede combat. When the chase terminates in a combat, all the preliminaries such as boxing, or hip throwing fail to occur. Instead, as soon as the pursuer catches up with the pursued there is a brief tumbling fight following which the loser flees. Chases may also follow a combat. In such chases, as well as in chases involving no fights, it frequently happened that the rat being pursued made successful its escape. It often happened that the pursued was younger and more agile. This enabled it to out-maneuver and out-distance the pursuer. The most frequent type of place where chases broke off was at the passages between the alley and areas. There were two main reasons why the breaks developed at these points.

Because of its initial head-start, or because of its greater speed the pursued rat would reach and pass through the passage from the alley toward the areas before the pursuer arrived. Here it was forced to turn left or right into one of the adjoining areas. The pursuer could detect this change in direction through the fence and would reorient its route of travel correspondingly. This reorientation would deflect the line of travel of the pursuer away from the passage with the result that the chase usually terminated after the two ran parallel for a short distance on opposite sides of the fence. Such an example is shown in figure 121.

A second factor influencing the termination of a chase at these passages was that they served as a sexual signpost. The pursuer frequently ceased
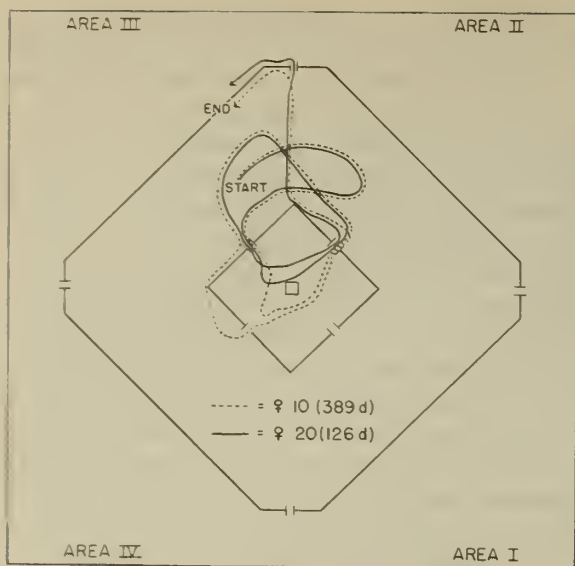
Figure 121.—Routes followed during one of three similar chases of female 20 by female 10 on October 3, 1947. Chases frequently terminated as did this one with the subordinate rat escaping into an area, with the dominant rat paralleling it, but traveling along the alley side of the median barrier fence.

chasing as soon as it reached or had just passed through the passage. In many such instances the pursuer would then engage in sexual rubs against the passage or pawings of the earth about it. This might happen whether or not the inception of the chase appeared to have any relevance to sexual behavior. Similar sexual behavior also frequently followed other types of aggression not characterized by chases. The association of these behaviors suggests that aggression increases erotic responses.

Chases which terminated at passages through the fences usually were initiated in the Food Pen or in the alleys and proceeded outward toward the areas. Less frequently rats in the areas chased other rats from one area into another or from an area into the alleys. Whereas most chases from areas appeared to have territorial implications, it was quite clear that as often as not, the outward chases from the alleys were merely expressions of dominance relationships. It might be added that, although chases might occur from the Food Pen or from the alleys through the Food Pen, they rarely terminated at the passages through the fence surrounding the Food Pen. Correlated with this was the fact that the territorial behavior of passage guarding (p. 187) rarely occurred at these Food

Pen passages. It may be seen from these comments that chases were a potent factor in dividing the population into the more favored alley inhabiting rats versus the less favored area inhabiting rats.

Certain conditions may now be listed which influence the occurrence of aggression in the form of chases.

1. Territorial defense.
2. The nonreceptivity of females. In the latter stages of estrous females were still attractive to males, but repelled their advances.
3. Lactation. Lactating females were particularly aggressive in defending the vicinity of their burrow against alien rats. Such aggression toward males was also expressed in the Food Pen to a lesser extent, but it is interesting that remarkably little aggression of any sort was exhibited between lactating females in the Food Pen, even though they inhabited different localities.
4. Antagonism of adults toward subadults ranging between 80 to 115 days, which were just becoming sexually mature. This category was primarily confined to male-male relationships.
5. The act of moving away by one rat may elicit the pursuit of it by another rat. This is a counterpart of fleeing by a previously stationary rat upon its approach by another rat running toward it. Either the pursuing or the fleeing in these cases, initiated by another rat in motion, may be entirely dissociated from recognition of social rank by this responding rat. Frequently the rat which is pursued after it moves away from another rat initiates its retreat at such an angle from the approaching rat as to make visual recognition of the pursuer difficult. The pursuits which arise under these conditions are usually of short distance (2–5 feet). It is as if pursuit is a learned response triggered by the movement away by another rat, but that pursuit is shortly terminated when the actions of the rat moving away in some manner convey to the pursuer that this is not the fleeing of a socially low-ranking individual. The moving away (usually 2–5 feet) from a rapidly approaching rat has the functional significance of giving the rat which moves away an opportunity to turn and recognize the approaching rat. Both of these behaviors were most frequently observed in the Food Pen, although they were noted elsewhere.

6. Closely allied to the situations discussed above under 5 is that of extremely low-ranking rats in the social organization. They exhibited a marked tendency to elicit pursuits by other rats. During many periods of observation the only chases from the Food Pen were of such rats. Several rats of both sexes and representing widely separated local colonies would be amicably eating or drinking together. Immediately upon the approach of a low-ranking rat one of the members of the feeding or drinking aggregate would turn and give chase. Such chases of markedly low-ranking rats were always of much greater length (see fig. 121) than between individuals of more nearly equal status. The pursuer would then return to the Food Pen, and amicably join the group which it had just left. If the low-ranking rat soon returned, pursuit would again be initiated by the same or another rat. It was undoubtedly as a result of these chases that such low-ranking rats fed during the day when other rats were asleep, or fed during those portions of the night when other rats were temporarily resting. The approach of such a low-ranking rat is characteristic. It moves forward hesitantly with neck and tail outstretched, and presents the appearance of crouching with the forelegs. The approaches were frequently punctuated with slightly sideways retreats. These behaviors announce in no uncertain terms that such an individual may be chased with impunity. Whereas chases of very low-ranking rats were most pronounced from the Food Pen, adult females who were lactating or who had established territorial rights in some locality, were particularly avid in chasing such individuals away from their territory.

7. See the following section "The relationship of estrous females to the frequency of fighting and chases."

e. *The relationship of estrous females to the frequency of fighting and chases.* When a female is in estrous, males are attracted not only to her but to those places where she leaves her scent. This attraction produced localized increases of contact rate between males. However, the increased aggression among males is not so much attributable to the increased contact rates as such, but rather derives from competition over priority of engaging in sexual activity.

Extensive observation made between October 6 and 8, 1948 (total of 19 hours and 40 minutes of observation) amply delimit the phenomena involved. During this time female 33 who lived at the South Alley Burrow was in estrous for at least 48 hours. The term estrous is here used in the sense of heightened attractiveness for males. During this entire period many males were seen to come and engage in sexual rolls at the entrances of the South Alley Burrow, at Passage 1, and at the passage into the Food Pen, at all of which places she had left her scent. Other courting behaviors were observed during this period, although sexual chases were only seen on the night of October 7 to 8. No mounts were observed. She apparently had just come into estrous on the afternoon of the 6th. On this date observations were made only between 3:20 and 6 p.m. Many rats entered or passed through the Food Pen. Most of them drank but very few paid any attention to the food. Nevertheless, there was an exceptionally large number of fights in or at the entrance to the activity recorders attached to the four passages into the Food Pen. These were places where females in estrous left their scent. When the general observation, that few fights occur at the food source, is coupled with the specific situation of lack of interest in food on this evening, it is probable that the antagonism did not arise over food. Although the initiation of fights in the activity recorders could only be heard and not seen it is presumed that they arose through competition over priority of action in engaging in sexual rubs against the walls of the recorder. Several fights or chases were observed to arise at the South Alley Burrow, when one male approached another who was engaged in sexual rolls at burrow entrances.

The males, which engaged in such fighting over estrous scent at the South Alley Burrow, were either a few of the males born in 1947, or some of the larger males born early in the spring of 1948 at the South Alley Burrow. Fights or chases between these same males subsequently occurred in the Food Pen. As a result of these interactions the aggressiveness of these males became heightened, and became directed toward other, and frequently much smaller males, who themselves were not involved in the sexual activity about the South Alley Burrow. These latter males were chased about or from the Food Pen, but apparently with no reference to direct competition over food.

That male aggression is heightened by the presence of estrous females is particularly well exemplified by male 22. He was the dominant male of

Area I during 1948, and there exhibited territorial defense. Although he was observed many hundreds of times in the Food Pen eating with other rats he was only noted to engage in fights or chases in the Food Pen on two dates, July 7 and October 7, 1948. On both of these dates female 33 was in estrous at the South Alley Burrow. This burrow lay along his most frequently traveled route between Area I and the Food Pen. He definitely dominated the South Alley Burrow at these times with reference to priority of action in engaging in courtship behavior. For this reason his territory of Area I might be considered as also extending over the South Alley Burrow. At least this dominance on his part may account for the fact that no other male developed a territory encompassing the South Alley Burrow during 1948. The range (fig. 109) of male 22 was normally restricted to Area I and the routes directly connecting it with the Food Pen. The only times he was observed roaming out of it as an adult was when he was attracted into Area III and IV by the presence of estrous females. On each of these three occasions he was noted to engage and win combats arising at scent "posts" left by the estrous females.

By the night of October 7 to 8, 1948, a general change in behavior of the rats had occurred. Even during the same hours on which observations were made on the previous day there was now a marked attraction of the rats toward the food and a nearly complete cessation of fighting in the activity recorders. The lack of fighting at these points is most probably attributable to the decline in attraction of estrous scent left at the passages into the Food Pen. By the second day of estrous the expanded range characteristic of females on the first day of estrous has not only been reduced; it is actively restricted to less than normal. This arises from the fact that she is essentially restricted to the vicinity of her home burrow by the persistent approaches of males who give her little opportunity to go to the Food Pen. On this night fighting again occurred among males about the South Alley Burrow. The males exhibiting this heightened aggression again transferred this aggression toward other males whom they chased from the Food Pen. However, the evidence again was that this aggression had only indirect relation to the procurement of food.

It might be added that aggression by females also appears to be increased at the time other females come into estrous. Females not in estrous are attracted to the places where estrous females

leave their scent. There they exhibit sexual rubs or rolls and give chase to males which encroach upon these activities. During such times the level of aggression of those females, who have had the opportunity to be stimulated by the estrous scent, becomes heightened to the point that aggressive actions, particularly against other females, occur in other places, such as in the vicinity of the Food Pen, where normally little interfemale aggression is expressed. The female who is in estrous exhibits heightened aggression at the terminal portion of the period when she is sexually attractive to males. At this time her receptivity toward males is extremely slight. She then actively repels their advances. She also may exhibit increased aggression toward other females at this time.

f. *Territoriality—expulsion of strangers from burrows or harborage boxes.* Occasionally rats, which were completely undisturbed by the observer, were noted to visit areas outside of their normal ranges and there enter places of harborage. The normal course of events was that the stranger would abruptly emerge squealing as if bitten by the resident rat, which normally emerged no farther than to protrude its head from the entrance. Occasionally such an invading rat would also be chased from the vicinity. A case in point is the following:

1. On April 29, 1949, at 4 p.m. male 669 was seen to enter Area I and enter Box 7. A fight could be heard inside (the observer had been standing quietly nearby). Male 669 emerged, followed by male 690, the dominant male of Area I, who chased him to Area IV. Male 669 was a member of the socially low-ranking aggregate (colony h, p. 212) inhabiting the central portion of Area IV during the spring of 1949.
2. Female 28, who was the dominant female of Area I; occasionally stopped in the South Alley Burrow on her way to and from the Food Pen. On May 18, 1948, she was seen to squeal and jump out of the SAB hole 8 as if she had been bitten on the rear. Presumably her ejection was by the lactating female 37 whose litter was located in this portion of the burrow.

These two records are typical of this expulsion. Although socially low-ranking rats were more frequently noted in such expulsions, it was quite apparent that regardless of the social rank of a rat about its own home, any invasion by it into the homes of rats in other localities was likely to result

in its expulsion. A much greater number of observations pertaining to expulsion following invasion of harborages was made at the time of marking and releasing rats. The reason for this was that following their capture rats normally avoided re-entering the harborage box from which they were removed, or from entering any place of harborage in the immediate proximity to the place where they were captured. This behavior frequently led the rats to enter harborages inhabited by rats with whom they normally did not have close associations. The events recorded in the following four examples are typical of a form of territorial defense which is certainly of equal importance to that exhibited by a few socially dominant individuals.

1. September 28, 1948. One-hundred eighty-eight-day-old female 75 escaped near Box 11 in Area II where I had been handling all rats captured that day. She was still slightly under the effects of anesthesia. She first went through two burrows along the northeast fence of Area II. Her departure from these two burrows was not observed to be associated with any antagonistic action toward her. From here she went up Path 3 to the Food Pen, from which she departed through Passage 5 and proceeded to the South Alley Burrow. Although this was the place of her birth she had not inhabited it since just before her first pregnancy 3 months earlier. She entered at the first hole she encountered and emerged 8 feet away being chased by an older female (one born in 1947) who trailed her to Passage 1. Female 75 was lost sight of as she headed through Area IV toward her home in the burrow opposite Box 28. This record is interesting from two viewpoints. In the first place, she was excluded from the place of her birth by an older female with whom she had close associations as a juvenile rat. In the second place she exhibited a retrogressive orientation when she arrived near the center of the Food Pen on her way home. Instead of departing through Passage 8 and going through the West Alley and Passage 4 to Area IV, as she had done for the past 3 months, she elected a route customarily utilized when she was a juvenile. This is one of the types of observation which has led me to believe that adults are more likely to exhibit juvenile behaviors when disturbed.

2. September 24, 1948. One-hundred forty-seven-day-old male 683 (born at the SAB) was released near the burrow at Box 29 where he was caught. He ran into Box 36 where a fight occurred. He was chased out by adult male 30. He then ran southeast along the fence. This male, who at this time had two large sores resulting from warble emergences, was destined by the spring of 1949 to become a member of the socially low-ranking all-male aggregate inhabiting the borderline region between Area I and IV (colony i, p. 212).

3. December 7, 1948. Two-hundred thirty-two-day-old male 97 (born in Area I) was inhabiting Box 25 in Area III. This was by far the worst place of harborage in the whole pen at this time. A large section of one side of the box had rotted away leaving any inhabitant exposed to inclement weather. Male 97 was inhabiting this place even though most rats were joining together in particularly large harborage aggregates, presumably for the purpose of conserving body heat. Upon my opening the lid of Box 25 he ran out into the Box 24 burrow, but was chased out. He then ran into the Box 19 burrow, where after a squealing fight it also ran out. By the next day he was again back in the exposed Box 25. During the winter and spring of 1949 this male joined the aggregate of outcasts and socially lowest ranking males inhabiting the collapsing burrow in the North Alley by Passage 3 as well as the extremely exposed harborage under the ladder in the East Alley (colony k, p. 213).

4. April 13, 1949. Three-hundred sixteen-day-old male 662 (born in Area III) was trapped and released at the burrow in the North Alley by Passage 3. He then entered this burrow momentarily, but left followed by another rat. It then entered the North Alley Burrow where it was chased out by a resident rat. The resident rat left its burrow only momentarily. Male 662 then entered the burrow at Passage 4, but remained there only a few minutes before going to and entering the South Alley Burrow. There it was chased out, fought by, then chased for about 25 feet by male 49, who dominated that burrow and its vicinity. The exclusion of 662 from burrows was so great that during

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April and May 1949, he lived under the exposed ladder in the East Alley with several other outcasts (colony k, p. 213).

These records help to emphasize an important point. This is that, although rats may be expelled from harborages which they do not customarily enter despite their social rank, the frequency of expulsion is greater for socially low-ranking rats. In fact, I have been lead to the hypothesis that the number of places of residence is inversely related to social rank of the individual (see discussion of the homogeneity index on p. 214). Certainly, much evidence of this relationship could be cited. Only the opposite extremes will be mentioned. On the one hand there were several females born at the South Alley Burrow which were practically never caught anywhere else but at the place of their birth, and for whom all lines of evidence point to their high social status. On the other hand, there were such individuals as the female sibs, 17, 20, and 25, who were practically never caught at the same place on two successive captures, and for whom all lines of evidence pointed to their extremely low-social status.

A striking example of the exclusion of other rats by the residents of a place of harborage is the following. On the night of January 6–7 a large nest of pine boughs was constructed in the activity recorder at Passage 6. This nest was utilized on that night and the following one by females 44 and 48, and males 29 and 670. Forty-four and twenty-nine were sibs, while 48 and 670 were not only sibs but young of 44 with whom they were remaining although 298 days of age. On January 8 this nest was examined in detail. It was both clean and well formed, thus indicating that the many rats which normally passed through this activity recorder had not done so during these two nights. This was the only record of rats building a nest in an activity recorder. Furthermore, these four individuals were among the eight taken out of Box 12 on January 6. Their movement as a group is one line of evidence which shows that rats do organize into groups which may maintain their integrity in moving through space.

g. *Defensive territoriality—hole-plugging.* From time to time rats plugged the entrances to harborage boxes or burrows with vegetation, soil or rocks. Such plugging inhibited the entrance by other rats. In this sense the rat exhibiting hole-plugging behavior is possibly defending the limited space it is inhabiting. This sealing of entries into harborages was previously discussed in detail in the section titled "Alteration of Burrows" (pp. 30 to 42). The one point which may be reemphasized here is that hole-plugging occurred three times as frequently in the north quadrant of the pen, which was inhabited by rats of relatively low status and who weaned only half as many young as the rats of higher status inhabiting the south quadrant.

This passive territorial defense was frequently associated with a lactating female, although even here it was affected by social status. Among the South Alley Burrow mothers, with their higher social status, there were only eight observed instances during 1948 of hole-plugging. These involved litters 10, 15, and 25b of females 33, 37, and 17. No pluggings were associated with litters 7, 17, 19, and 32–37. In contrast to this there were 13 records of hole-plugging by the socially lower ranking female 42 at the North Alley Burrow. Covering of holes by her was more marked right after the birth of the young. Yet she persisted in this activity during the entire period of lactation. It is also of note that the two females, 37 and 75, who were excluded from the South Alley Burrow during the summer of 1948 did cover entrances to their burrows in Area IV when they had litters. There was also a qualitative difference in the coverings between the North and South Alley Burrows. Those at the North Alley Burrow were much larger and functionally more effective.

h. *Offensive territoriality.* Included under this topic are all those instances where an individual repeatedly and aggressively drove off other rats which invaded the general locality about a single burrow or a group of neighboring harborages. Unless occupancy of a particular space may be considered a goal in itself, territorial behavior of this type is in quite a different category from the more frequent combats associated with priority of action such as involved in the competition of males over a female in estrous. Territorial defense was exhibited by most lactating females, and by those few males who were able to dominate a harem of females to the nearly complete exclusion of all other adult males. The most characteristic aspect of this territorial behavior was that the rat exhibiting territorial defense rarely showed any antagonism to rats it encountered while outside the territory, not even toward individuals whom it may have

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driven from its territory previously. A few examples will help to clarify this point:

1. During the spring of 1949 male 49 dominated the area about the South Alley Burrow and its extension in front of Passage 1. Nevertheless, and despite the fact that he was observed in the Food Pen hundreds of times in close association with other rats, only once was he observed to fight another rat there. On this one occasion he chased male 707 out of the garbage pail placed there for the purpose of photography. Male 707, who was the dominant male of the neighboring burrow by Passage 2, and who was a younger sib of male 49, was the only male who persisted in invading the vicinity of the South Alley Burrow, particularly at times when females were in estrous. Such a period of invasion occurred during the evening of April 25 when the conflict in the Food Pen occurred. Thus, this single aggressive action by male 49 outside his territory was probably an extension of a specific social relationship involving territorial rights rather than resulting from competition over food.

2. During 1948 male 22 established Area I as his territory and consistently chased out all adult males which invaded it. He was also a persistent storer of food. On one such trip on June 28 he was carrying a large piece of cake. Just before he reached Passage 1, as he was going up Path 1, the cake crumbled into several pieces. He then began making the several trips requisite to retrieve the pieces. On one of the last trips, while he was still in his harborage, adult male 30 invaded Area I. The latter was immediately chased out of Area I and through Passage 1 by male 22. Although male 30 went over a few feet into the West Alley, he returned in a few seconds to Path 1. There he and 22 sat amicably side by side and ate the remaining pieces of cake. Here male 22 failed to exhibit any aggressive action outside his territory even when a piece of food was involved toward which male 22 might have been expected to exhibit some "property rights."

3. On May 18, 1948, female 28, who had 31 day-old young in Area I, stopped and entered several holes of the South Alley Burrow. While this was going on female 37, who had 19 day-old young in this burrow, came from the Food Pen. She jumped on 28 and bit her. The latter fled. Later in the evening they were observed feeding together in the Food Pen with no show of animosity. Similar observations are available for other females.

There is one main difference between the territorial defense exhibited by lactating females and that by males with a harem. This is that two or more lactating females may simultaneously inhibit the same burrow system without showing any animosity toward each other. Males exhibiting territorial defense rarely permit the presence of another adult male. However, when more than one lactating female simultaneously inhabits a burrow it is characteristic that each confines its activities primarily to a restricted portion of the burrow. Where a territory was held by a single male (such as by 22, 49, or 690) (pp. 198 to 202) it was quite apparent that the adult females who lived in it were subjected to much less stress than females living elsewhere. This was because they were bothered less by the sexual advances of males, as well as because of the reduced necessity of defending a terriotry.

There was one behavior associated with territoriality which became highly developed in male 49 This was the behavior, which I have designated as "passage guarding." It consisted of a passive phase in which a rat stood in, against or near a passage through the fence. When so blocked, any more subordinate individual had to wait for the dominant rat to move, or it had to take a more circuitous route to its goal. The active phase consisted of exhibiting threatening motions, or actually giving chase to rats who approached. When a territory included a passage, the focus of the defender's attention to that point enabled it most effectively to keep away other rats. Passage guarding occured primarily at the passages through the central barrier fence, although it was occasionally exhibited at the passages into the Food Pen (probably as a sexual response). Two conditions contributed to the origin of the passage guarding repsonse. They were that chases frequently terminated there, and that these spots were favorite ones for the depositing of estrous scent.

For rats one can make the distinction between territoriality and dominance on the basis of exclusion from a space. Among males it is difficult to assign territoriality unless there is complete exclusion of other males. Among females there must be the exclusion of females who are not members of

the harem. There were instances where a female alone was rather effective in keeping away other rats of both sexes from her territory both during and following lactation. Dominance and the social rank ordering of local groups did occur, but most particularly it occurred among groups which did not exhibit territorial defense. Aggression and the formation of hierarchies without the concomitant development of territoriality is detrimental. This is documented in the later sections, Stress and Reproduction (pp. 214 to 216) and the Development of Local Colonies during the spring of 1949 (pp. 203 to 213).

E. *Conditions Influencing the Frequency and Outcome of Aggression.* In addition to the conditions which influence aggression mentioned in the previous discussion there are others which operate:

a. *Sex.* There were 88 paired conflict situations in which each member of the pair was known, and in which both rats were born in the pen. The number of instances and the sexes involved are listed as follows. The sex of the winner is listed first and the expected number is given in parenthesis: male-male: 53 (26); female-female: 20 (18); female-male: 12 (22); male-female: 3 (22). Expected numbers in each catagory were derived on the basis of their dependence upon chance interactions among the 87 males and 72 females which were born during 1947 and 1948 and lived for more than 150 days. The proportions of the interaction will be male-male (a^2): 0.299; male-female plus female-male (2ab): 0.496; and female-female (b^2): 0.205. Differences between the observed and that expected, on the basis of proportionality to the chance encounter rate, are of such magnitude as to indicate significance without recourse to a statistical test.

From the fact that the frequency of intermale antagonistic encounters is so much greater than expected it is concluded that males actively "seek" competitive situations. Fights between females were in proportion to a chance contact rate. Intersex fights, regardless of the sex of the winner were so reduced that one might say that males and females "avoid" competitive situations.

"Seek" and "avoid" are understandable in terms of alterations in extent of home range and the attitude of the sexes toward each other as goals. Females maintain a more stable extent of home range than do males. Also, female members of the same local colony are remarkably tolerant of each other. That is, they exhibit neither attraction or repulsion of each other as goals. Thus, fights between females primarily involved contact between members of different colonies when one chanced to approach the place of residence of another. Under such circumstances fights approximating a chance contact rate is logical.

When females are in estrous, males are attracted to their vicinity. Some males depart from their normal home range. This and their simultaneous attraction to the female or her scent posts increases the contact rate between males above the customary rate. The frequency of fighting certainly increases at these times of increased contact rates. In a few males this temporary increase of aggressiveness toward other males becomes transformed into a conditioned territorial behavior, in which increased aggression about the burrow is elicited even in the absence of estrous females. In such a system antagonistic encounters among males would be expected to exceed the proportionality to chance contact rate.

Contact between males and females are reduced because of the development of local colonies, whose adult members are either largely male or largely female. See the section "The Development of Local Colonies" (pp. 203 to 213). This alone would account for a reduced frequency of fighting between the sexes, if fighting is proportional to contact rate. Furthermore, the attitude of the sexes toward each other, particularly of males toward females, must further reduce fighting. Were there not some such ameliorating attitude the act of copulation would rarely be consummated.

The complete data on the observed frequency of intersex and intrasex encounters is given in table 41. This includes encounters involving the introduced rats. From this table sexual differences in the number of wounds are apparent. Males which win receive more wounds than do females. This difference is probably completely dependent upon the greater frequency of fighting by males. In fact, the more dominant males (the winners) frequently were characterized by more wounds than were their lower ranking associates. Those individuals with the most wounds represent the extremes of the social scale. The few most dominant males received a large number of wounds because they engaged in frequent combat with a larger number of other males who fought back. At the other extreme there were a few males which were frequently attacked, but which prac-

TABLE 41.—*Characteristics of rats engaged in paired conflict situations*

Sex	Type of pairing	N	Means ± 2 standard deviations			Maturity[1] index
			Age in days	Weight in grams	Number of wounds	
M	Winner...............................	67	371±158	480±122	7.2±11.8	I.64
M	Loser................................	67	285±270	427±122	6.2±13.4	I.68
M	Winner...............................	4	248	489	3.8	I.71
F	Loser................................	4	305	376	12.5	I.76
F	Winner...............................	29	304±158	412±164	2.5± 5.0	I.59
F	Loser................................	29	289±228	373±176	9.6±12.1	II.09
F	Winner...............................	29	298±152	408± 98	2.4± 4.8	I.49
M	Loser................................	29	340±398	406±150	7.6±15.4	I.54
M	Winner (Loser unknown)....................	37	383	499	11.5	I.31
M	Loser (Winner unknown)....................	9	398	443	8.1	I.96
F	Winner (Loser unknown)....................	13	348	440	2.3	I.77
F	Loser (Winner unknown)....................	10	310	376	11.5	II.05
	Total of M winners........................	108	371±142	486±128	8.6± 9.4	I.51
	Total of M losers.........................	105	310±230	421±144	6.9±14.2	I.68
	Total of F winners........................	71	310±150	416±124	2.5± 4.6	I.62
	Total of F losers.........................	43	296±232	373±154	10.4±16.0	II.05

[1] The number of animals for which data on wounds or maturity index were available was somewhat less than for age and weight.

tically never fought back. Among females there were also a few such individuals as these latter males, and they formed by far the bulk of the females which lost combats. Female winners were characterized by few wounds since they rarely engaged in combat except under situations in which the opponent did not fight back. The generally lower number of wounds in females than on males is particularly well shown in Figure 122.

b. *Age and size*. The typically small combat-incurred wounds healed within 2-weeks time. Thus, by the time a rat was retrapped during a later trapping period the wounds recorded represented those received in recent combat. Therefore, it was possible to construct figure 122 showing the change in mean number of wounds with age. Six clear-cut periods are discernible for each sex. Each period is characterized by a specific rate of change in the mean number of wounds. These changes may be viewed as an indication of the maturation of aggressive behavior.

Period one, when no wounds were received, lasted to about 40 days of age and coincided with the time of nursing and close association with the mother. Period 2, circa 40 to 60 days of age was the time the maternal ties were beginning to break, and a very few individuals received their first wound. Period 3, lasting from 60 to 115 days of age for males and to 150 days of age for females, is the time during which most individuals receive their first wounds. For males, this coincides with the period of sexual maturation to the point of exhibiting the nearly complete repertoire of courtship and copulatory behavior. Period 3 may also correspond to sexual maturation in the female since it was quite apparent that females under 115 days of age were not so frequently as attractive to males as were older females. Although the rate of increase in aggression was slower for females, Period 3 terminated at approximately the same mean wound level as for males.

There is no plausible explanation as to why there was no apparent change in intensity of
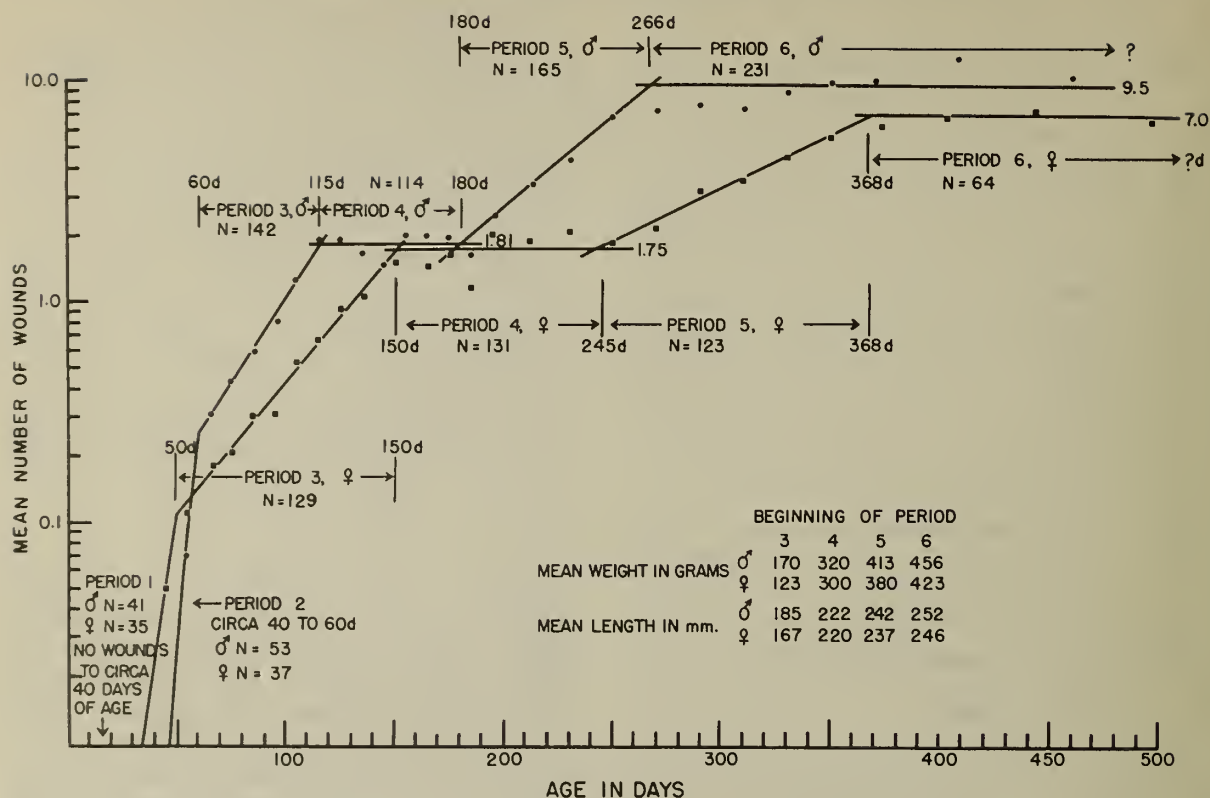
Figure 122.—Prevalence of wounds with age.   The data are shown as a three-point moving average of the means.   N=number of observations.   Note that each of the periods for males is of shorter duration than for females.   This indicates that males have a more rapid rate of maturation of aggression than do females.

aggression during Period 4 (115 to 180 days for males, 150 to 245 days for females). The intervals approximate the ages during which each sex is in its prime pelage (see fig. 144 and 145). This Period 4 with its constant low level of aggression is one which I have thought of as a period of behavioral maturation, such that by the end of the sixth month for males and the eighth month for females the rats may be said to be fully adult and prepared to fully engage in courtship, mating, and defense of territory.

There follows Period 5 (180 to 266 days for males: 245 to 368 days for females) during which aggression increased to a high constant level, which has been designated as Period 6. By the beginning of Period 6 each sex has just attained 0.9 of the post-weaning increment in weight (Figs. 130 and 131).

In the preceding paragraphs certain events associated with the periods of aggression were presented, without necessarily implying any cause and

effect relationships. There is a strong suspicion that these periods do have casual relationship with physical size. Three facts fostered this suspicion: (a) Males grew faster than females and likewise exhibited more rapid rates of increase in aggression. (b) The two sexes were more nearly identical in weight at the ages corresponding to the beginning of their periods, 4, 5, and 6 than they were at identical ages corresponding with any of these periods for either sex. For example, the mean weight of females at 115 days was 250 grams and at 180 days 346 grams. Contrast this to the data in the table on figure 122. These weights are for the ages at the beginning of periods 4 and 5 for males, and represent much smaller size for females than for the later ages (150 and 245) at which females also begin these two periods. (c) Table 41 shows that those individuals winning a conflict were generally both older and larger than their losing opponent. At least among males the loser was not only smaller because he was younger, but his weight was even

less because of loss of weight. From the mean Maturity Index (see pp. 220 to 221) the expected mean weight may be calculated. For the male: male encounters the observed mean weight for winners was only 15 grams less than the expected, whereas for the losers it was 48 grams less than the expected. Similarly for female: male encounters the respective reduction in weight of the observed from the expected was 24 and 92 grams. In female: female encounters the respective losses were only 10 and 12 grams. Thus, it may be seen that males who lose in conflict situations have lost proportionately more weight than their winning opponents of either sex. I am convinced that this greater loss in weight is not a result of an inability to obtain sufficient food but in some way depends upon the greater stress experienced by losers.

In order to obtain more insight into the relationships of age and weight to success in conflict the data forming table 41 was separated into subgroups and plotted in figures 123 to 125.

Males under 150 grams, which engaged in conflict situations with older, larger rats, were those whose mean weight far exceeded the mean weight for that age. This is important despite the fact that they always lost such encounters, because it indicates that an early expression of aggression is more likely, provided the individual has a rapid rate of growth. The only other category of losers whose mean weight exceeded that for the mean of the population at that age was for sibs. Most of the sibs involved in observed paired conflicts were born during 1947. This fact certainly contributes to the increased weight of sib losers. However, it is also probable that slowly growing sibs infrequently fight among themselves. Females 28, 33, 37, 42, and 43 of litters 5 and 6 were involved in the five female: female sib conflicts. Their Mean Maturity Index was I.64. These same 5 females were involved in 12 conflicts with the female sibs 17, 20, and 25, over whom they always won. The Mean Maturity Index for these latter three females was II.47, and they were never observed in conflict among themselves, although they often came in contact.

Regardless of the age differential between loser and winner, the following general conclusion may be made concerning the conflict categories 3 and 4 shown in these figures: For their respective ages, winners have greater than mean weight and losers less than mean weight.

c. *Season*. I soon came to the conclusion that fighting was less intense during the winter months. This was a time when rats formed exceptionally large harborage aggregations and when sexual activity was nearly inhibited. Males between 8 and 12 months of age were selected as the most likely group to reflect a seasonal variation. The results of this analysis are shown in figure 126. It is quite apparent that during the breeding season the intensity of antagonism is something of the order of twice that during the winter months.

The fact that rats assemble in larger harborage aggregations during the winter months does not prevent them expressing antagonisms following departure from their place of rest. Several instances such as the following were observed: There were approximately 20 rats staying in Box 31 and its adjoining burrow on February 1, 1949. Shortly after dusk they began to emerge and 12 were seen to proceed to and underneath a group of traps piled near Box 36. Occasional fights were heard immediately after they had assembled there.

d. *Availability of food*. It was the customary policy to make available an abundance of food at all times. Under these conditions the most frequently recorded observation was that several rats, usually not over 10, were feeding together amicably. This held true even though fights were occasionally occurring as rats met in the activity recorders at the passages into the Food Pen, or when fights were occurring more frequently in the vicinity of the burrows or harborage boxes. This typical amicability characterized both the permanent supply of laboratory food pellets as well as temporary additions of scrap table wastes and similar garbage.

However, on a few occasions the food was accidently or purposely permitted to become exhausted. These few instances provided important information concerning the role of food to aggression. On one night, while movies were being made during April 1949, the only food provided was a large pile of garbage. Many pieces of the food such as halves of oranges or fresh ears of corn were nailed to a board. During the early part of the night, while the food was in abundance, up to 20 rats fed together with little show of antagonism, despite the fact each rat was frequently in actual contact with others. As the food supply dwindled more and more fights at the food source occurred. Evidence of a similar situation was observed on November 15, 1948. When I left town on November 10 the hopper contained nearly 50 pounds of food pellets

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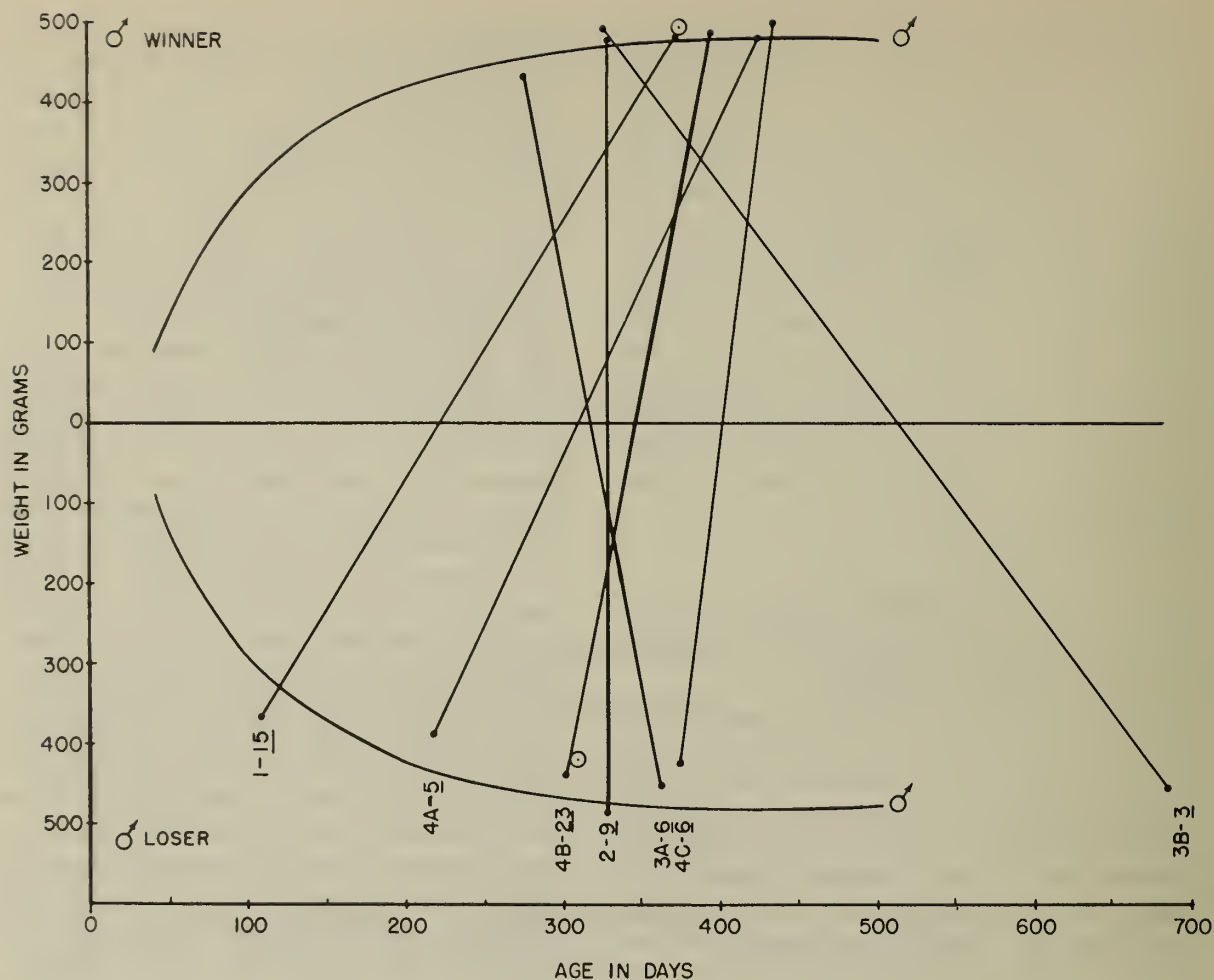
Figure 123.

Weight and age differentials between pairs of males engaged in conflict situations. Arbitrary age class intervals for losers were selected. The straight lines connect the winners and the losers in each category. The curves represent the mean growth rate for all males in the pen. They are presented for the purpose of rapid comparison with the selected subgroups. Just below the point for the losers are two numerals. The first (not underlined) indicates the arbitrary age class interval of the losers; see below. The second number (underlined) indicates the number of conflict situations, each involving two individuals, from which the means of age and weight were determined. The two circled dots represent the means of all losers or all winners.

Arbitrary age class intervals for losers:
1. Loser is the younger and under 150 days of age.
2. Sibs of all ages.
3. Loser is the older.
      A. 300–450 days of age.
      B. Over 600 days of age.

4. Loser is the younger.
      A. 150 to 250 days of age.
      B. 250 to 350 days of age.
      C. 350 to 450 days of age.

but upon my return on November 15 it was empty. The earth about the base of the hopper had been scratched up in the rats' efforts to glean the last morsel. There was fresh blood about the hopper and several spots of blood about the Food Pen. Similar spots of blood indicating intense fighting, was observed on another occasion after the food had become depleted.

In these instances there were two conditions, which contributed to the increased antagonism. They were hunger and competition over a limited supply of food. The following observation indicates that the latter of these two conditions was the more important one. During the nights of July 10–11 and 11–12, 1948, there was no food available to the rats in the Food Pen. Through these 2 nights
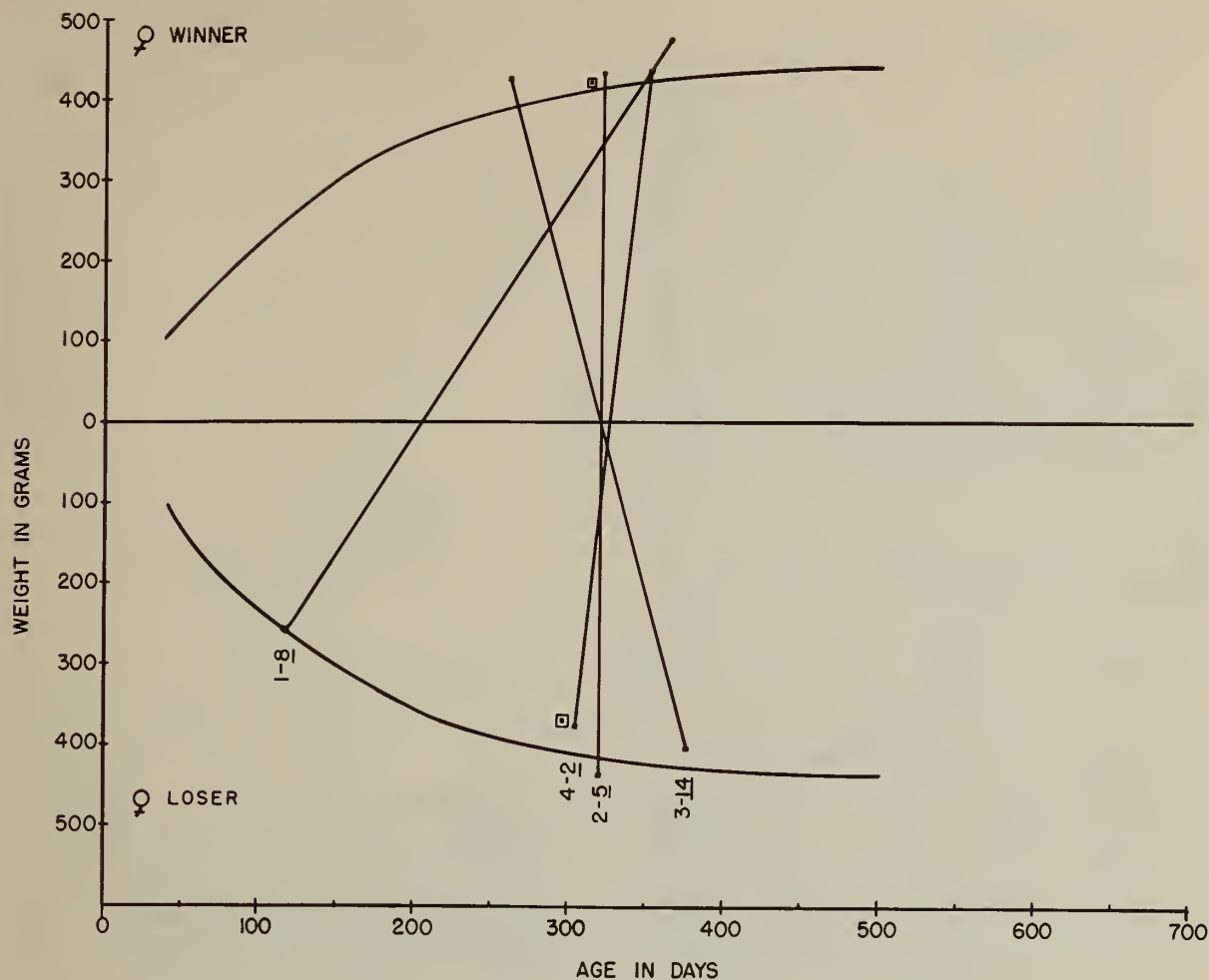
Figure 124.

Weight and age differentials between pairs of females engaged in conflict situations. See figure 123 for additional explanation. The large squares represent the means of all losers and all winners.

Arbitrary age class intervals for losers:
1. Loser is younger and under 150 days of age.
2. Sibs of all ages.
3. Loser is older and over 300 days of age.
4. Loser is younger but over 150 days of age.

the rats were forced to eat bark of black locust trees. A number of these trees from 8 to 13 feet high even had their uppermost branches stripped. An abundance of food pellets and sections of oranges were provided on the evening of July 12. There immediately began intense activity relating to the acquisition of food. This included both consumption and transportation. Very few fights were observed anywhere in the pen. A nearly identical set of observations were made on June 1, 1948. There had been practically no food available to the rats during the previous 3 nights.

During this evening there was a period of intense transportation of food throughout the 4 hours of observation. The only observed antagonisms pertained to lactating females chasing the three socially low-ranking female sibs 17, 20, and 25 at other places than in the Food Pen. On the following evening transportation of food was greatly reduced, several rats would feed together amicably, sexual activity was increased, and there was an increase in fighting outside the Food Pen, associated with territorial defense and sexual activity.
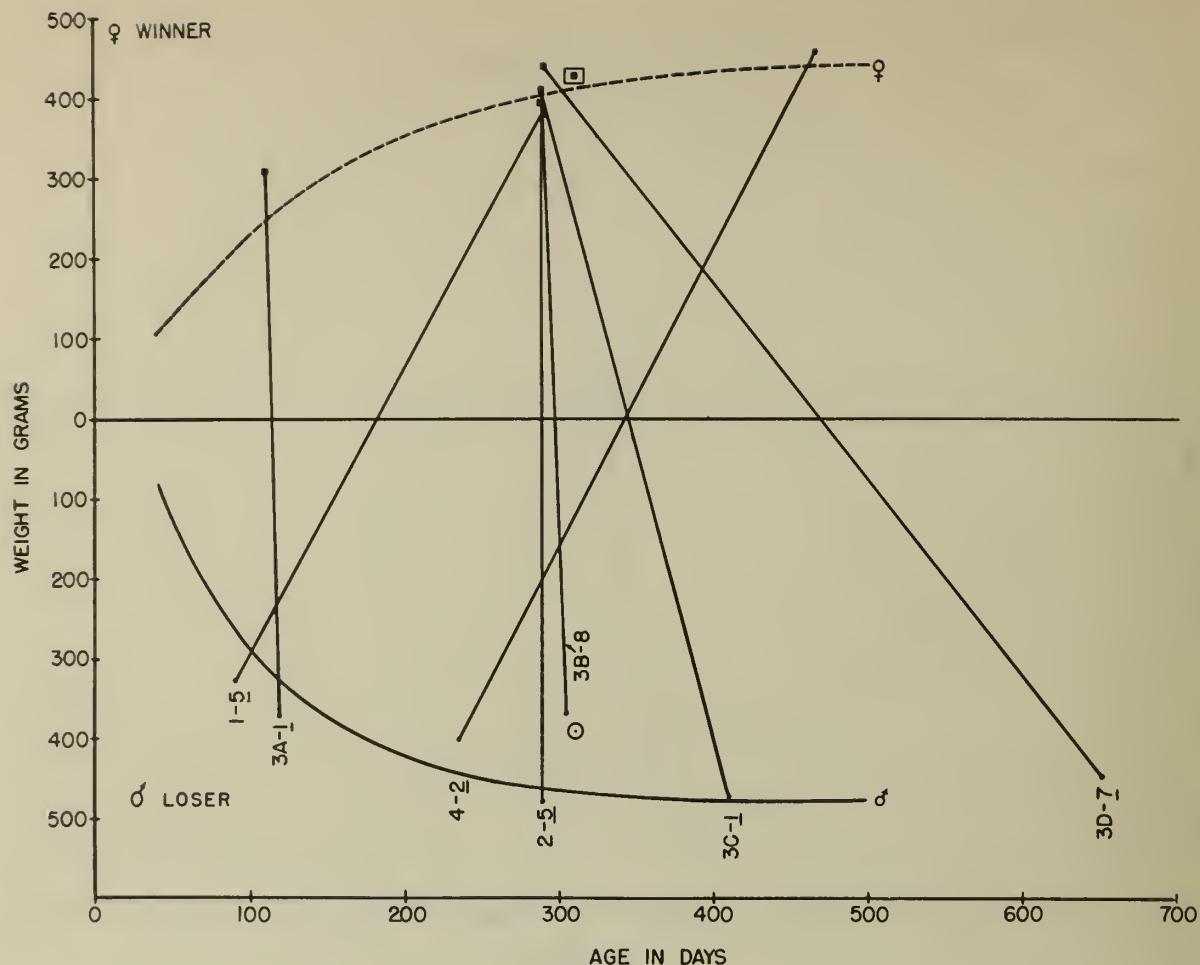
Figure 125.

Weight and age differentials between males and females engaged in conflict situations in which the male was the loser. There were too few instances in which the male won over a female to justify their inclusion in a graph. See figure 123 for additional explanation. The large square represents the mean for all these winning females, and the circled dot represents the mean for all these losing males.

Arbitrary age class intervals for losers:
1. Loser is younger and under 150 days of age.
2. Sibs of all ages.
3. Loser is the older.
      A. Under 150 days of age.

B. 150 to 350 days of age.
C. 350 to 600 days of age.
D. Over 600 days of age.
4. Loser is younger and from 150 to 350 days of age.

As a result of these and similar observations the following conclusions are warranted: When the amount of food is restricted, fighting at the food source increased. When the food supply is ample, there is little fighting about the food but an increase elsewhere.

e. *Social rank and the acquisition of food.* At several places in the previous discussions, it has been pointed out that individuals of low social rank (a) exhibited marked avoidance of other rats,

(b) were extremely wary in their approach to the Food Pen even when other rats were absent, and (c) frequently were chased by their higher ranking associates, even when no competitive situation existed. Although most individuals, regardless of social rank, did not appear to experience undue difficulty in obtaining food, the peculiar set of circumstances relating to the few individuals at the very bottom of the social hierarchy were quite striking. The following set of observations succinctly

SEASONAL INCIDENCE OF WOUNDS: MALES—
240 TO 359 DAYS OF AGE

	N	MEDIAN	MEAN	σ
OCT.–MAR.	122	3	7.1	9.8
APR.–SEP.	70	9	10.0	9.8

MEDIAN OF 3-POINT CLASS INTERVAL
NUMBER OF WOUNDS

Figure 126.—The effect of season on the prevalence of wounds among mature male Norway rats.

describe the end result which arose from the consistent aggression expressed toward these individuals:

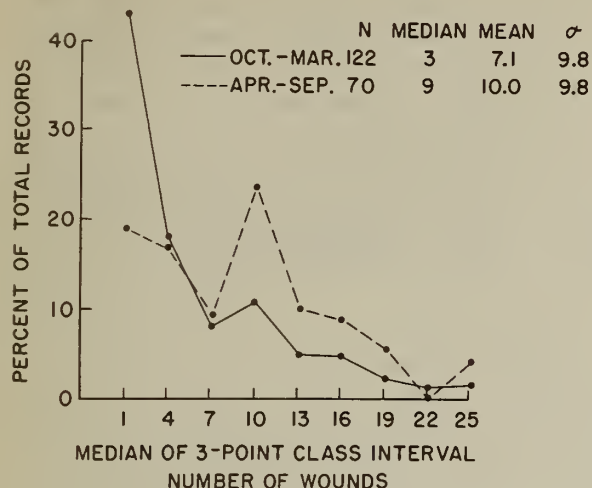January 23, 1948. Snow on ground. Female sibs 17, 20, and 25, which are the socially lowest ranking rats in the pen, have been harboring in Box 9 for the past 3 days. This was one of the four most distant harborage boxes from the Food Pen. I do not know which member or members of this trio the described events pertained to. *Trip No. 1 to Food Pen:* Box 9 to Passage 1, through West Alley to Passage 8, which was blocked by another rat. Thence around to Passage 7, which was also blocked by a rat. There was no indication that either of these rats actively threatened this female. Rather it was a case of the female avoiding close association with another individual. From Passage 7 it proceeded toward the North Alley Burrow where it was attacked and chased a short distance. It then went into the East Alley where it rested for 10 minutes under a clump of small pine trees just in front of Passage 6. From here it went back to Box 9 through Passage 2 without making any further attempt to enter the Food Pen. *Trip No. 2 to Food Pen:* Box 9 to Passage 1, down Path 1 and through Passage 8 to food hopper. Here it paused for 20 seconds without eating. Although no other rats were in the Food Pen, it retreated under the platform of the activity recorder at Passage 8. A rat from the South Alley Burrow entered, smelled at the female under the platform,

and as it emerged chased it across the Food Pen, and through Passage 2, from which the low-ranking female proceeded to and into Box 4. *Trip No. 3 to Food Pen:* Box 4 to Passage 1, down Path 1 and through Passage 8 to food hopper. It paused here only momentarily, since there was another rat there, before going out through Passage 6 and around to the outside southeast corner of the Food Pen. Here it paused for 2 minutes before entering the Food Pen through Passage 5, and again went to the food hopper. The rat at the food hopper immediately chased it out through Passage 5. The rat doing the chasing stopped at Passage 5; while the low-ranking female proceeded back up Path 1, through Passage 1 and over into Box 3.

In these trips the female or females traveled 665 feet without ever obtaining any food, whereas a round trip of 200 feet would have sufficed to satisfy its temporary food needs, had the behavior of the rat permitted it to go to and remain at the food hopper. The above events included practically all of the aboveground activity of all rats during the first 45 minutes of activity on this evening. During the next 35 minutes there was a marked increase of activity by all of the rats in the pen except the three low-ranking females living in Area I. On this date the rats were concentrated in the North and South Alley Burrows, the burrow by Passage 3, and the burrow by the fence opposite Box 14. Despite this dispersion of places of living, and despite the fact that both high and intermedite levels in social rank were represented, none of these rats exhibited any hesitancy in going to the food hopper to eat, nor were there any antagonisms expressed upon encounters.

F. *The Syndrome of the Social Outcast.* The three females discussed above were definitely social outcasts. Other individuals over the history of the colony fell into the same category. Certain characteristics of these individuals were sufficiently general to classify them into a syndrome. They were:

1. Slow growth rate, and low adult weight. These animals which grew slowly had a more juvenile body length: body-weight ratio in comparison with faster growing individuals of the same age (see figs. 134 and 135).

2. Marked tendency to reenter traps (see pp. 94 to 99).

3. Were difficult to remove from traps. In contrast to most of the other rats which

immediately ran into the gathering sack, as soon as the door of the trap was opened, these rats had to be shaken into the sack.

Items 1 to 3 pertained primarily to those individuals which became social outcasts sometime between weaning and the time of physiological sexual maturity at about 115 days of age. The remaining items pertained to most social outcasts regardless of the age at which they became outcasts.

4. Marked diurnality of activity or the rat became active during those periods of the night when most other rats were temporarily inactive (see pp. 112 to 135).

5. Tendency to approach hesitantly or retreat from nonoutcast rats. It is presumably by such behavior as this that the outcasts elicit frequent attacks upon them by other rats (see pp. 179 to 180).

6. Tendency to repeatedly approach and then withdraw from the Food Pen without entering, it, even when no other rats were active (see pp. 179 to 180).

7. In the Food Pen they frequently took a pellet of food over into one corner to eat. This was never observed for any of the nonoutcast rats.

8. Nonharborage food cache formation (see pp. 102 and 106 to 109). Outcasts would come into the Food Pen, when no other rats were about, and transport pellets to one or more places within the Food Pen. These were usually deposited in piles either under the platforms to the activity recorders or just out on the bare ground. The most extreme case was for a rat which made a number of consecutive trips taking pellets from the base of the hopper, climbing up the side of the hopper, and depositing them on top of the mass of pellets inside the hopper. After completing such a period, these individuals would depart for their place of harborage, even though no other rats were about.

9. Marked tendency to harbor in unfavorable situations. (See account of males 97 and 662, p. 185, and female sibs 17, 20, and 25, pp. 193 to 195, and colony k, p. 213.) By unfavorable is meant that the place of harborage was farther from the food source or was more exposed to inclement weather such as a collapsing burrow, or a harborage box whose sides had rotted through.

10. Formation of nonreproducing aggregates (see tables 56 and 57, and discussion of colonies g to k, pp. 210 to 213). The aggregates were nonreproducing in the sense that they were usually composed mostly of males. The females present were either never seen to be courted by males, or if they conceived they failed to rear young, nor were the males from the all male groups seen to participate in the sexual attention toward females in estrous in neighboring colonies. The only instance of homosexual behavior, involving two males, was for one of these aggregations of outcasts.

Only the members of one litter were characterized by item 8 as well as the first three items of this syndrome. This was Litter 13 (see section on the history of the "Three Litters of Female 43," pp. 147 to 148). This was the only litter born in the pen which was conceived on the date of parturition of a previous litter, and which during their nursing period was subjected to competition from older sibs. Female 7, the smallest of the introduced rats, and male 83, a low-ranking, average-growing male born at the North Alley Burrow, were the only two other rats to be observed as adults engaging in the aberrant type of storage indicated in item 8.

Male rats which as adults might have been dominant, or at least had matured under such favorable conditions as to engage in competition for dominant status, eventually were characterized by this syndrome of the social outcast. The introduced male 12, who was dominant during the summer and fall of 1947, was such an example. The males which had a better than average growth rate, and which became members of colonies h to k (pp. 212 to 213) were also individuals which exhibited this transition in behavior to that of the social outcast as a result of their unsuccessful attempts to attain favorable status.

G. *Locality of Birth and Social Status.* From time to time through this account of the history of this experimental population, mention has been made that rats born in the southeast half of the pen held higher social status than those born in the northwest half (see especially pp. 38 to 41, 117 to 123, 138 to 143, 164, 186). In order to learn more of the effect and implication of this social stratification a tabulation was prepared (see table 42) of all combats for which there was a decisive termination. However, this tabulation is relatively meaningless

			WINNER	
		Sex of the pair	Born in southeast half of pen	Born in northwest half of pen
LOSER	Born in southeast half of pen......	Male-Male...................	30 (23. 9)	5 (11. 7)
		Female-Female...............	4 (6. 2)	1 (5. 0)
		Female-Male.................	8 (4. 5)	1 (3. 6)
		Total.................	42 (34. 6)	7 (20. 3)
	Born in northwest half of pen......	Male-Male...................	16 (11. 7)	2 (5. 7)
		Female-Female..............	14 (5. 0)	1 (3. 9)
		Female-Male.................	2 (2. 2)	1 (1. 7)
		Total.................	32 (18. 9)	4 (11. 3)

unless the number of sexually mature animals born in each half of the pen is taken into consideration. On the southeast side, 51 males and 34 females, who were born there, lived more than 150 days. Correspondingly, there were 25 males and 27 females from the northwest side. This refers to individuals born in 1948. Inclusion of the 22 rats born during 1947 does not materially affect the proportions of sex to locality of birth.

The hypothesis used for determining the expected frequency of interactions was that they should be dependent upon the relative numbers of each sex and place of birth available for interaction. Thus, if a denotes the number of southeast males and b the number of northwest males, the interactions would be proportional to a^2 (southeast with southeast)$+2ab$ (southeast with northwest) b^2 (northwest with northwest). Furthermore, the ab's on a purely random basis should be divided between southeast winners and northwest winners. The 53 observed male-male encounters would be $(0.450a^2)+(0.441ab)+(0.108b^2)$. The expected female-female and female-male encounters were similarly derived.

Certain general conclusions may be drawn from the table: (a) There were more antagonistic interactions than expected, when both members of the pair were rats of higher social status from the southeast half of the pen; while there were fewer encounters than expected when both members of the pair represented rats of lower social status from the northwest half of the pen (Chi Square 6.30, P between 0.02 and 0.01). (b) Among the pairings involving one rat from each half of the pen there was a greater than expected number of winners representing the rats of higher social status from the southeast half of the pen (Chi Square 17.80, P less than 0.001).

There is one question left unanswered in this study. This is: Do rats which engage in fewer antagonistic interactions also have fewer social relations of all kinds? In this connection it is worthwhile to mention the results of some studies (16) I conducted at the Roscoe B. Jackson Memorial Laboratory during 1950 and 1951. Two groups of free-ranging house mice were studied. One contained 8 males and the other 11. The status of the individual in every observed interaction was recorded; whether it was dominant, subordinate, or neutral. In each colony the following relationship was exhibited. As the number of positive interactions (dominant or subordinate) per individual declined there was a decline in total interactions. In other words, in the absence of positive interactions there was not a corresponding increase in neutral interactions. Furthermore, those individuals with the most total interactions had the greatest percentage of these dominant.

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There is reason to suspect that the socially lower ranking rats in addition to engaging in fewer positive encounters also engaged in fewer neutral social interactions. This belief is based upon the regularly observed fact that rats of known low social status customarily became active when most other rats had retired to their burrows. However, this tendency toward a reduced number of total social interactions characteristic of socially low-ranking rats must have been reversed following the invasion of the northwest half of the pen by rats forced from their place of birth in the southeast half of the pen by early in the winter of 1948. I, furthermore, strongly suspect that it was an attempt to reduce social interactions as much as possible that led to the formation of all male aggregates in the spring of 1949. The members of these groups were such definite outcasts that they never engaged in sexual relations with females.

H. *History of Male Dominance.* The largest of the introduced males, No. 6, was clearly the dominant male until his death from unknown causes on July 19, 1947. There was nothing in his behavior to indicate defense of territory; there was merely an expression of dominance in fighting encounters, wherever they might occur.

His presence for two-thirds of the time in the southeast half of the pen during this time may well have been an important factor in making this half of the pen the more favored one in the latter history of the colony. Following his death there remained only two of the original males, Nos. 8 and 12. Marked antagonism existed between these two individuals although it took the form of male 8 avoiding male 12 whenever possible, and male 12 attacking male 8 whenever they met. There was never any expression of tolerance between them. This complete lack of tolerance was never noted for males born in the pen, and it is therefore assumed that this lack of tolerance may be attributed to the lack of opportunity of developing mutual adjustments of noncombative behavior during early life. All introduced rats, if not actually total strangers, were strangers in the sense that they were thrown into a new environment in which there were no previously established priority rights to places and objects. Thus, the initial adjustment was one of fighting to establish priority rights. This initial behavior was the one which then became the established one when any two of the introduced males encountered each other, and probably accounts for the relatively greater antagonism which occurred

among the introduced rats, both male and female. This marked antagonism among the colonizing adults during 1947 was also extended to encompass many of the relations between these adults and the young born during 1947. After male 12 assumed his dominant status during July he persistently fought or chased young males between the age of 60 and 200 days. This lasted until the cessation of sexual activity in late October 1947. I strongly suspect that it was this extreme punitive action received by these young rats, who became the adult males of the 1948 season, that inhibited their expression of any clear-cut territorial dominance in most areas inhabited by breeding females. Furthermore, these experiences probably contributed to the lessened antagonism of adult males toward juvenile and subadult males during 1948.

Male 12 also can hardly be said to have had a territory unless his territory was nearly the whole pen. During most periods of observation he was seen to wander leisurely over most of the pen, and 1 night he was seen to cover every portion of the pen. No rat born in the pen was seen to exhibit such an extensive home range. When both captures and visual observations of his presence were included he exhibited the following distribution: southeast half of pen, 43 (South Alley, 14; Area I, 17; Area II, 12); northwest half of pen, 25 (North Alley, 12; Area III, 3; Area IV, 8). These records are for the period March 27 to October 29, 1947, which approximates the breeding season. However, trapping records (fig. 107) which more closely approximates places of harborage indicate a strong preference for the southeast half of the pen.

During the nonbreeding winter season of 1947–48 male 12 lost his prior dominating status. By April 17, 1948, when he was approximately 605 days of age he was emaciated and arthritic to the extent of having a permanently arched back. There was much scar tissue and fresh wounds over his lumbar region; his pelage was extremely sparse; and he had only one descended testis, which was no more than 10 mm. long. From this time until his last record on October 28, 1948, he showed a marked shift in his place of residence (fig. 107). During April, May, and June he lived mostly in Area III. His presence there during the time female 43 was rearing her litters Nos. 8, 13 and 18 at least reflects the lower social status shared by other rats inhabiting this northernmost portion of the pen. To what extent he also served to mold the behavior of the young of female 43, I do not

know. However, her recently weaned young were on several occasions found harboring with him, and I am inclined to believe that the type of behavior exhibited by adults does influence the subsequent behavior of juveniles who associate with them.

By July 1948 male 12 exhibited three major symptoms of the syndrome of the social outcast (pp. 195 to 196). These included transporting food to one side of the Food Pen to eat rather than eating at the hopper, hesitancy to enter the Food Pen, and marked diurnal activity after the other more dominant rats had retired to their burrows. By this time he was also an avid storer of food, a characteristic which he had not exhibited previously and which is common among socially lower ranking rats. From July through October, 1948, 1948, male 12 centered his residence in Area II. He was still frequently chased or fought by other rats. His presence there is one indication that, although the southeast half of the pen developed a more favorable social organization, conditions in Area II were in general less favorable than in the South Alley and in Area I. During the April to October period male 12 was recorded 39 times in Area III and 28 times in Area II. This includes a few observations in addition to those shown in figure 107.

By April 1949 10 of the males born during 1947 still survived. Only one of these exhibited defense of a territory. This was male 22, a member of the first litter born in the pen. From April through October 1948 he repelled all males who invaded Area I. His dominancy was also occasionally expressed in the Food Pen, although in general his associations with other males outside of Area 1 were amicable. Those aggressions exhibited by male 22 outside of Area I occurred only at times when a female was in estrous. Since he always dominated the males attracted to females in estrous at the South Alley Burrow, his territory might be considered as having encompassed it during these times.

None of the other nine 1947-born males exhibited territorial defense, nor was there any clear-cut hierarchy among them. During adult life they resided at other places in the pen than in Area I, or at the South Alley Burrow where all were born or had spent much of their juvenile life As mentioned above they were repelled by male 22 whenever females came into estrous, even though several of these males were larger than he. Territorial defense in all parts of the pen during 1948

other than in the south quadrant was entirely by lactating females.

The approximate areas controlled by males during 1949 are shown in figure 127. They may be ranked in descending order as follows with their life span mean Maturity Index shown in parenthesis: 49 (I.0), 690 (I.0), 786 (I.20), 82 (I.11), 707 (I.86), 751 (II.0), 74 (I.68), 97 (I.90). This ranking is based upon outcome of combats, number of young per female in the area, and ratio of males to females in the area. The more males to females the lower the status of the group is assumed to be. The details of these criteria are discussed on pages 203 to 216.
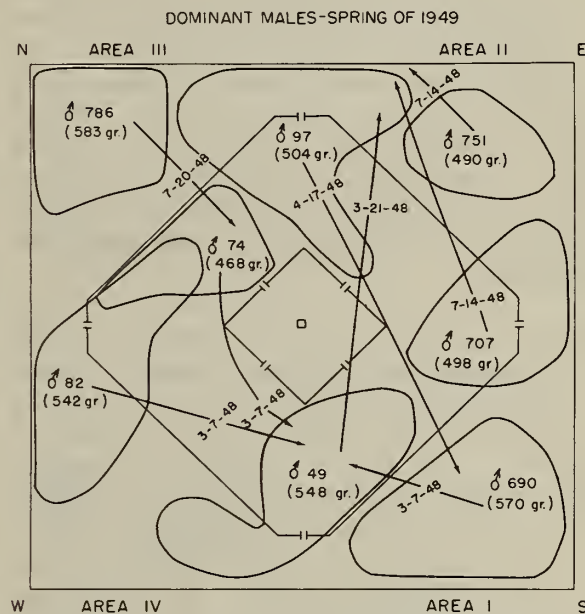
Figure 127.—Approximate areas controlled by males during the spring of 1949. Arrows point to place of birth. Note that none of these high-ranking males resided at the place of their birth. Weights are for May 1949. Compare this with the local colonies as they existed in the spring of 1949 (figure 128).

That male 49 was the dominant male of the whole pen there is absolutely no doubt. Observation concerning him was facilitated by the fact that a crumpled left ear and a V-shaped bare spot on the lumbar region enabled identification at all times. He was observed in hundreds of fights, all of which he won. In fact, he would sometimes take on two or three males simultaneously. Even the next highest ranking male, number 690, did not seriously contend his position. A great majority of interactions, however, were of other males

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avoiding male 49. He remained near the place of his birth in Area II in close association with his mother, No. 44, into January 1949. At about the same time she shifted her place of residence back into the South Alley Burrow. However, she remained with the lower ranking colony inhabiting the burrow in the South Alley near Passage 2. At this point the question may be raised as to why this male, who was born in Area II, became the dominant male with a harem of 13 females at the South Alley Burrow, rather than any of the many males born there during 1948. I believe that there are three major contributing conditions or situations. First, male 49 was one of the only four males whose growth was so rapid that at every capture he fell into the Maturity Index Channel I, and only three of these males survived through the 1949 spring breeding season. Second, because of his close ties with his mother, his shift in place of residence back to the South Alley Burrow may have influenced her return to the South Alley. Three, conditions about the South Alley Burrow during 1948 were unfavorable for males born there remaining.

TABLE 43.—*Data concerning the males who were born at the South Alley Burrow during 1948 and who survived longer than 150 days*

Litter number	Date of birth (1948)	Number of males surviving longer than 150 days	Average maturity index
7.............	Mar. 7.......	6	I.26
10............	Mar. 16......	5	I.79
14............	Apr. 30......	1	II.14
17–19........	May 18......	8	I.50
22a..........	June 1.......	1	I.83
25b..........	July 15.......	5	II.30
32 and 37.....	Sept.........	3	II.62
		29	

An understanding of why this was so may be facilitated by examining table 43. It will be seen that the timing of the litters was such that by the time each reached approximately 60 days of age some other female than their mother was lactating at the South Alley Burrow. Thus, these males were becoming independent of their mother just at the time when they were most likely to receive psychological drubbings from these lactating females.

This and the competition among the males as they matured exerted pressure to disperse. The males born at the South Alley Burrow during March 1948 were captured or observed between June 19 and July 31, 1948, 40 times at the South Alley Burrow and 54 times elsewhere. Actually, the amount of dispersal was greater than these records indicate since observations of movements produced a pattern of residence elsewhere, particularly Area IV, with rather frequent return visits to the place of their birth. These induced shifts in place of residence are shown in figures 114 and 116. Toward the end of the summer of 1948 conditions of competition had become so severe that there was an inhibition of growth to the extent that none of the later born males could offer effective competition to those born earlier.

Thus, by the winter of 1948–49 the situation of the South Alley Burrow was one of inhabitance by several females who were born there and who formed a rather stable group despite the lack of permanent residence of any males. During the latter portion of this winter, old female 44 and five (males 49 and 707, and females 48, 875, and 925) of her nine surviving progeny moved from Area II into the burrow by Passage 2 in the South Alley. Due to his proximity to the South Alley Burrow and because all males who were large enough to offer him any serious competition had long since developed attachments elsewhere, it was only natural that male 49 should assume territorial defense of the South Alley Burrow as soon as some of these females came into estrous during the latter part of February 1948. He and these 13 females formed the colony of highest social status of the entire population (colony a, pp. 204 to 205).

One of the other two surviving males, No. 690, whose growth was so favorable as to have always been classified in Maturity Index Channel I assumed control of Area I, which was the second most favored area through the history of the pen. Along with two other (males 82 and 74) and slightly smaller of his five brothers, he remained mostly at the place of his birth, the South Alley Burrow, well into his 4th month (June 1948). Their remaining here was probably attributable to their remarkably rapid growth. At 113 days of age (June 30, 1948) male 690 was seen to follow the dominant female of Area I, No. 28, into Area I. However, he remained as a marginal member of this Area I colony until the death of the then dominant male of Area I, No. 22, sometime during December 1948.

During this early adulthood before male 22's death, male 690 harbored in the burrows in the south corner of Area IV or at the South Alley Burrow. At the time of male 22's death there were residing in Area I in addition to the dominant female 28, five females and eight males who were born there as well as one male (No. 52, who was the dominant male 49's brother) from Area II. It will be noted that male 22 was tolerating the presence of several rats which had grown up in his presence to adulthood but who were sexually inactive (testes withdrawn into the abdominal cavity) because of the cold winter weather. Male 690 also tolerated these males through January and February 1949 after he moved into Area I. During these months he lived solitarily and never joined in the harborage aggregations maintained during the winter of 1948–49 by the rats which were born in Area I. However, with the advent of the breeding season in late March of 1949 all but one of the eight males were driven from Area I by male 690. This one male (No. 737) was an extremely small individual having a mean life span Maturity Index of II.75, so that he certainly offered 690 no serious competition over the control of the four of the six females who survived through the spring breeding season.

The dispersal of these eight males as a result of male 690's action is interesting. Five of them became members of the all-male colony, which in its physical position opposite Passage 1 was marginal to the two highest ranking colonies, that of the South Alley Burrow and of Area I (see colony k in fig. 128). One joined colony c which inhabited the burrow in the South Alley by Passage 2, and one, No. 95, shifted to Area II. Thus these seven males (Nos. 732, 735, 736, 739, 760, 799, and 95) settled in localities immediately adjoining the place of their birth. The ninth excluded male, No. 52 who had originally joined the Area I winter aggregation from elsewhere (Area II) made the greatest shift in range to the senescing North Alley Burrow which housed an extremely socially low-ranking, all-male aggregate (see colony i, fig. 128). Thus the assumption of dominance over Area I by male 690 illustrates how the establishment of territorial defense of an area influences the lives of other males. The typical interaction of male 690 with the higher ranking male 49 of the South Alley Burrow was generally one of 690 avoiding or retreating from 49 in instances involving priority of action, although they frequently ate or drank amicably together in the Food Pen.

Concerning the males of the colony in Area III in 1949, there were no behavioral records indicating dominance despite extensive observations in this colony during April when filming by the U.S. Army Signal Corps was underway. The lack of observed fighting during a time when male 49 consistently defended his territory of the South Alley Burrow and its environs at least indicates that there was less territorial defense. Further evidence of lack of fighting among the males of Area III is the fact that three of the only five males who had no wounds in May 1949 were members of this colony. A fourth male, No. 703, who had a fairly good growth (mean life span Maturity Index of I.75 with a May 1949 weight of 510 grams) and who with the other three slightly smaller males was accepted in the burrow by the nine females, might have been the dominant male, although I doubt it. He had nine body wounds. The fifth male, No. 786, was more likely the dominant one. During May 1949 he was the heaviest male in the pen, 583 grams, despite the fact that he had a less favorable earlier growth than several of the other males. His 25 wounds in May 1949 (male 49 had 26) certainly did indicate that he frequently engaged in combat and it is unlikely that he lost since he weighed from 40 to over 100 grams more than any other male with whom he had occasion to come in contact. During the 1949 breeding season he lived a solitary life residing in harborage boxes away from other rats. Assuming that he was the dominant male and that it was his activities which maintained the exclusion from Area III of the many males inhabiting the immediately adjoining localities, his past history becomes particularly interesting. He was a member of the last litter born in 1948 at the North Alley Burrow and all of his three sibs were females. This reduced competition. Furthermore, the lateness of his birth precluded the possibility of his receiving aggressive action from lactating females following his own weaning. He remained at the North Alley Burrow until about the time in 1949 when the reproducing females in Area III began coming into estrous. Just preceding the breeding season there were 10 males residing in Area III. Five of these (Nos. 74, 82, 89, 657, and 909) were among the 15 males weighing over 525 grams. This formed quite a concentration of large males in Area III when one considers that there were 69 adult males at that time in the pen. Their being here also indicated that Area III had become a more favorable

area, particularly with reference to Area IV and and the North Alley. Male 786 must have dispersed this aggregation of large males at the beginning of the breeding season. Males 82, 74, and 89 went to the adjoining Area IV and the North Alley where 82 and 74 were presumably dominant males (see colonies f and j, pp. 209 to 212). Male 909 moved back and joined the marginal all-male group opposite Passage 1 (colony i, p. 212). Male 657 became one of the outcast members of the East Alley Group. Thus large size did not insure a dominant place for these males (colony k, p. 213).

Since males who were dominant in different localities were rarely observed together it is difficult to assign an exact rank order to them. However, I am inclined to believe that male 82 was the next highest ranking male after 49, 690, and 786. These were the only males exceeding 82 in weight and 82 had apparently been excluded from Area III by 786. The basis for designating him as the dominant male over the area shown in figure 127 was that he was observed to repeal other males engaged in chases of estrous females, although he apparently rarely mounted the estrous females. However, his dominancy was not one of territorial defense as was that of males 49 and 690. He tolerated the presence of several other males in this central portion of his home-range, nor could he prevent the passage through it of males from all immediately surrounding regions. Two factors contributed to this apparent quasi-dominant status. He was the oldest and largest male born in 1948, who later most frequently inhabited Area IV. He was born in the socially most favorable colony of the pen at the South Alley Burrow.

Regardless of his actual rank among the dominant males, No. 707 exhibited an interesting relationship in his dominancy over the burrow in the South Alley by Passage 2. He was a younger brother of male 49 who dominated the neighboring South Alley Burrow and with whom he must have had considerable interaction during his early life (see p. 200). By February 1949 he and three of his sisters as well as his mother had moved to this location from Area II. All during the breeding season he persisted in invading the surface area of the South Alley Burrow, when females residing there were in estrous, and when male 49 was absent. However, he exhibited marked avoidance behavior whenever male 49 approached, or when they encountered each other in the Food Pen.

Although none of the 10 females of the South Alley Burrow, who conceived one or more times during the 1949 spring breeding season were ever seen in the act of copulation, and although male 707 was only slightly greater than average size (mean life span Maturity Index of I.86) it is highly probable that if any male other than 49 contributed to these conceptions it was male 707.

At the North Alley Burrow there was no clear cut dominance. As has already been mentioned, male 82 from Area IV partially shared control of this burrow. Of the 12 males (tables 52 and 53) residing in this general locality male 74 probably held the most dominant status. Although 4 of the other 11 males were of approximately the same weight as male 74, he was repeatedly observed to whip in combat other males who participated in the sexual chases of estrous females about the North Alley Burrow.

The designation of the dominance of the final two males was based upon more circumstantial evidence. Male 97 was assigned as the dominant male of the all male aggregate inhabiting the alley region about Passage 3 solely on the basis that he was the heaviest of the 13 males (table 55) and was the only one that had not lost considerable weight. Of the two males inhabiting Area II (table 47), male 751 was assumed to be dominant over male 95. Three lines of evidence lead to this conclusion. First, male 751 continued to grow during the 1949 spring breeding season until he surpassed male 95 who had declined in weight. Second, male 751 had continued to reside near the place of his birth while male 95 was known to have been driven from his place of birth, Area I, by male 690. Third, two of male 751's sibs, males 49 and 707 were definitely known to have dominated local areas. This points to the favorable condition of his early life.

a. *Summary of Male Dominance and Its Implications.* It was impossible to determine all the conditions which influenced the acquisition of dominance or the selection of an area to be defended. However, the histories of the males discussed above strongly suggest certain conditions.

1. *Weight.* During the 1947 season weight alone seemed to determine dominance. It is to be noted that because these rats were colonizers there was little likelihood of culture influencing the outcome. Later other factors than weight certainly operated. Male 22 defended Area I in 1948 despite the survival of two of his larger brothers who did not

defend territory. However, it is to be noted that the two males, Nos. 49 and 690, who most markedly defended local regions in 1949 were respectively the third and second heaviest of all the males. Even so, the lighter of these two dominated the other.

2. *Age*. If this really is an influencing factor it probably operates through the greater weight of the older rat and as a result of the older rat with its greater experience having an advantage over its younger antagonist. Figure 123 supports the contention that age is a factor. In 1948 it was one of the three oldest males who dominated the 10 adult males. In 1949 the most dominant male was a member of the first litter of the season in Area II. Three of the other seven dominant males of 1949 were members of the first litter born in 1948.

3. *Culture*. The characteristics of the mother as well as the social condition of the other rats inhabiting the vicinity of the place of birth appear to provide an important part of the determinants which incline a male toward becoming a dominant individual. Female 15 was the mother of three of the males (Nos. 690, 82, and 74) judged to be dominant in the spring of 1949. She was the oldest female to breed in 1948, and she selected the South Alley Burrow as the place for her litter (Litter No. 7). It will be noted that several lines of evidence showed that the South Alley Burrow was the most favorable locality in the pen for rats to live. Female 44 was the mother of three of the other males (Nos. 49, 707, and 751), who were judged to be dominant in the spring of 1949. She was by far the largest of the females breeding in 1948. This certainly must have contributed to her ability to defend her young, for whom she was also an excellent provider of stored food. Female 44 had moved to Area II shortly before she was 4 months of age. This move to a locality inhabited by no other breeding female in 1948 enabled her to rear her young without the added competition of social pressure from other juveniles or from lactating females. Whereas, such rather indefinite cultural attributes as discussed above may at first appear to form a rather frail basis for judging their importance in contributing to the eventual dominant status of a male, it

is noteworthy that for practically all other litters born in 1948, and which did not produce dominant males, there were one or more unfavorable conditions surrounding the early life such as excessive competition with other juveniles or lactating females, low weight of the mother, or past history of social subordinancy of the mother.

If the pattern of male dominancy revealed in this study is also true of rats living under other wild states, it has particularly relevance to gene flow through the population. Wheras, females, particularly those that are successful in rearing young remain at the place of their birth, males tend to become dominant in some other area than their birth. Furthermore, since those males which are quite dominant do exclude other males, including the sibs of the females in question, the degree of inbreeding (see pp. 142 to 143) will be lessened.

I. *Development of Local Colonies.* During the breeding season of 1948 and continuing through the nonbreeding winter season of 1948 to 1949 shifts in place of residence occurred (table 30). These were primarily from the southeast half of the pen toward the northwest half. This shift was from the area of higher social status, with its higher rate of production of young, to the region of lower social status, with its lower rate of production of young. Gradually through the winter the shifting about lessened, and local aggregates or colonies developed more constancy of membership. In fact, by the beginning of the breeding season in early March, the membership of local colonies (fig. 128) became so rigidly fixed that there were few further changes through the remaining history of the pen to late May 1949, at which time all rats were captured and killed.

The composition and history of these local colonies throws considerable light upon the nature and implication of social organization in the Norway rat. A local colony is considered as any group inhabiting a single burrow system, or as any group in which, for whatever reasons, the members had much more frequent associations with each other than with other rats.

Six criteria were used for judging the relative social rank of a colony. They were:

1. Proportion of the group which remained near the place of birth. The greater the proportion remaining near the place of birth, the higher the social rank.
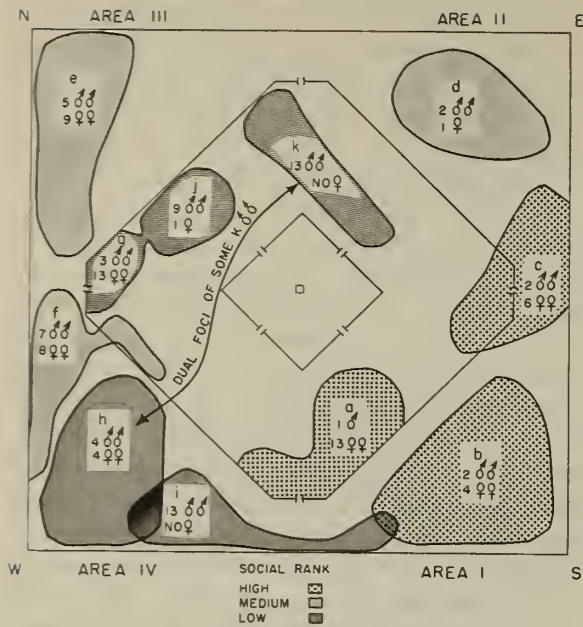
Figure 128.—Discrete colonies during the spring of 1949. See tables 44 to 56 for characteristics of the members of these colonies.

2. Number of places of birth represented by members of the group. The more places of birth, the lower the social rank of the group (see p. 214).

3. The location of the colony. This takes into account the whole history of the population, which indicated that the southeast (particularly the south) side of the pen was the favored region, and that proximity to the food source favored high social rank.

4. The proportion of the group formed by females. The higher the proportion of females, the higher the social rank of the group.

5. The reproductive success of females on the basis of number of conceptions and successfully weaned young.

6. The number of wounds.

On a rather intuitive basis these criteria were weighted to form the ranking of the colonies from a to k in a descending order of social rank. See tables 44 to 48 and 50 to 55, and figure 128.

Explanation of tables 44 to 57. S.A.B. and N.A.B. refer to birth at the South and North Alley Burrow. The Maturity Index reflects the mean growth rate. At each time of capture each rat was assigned as being characterized by rapid growth (I), moderate growth (II), or slow growth (III). These readings

were averaged to give a Maturity Index which most nearly reflected the growth rate of the rat during its entire life span. Thus I.38 represents greater than average growth rate while II.10 represents slight less than average growth rate. For further details on growth and this index see pages 216 to 236. The May 1949 weight for certain females is shown in italics. These rats were pregnant. Their weights were excluded in deriving data pertaining to weight in tables 55 and 56. Information on placental scars is incomplete since the uteri of only a portion of the females were were preserved for later counts.

a. *General Remarks about the Colonies as they Existed in the Spring of 1949.*

Colony a: *South Alley Burrow*—(table 44, fig. 21).

An appreciation of the formation of this most favored colony requires consideration of those rats who were born here but later emigrated. None of the 22 males which were born here in 1948 and which survived into the spring of 1949 remained here. See comments under prior discussion (pp. 199 to 200) of the dominance of male 49 for some of the reasons for their dispersal. Also see the comments under colony i for the males who remained as marginal members. I was never able to determine why some of the females born at the South Alley Burrow remained, whereas others emigrated. Among those which bore litters, there was no difference in growth and maintenance of weight between those who remained and those who emigrated. However, 78 percent of these females who remained in the southeast half of the pen successfully reared young, whereas only a 50 percent success characterized the females who emigrated (table 31). Some of the characteristics of this colony, not included in table 44 are:

1. The entire past history of this colony indicated a most favored status.

2. The females were protected by the single most dominant male of the pen from excessive disturbance by other males.

3. The rats of this colony, with their more stable social structure, were able to maintain the physical structure of their burrow. Compare figures 21 and 22 and the remarks under colony j.

Only 3 of these 13 females failed to have any surviving young at the end of May 1949 which were born during the preceding spring breeding season. Two of these, 778 and 704, had exhibited the

Table 44.—*Colony a: South Alley Burrow, April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (56)	Placental scars
Males: 49..............	Area II...........	I.00	548	26	....	....
Females:						
80................	SAB.............	I.07	568	7	Yes................	12
767...............	SAB.............	I.40	438	2	Yes................	....
98................	SAB.............	I.80	*472*	5	Yes................	28
778...............	SAB.............	II.60	390	2	No................	15
676...............	SAB.............	I.38	435	0	Yes................	7
689...............	SAB.............	I.50	488	24	Yes................	....
700...............	SAB.............	II.00	436	2	Yes................	....
702...............	SAB.............	II.00	435	0	Yes................	17
704...............	SAB.............	II.10	478	0	No................	6
705...............	SAB.............	II.00	468	1	Yes................	....
1075..............	SAB.............	I.00	402	5	Yes................	....
93................	Area I............	I.33	493	0	Yes................	11
39................	SAB.............	(1)	....	....	....	....
Mean...........	....	I.68	457	4	....	13.7

1 She is a senescent female too old to breed.

slowest growth rate of any of their associates. Thus, within a single colony reproductive success appears to be correlated positively with growth rate just as this relationship is indicated with more inclusive groupings shown in table 56. The third nonreproducing female was No. 39. She was one of the mothers of these other females. By May 1949 she was over 600 days of age and can be classified as a senescent, postreproducing rat on the basis of sparse pelage and relatively minute uterine horns. This inclusion and presumably tolerance of an old female suggests a rudimentary phenomenon among rats in harmony with the ethic of honor thy father and mother.

Although no males born in 1947 survived to May 1949 there were four other females which did. Each of these was accepted by the members of a local colony. See female 44, colony c, table 46; female 37, colony e, table 48; female 43, colony f, table 50; female 42, colony g, table 51.

Colony b: Area I (table 45).

Like colony a the majority of this colony were also born in the locality of later residence. Thus, the colony was not only homogeneous in membership, but was composed of nonemigrants. One situation which may have detracted from the stable organization of this group was that there were four separate burrows. Two were adjoining Boxes 6 and 9, the third was connected to both Boxes 2 and 3, and the fourth was by the fence opposite Boxes 8 and 9. There was less opportunity for these rats to develop mutual tolerances and associations, than was true of colony a at the more communal South Alley Burrow. A further disadvantage experienced by members of colony b was that they had to travel farther for food than did members of colony a, and in doing so they had to pass through Passage 1, which was so frequently defended by male 49, the dominant male of the South Alley Burrow. Male 690 protected the four females of colony b through his persistent chasing away of other males who entered Area I. I believe that the presence of the small male 737 in Area I resulted from the development by him of such a docile behavior as not to elicit aggression by 690. Despite the presence of seven wounds, the very fact that his pelage was in good condition reflects the fact that he had experienced less stress or aggressive action. In contrast to him, all members of the neighboring all-male colony i had much thinner pelage.

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TABLE 45.—*Colony b: Area I; April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (15)	Placental scars
Males:						
690	SAB	I.00	570	7		
737	Area I	II.75	453	7		
Mean		I.88	511	7		
Females:						
92	Area I	I.36	501	2	No	
96	Area I	I.17	506	14	Yes	2
734	Area I	II.62	340	2	Yes	7
733	Area I	I.50	*512*	4	Yes	
Mean		I.66	449	5. 5		4. 5

Colony c: Passage 2, burrow and burrows by Box 10 and by the gate (table 46).

Despite all of these rats having emigrated from their place of birth, the fact that five of the seven members consisted of four sibs born in Area II and their mother, female 44, indicates that this was a fairly well-knit group. However, their in-inability to prevent their major burrow by Passage 2 from disintegrating into separate segments suggests that the group was sufficiently disharmonious in their relationships to maintain the continuity between the separate regions in which the different rats lived. Female 378, although living close to the others, actually remained somewhat aloof from them. Her history is given in detail on pages 27 to 29.

TABLE 46.--*Colony c: Passage 2, burrow and burrows by Box 10 and by gate, April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (15)	Placental scars
Males:						
736	Area I	II.00	538	8		
707	Area II	I.86	498	12		
Mean		I.93	518	10		
Females:						
378	SAB	II.17	450	4	Yes	21
48	Area II	I.19	525	4	Yes	16
875	Area II	II.10	441	2	No	27
925	Area II	I.50	492	26	No	5
63	Area III	I.14	530	4	No	6
44	SAB	(1)				
Mean		I.62	488	8		15. 0

[1] She is a senescent female too old to breed.

Colony d: Area II, except Box 10 (table 47).

Why so few rats inhabited Area II during the spring of 1949 is somewhat of a mystery. The following train of events certainly contributed to their absence. During the winter, until mid-January, female 44, who had been the dominant female of the whole pen, and her 600 gram son, No. 49, who was becoming the dominant male of the whole pen, lived here. Their presence probably kept down the invasion to five rats. Actually, three of these were hardly invaders. They were Area III rats which had lived with the young of female 44 since they were juveniles. None of

female 44's young, born in Area II, were still here with her. The migration of female 44 back toward the South Alley Burrow in late January along with six of these nine young of hers, including male 49, left Area II without any controlling individuals. In fact, once these two rats left all the remaining rats also soon left Area II. Practically no rats were observed here during February and March. Up until mid-April female 75 was residing in the adjoining Area III, where she had moved earlier from Area IV with her three surviving adult progeny. She moved over into Area II about April 18, when she had her litter in Box 13 burrow. See page 202 for comments concerning male 95.

TABLE 47.—*Colony d: Area II (except box 10), April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (9)	Placental scars
Males:						
95................	SAB...............	I.50	472	13	....	....
751..............	Area II............	II.00	490	0	....	....
Mean...........	....	I.75	481	6. 5	....	....
Female: 75............	SAB..............	I.00	*644*	8	Yes................	[1] 16

[1] Includes the scars of the pregnancy upon last handling before shipping her to the National Institutes of Health. This second litter was born in transit to NIH.

Colony e: Area III (see table 48).

The most striking thing about colony e was that none of the 14 rats born in Area III during 1948 and which survived to May 1949 still lived in Area III. Ten out of the 16 rats born in Area III and alive to mid-January 1949 still resided in Area III. All were excluded by the beginning of the breeding season in March 1949. Five of the surviving males became members of the lowest ranking and all male colony k. A sixth, and largest of the Area III born males became a member of colony j. The seventh surviving male, 59, although apparently in a more favorable situation than his sibs, that is in colony g, was functionally an asexual runt. Although none of the Area III born females produced surviving young from March through May 1949, their dispersal is instructive (see table 49).

The point of interest is that the more inhibited was their physical maturation, the lower was the social rank of the colony they joined after being excluded from Area III.

Even as the replacement of Area III born rats began to occur, principally by Area IV rats, there was local segregation within Area III. In February 1949 the two local colonies living in burrows leading from Boxes 23 and 25 illustrate this. Among the 16 rats in Box 23 burrow there were four of the to-be-excluded Area III rats (female 43 and three of her progeny), but only two of the invading Area IV rats. In contrast to this, six of the nine rats in the adjoining Box 25 burrow were Area IV invaders (females 37 and 75 and four of their progeny), while there were no Area III rats here. See figure 129 with its indications that the Box 23 Burrow rats were the lower ranking of the

Table 48.—*Colony e: Area III burrow (including boxes 23, 26, and 27) April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (21)	Placental scars
Males:						
703	SAB	I.75	510	9		
462[1]	Area IV	II.17	490	0		
786	NAB	I.20	583	25		
742[2]	Area IV	II.25	470	0		
Tag lost			508	0		
Mean		I.84	512	6.8		
Females:						
71	SAB	I.25	520	5	Yes	10
655	SAB	I.40	428	6	Yes	15
749	Area II	II.00	434	3	No	
766[2]	Area IV	II.13	*440*	0	No	*11+*
740[2]	Area IV	II.00	414	7	Yes	
352[1]	Area IV	I.20	484	4	No	
915[1]	Area IV	II.25	332	5	do	
797[1]	Area IV	II.70	*426*	0	do	*11+*
37	SAB	(3)				
Mean		I.87	435	3.8		12.0

[1] These rats were either the young of female 37, or at least were closely associated with her in the same burrow with her young of a similar age.

[2] Young of female 75; see colony d.

[3] She is a senescent female too old to breed.

two colonies. Furthermore, 6 of the 9 invading rats forming the Box 25 burrow aggregate in February 1949 were still in Area III during March to May 1949; but none of the 16 rats forming the lower ranking Box 23 burrow aggregate in February 1949 were here during the following spring. This difference has a Chi-Square of 5.579 with a probability of less than 0.02. Thus, even during the prebreeding season, there was local differentia-

tion into subcolonies of rats inhabiting Area III. This differentiation was on the basis of which rats were to remain here, and which ones these were going to exclude by the beginning of the breeding season.

Colony e demonstrates that a marked homogeneity of origin of members of a colony does not not necessarily confer upon them a favored status. The majority of the members of this colony came from Area IV, which historically was composed of socially lower ranking rats than those from Area I or the South Alley Burrow. In line with this difference in place of birth both of the colony e females born at the South Alley Burrow had surviving litters, whereas only one of the colony e five females born in Area IV did.

The influence of male 786, as presumably the dominant male of colony e, in the formation of this colony was discussed on page 202. One further comment about him is pertinent. He and five other males born at the North Alley Burrow during 1948 survived into the 1949 breeding season. All remained at or frequently

Table 49.—*Growth and later residence of those females born in Area III during 1948 and who survived to May 1949*

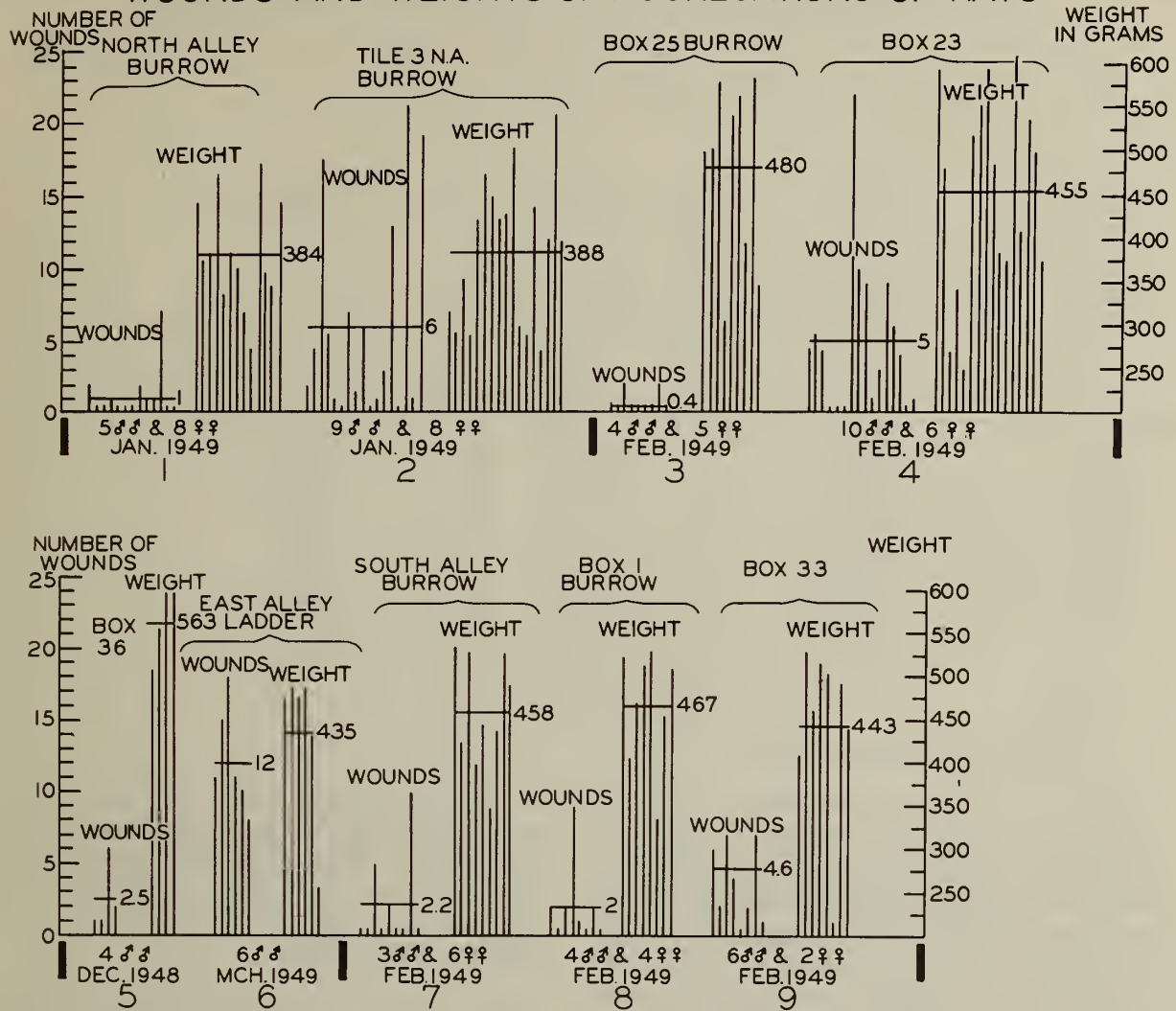| Number	Maturity index	Member of colony
63	I.14	c
62	I.81	f
658	I.90	g
661	II.25	g
60	II.56	h
58	II.67	h
659	II.83	j

WOUNDS AND WEIGHTS OF AGGREGATIONS OF RATS

Figure 129.—Comparative differences between aggregations of rats whose past histories differ. Groups between which the major comparisons are intended are set off by heavy bars at the base of the histograms. The four sets of aggregations are: 1 and 2; 3 and 4; 5 and 6; and 7, 8 and 9. Within each grouping the aggregation with the most favorable past history is placed on the left. Each individual is represented by a vertical bar. Means are indicated by horizontal lines cutting across the histograms. Three trends stand out: (1) fewer wounds, (2) greater weight, and (3) more females among those aggregations with the more favorable past histories. These are some of the aggregations as they existed prior to the reorganization of groups at the beginning of the 1949 spring breeding season. They show that even during the winter, when breeding had ceased and fighting was reduced, there were marked differences even between neighboring aggregations.

returned to the place of their birth up until the beginning of the 1949 breeding season. Of these males, 786 weighed from 100–150 grams more than any of these five males during May 1949 despite the fact that he was younger than they. The advantage of increased size is reflected by the fact that during the reorganization of the population coincident with the beginning of the breeding

season, male 786 moved to a more favorable situation and assumed control of Area III, whereas the five smaller males became members of the lower ranking colonies h, j, and k.

The formation of colony e epitomizes the results of many of the forces determining social oranization in the Norway rat.

TABLE 50.—*Colony f: Area IV burrow colony including Box 28, and burrow in West Alley*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (16)	Placental scars
Males:						
82................	SAB..............	I.11	542	14	....	....
89................	SAB..............	I.15	524	20	....	....
675...............	SAB..............	I.50	480	14	....	....
677...............	SAB..............	I.67	418	....	....	....
862...............	SAB..............	II.79	423	5	....	....
874...............	Area I.............	III.00	402	10	....	....
436...............	Area IV...........	II.60	400	25	....	....
Mean.............	....	I.97	456	14.7	....	....
Females:						
477...............	SAB..............	II.80	354	1	No..............	18
383...............	SAB..............	II.30	409	7	Yes.............	12
697...............	SAB..............	I.50	526	4	Yes.............	17
686...............	NAB.............	II.00	482	3	No..............	....
694...............	NAB.............	I.75	440	13	No..............	....
62................	Area III..........	I.81	347	21	No..............	3
354...............	Area IV..........	II.25	426	7	Yes.............	19
43................	NAB..............	(1)	....	....	....	....
Mean.............	....	II.06	427	7.5	....	13.8

[1] She is a senescent female too old to breed.

Colony f: Area IV Burrow Colony including Box 28 and the Burrow in the West Alley (table 50).

Two of the 15 rats of this colony actually had very little association with the remaining 13. These were females 383 and 697 who were born at the South Alley Burrow. During the spring of 1949 they established a burrow in the West Alley where each had a litter. This position brought them in closer association with the Area IV Burrow colony than with any other rats. In contrast to these two females, only one of the five nonsenescent females in the burrow opposite Box 28 in Area IV had a surviving litter, and this was the only one of the females which was born here. Whereas, birth at the South Alley Burrow favored reproduction, even elsewhere, it is important to note that the colony f S.A.B. female, who did not produce surviving young, was an extremely small, slow maturing individual.

One line of evidence supporting the belief that colony f was lower ranking than colony e in Area III, was that it contained the senescent female 43 and one of her adult progeny who had earlier been excluded by the rats invading Area III from the direction of Area IV. Even though a majority of the members of colony f were born at the South Alley Burrow, this does not overly accentuate the status of this colony, since most of them were individuals who were excluded from their place of birth, and were unable to establish themselves in a more favorable locality.

Colony g: Passage 4 burrow and its North Alley extension (table 51)

and

Colony j: North Alley Burrow (table 52).

Although listed as separate colonies, their proximity and prior history require discussion together. See figure 22 which shows the details of their burrow system. A number of lines of evidence have been given which indicate a considerable stress having been placed on the rats living at the North Alley Burrow. This stress led to social disorganization. Members born there departed, while rats born elsewhere moved in. Coincident with this social disorganization the burrow began to disintegrate into isolated segments. By June 1949 there was only one place in the burrow where an alternate route along tunnels was possible.

TABLE 51.—*Colony g: Passage 4 burrow and its North Alley extension, April–May 1949*

Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (0)	Placental scars
Males:						
59	Area III	III.00	395	12		
385	SAB	II.40	464	11		
879	SAB	II.50	438	15		
Mean		II.63	432	12.7		
Females:						
72	SAB	I.90	378	5	No	
851	Area I	II.80	322	3	No	2
77	NAB	I.00	570	20	No	
691	NAB	I.60	470	9	No	0
674	NAB	I.58	471	4	No	7
792	NAB	II.63	406	1	No	9
894	NAB	I.67	486	7	No	
791	NAB	II.37	396	3	No	3
886	NAB	I.33	392	0		12
658	Area III	I.90	420	5	No	9
661	Area III	II.25	458	5	No	12
370	Area IV	II.17		3	No	
42	NAB	(1)				
Mean		I.93	413	5.4		6.8

[1] She is a senescent female too old to breed.

TABLE 52.—*Colony j: North Alley Burrow, April–May 1949*

Rat's No.	Place of birth	Maturity index	May weight	May wounds
Males: [1]				
74	SAB	I.68	468	62
66	SAB	I.73	445	42
897	SAB	I.50	473	16
99	SAB	II.00	430	3
696	NAB	II.22	435	11
757	Area I	III.00	390	9
52	Area II	II.20	470	22
660	Area III	I.50	478	14
464	Area IV	II.80	446	16
Mean		II.07	448	21.7
Females:				
659	Area III	II.83	413	16

[1] Male 69, born at SAB., M.I.: I.40, probably belonged to this group. He was found partially eaten by other rats on May 26, 1949, along the path from the Food Pen to the North Alley Burrow.

The nearly all-male aggregation, designated as colony j, inhabited that portion of the burrow which had disintegrated into the most isolated parts. As shown in table 57, these males represented so many places of origin that colony j had the lowest homogeneity index (p. 214) of any of the colonies. This lack of common background is presumed to be a contributing factor in the lack of maintaining tunnels between adjoining nest cavities. The unkempt nature of their nests points to the fact that the members of socially disorganized groups lose the motivation or ability to maintain repair of the burrow system or to expand it. Actually this section of the North Alley Burrow had been disintegrating even during 1948 while female 42 and her several litters lived here. Compare figures 25 and 26. Therefore, the important point of interest may be simply the aggregating of these low-ranking males at this disintegrating burrow. Most of them had certainly been forced from more favorable localities. To what extent rats of disturbed past history are attracted to each other is unknown. The only female residing with these males was slower growing than any in the adjoining North Alley Extension of the Passage 4 burrow.

The females of colony g were probably a discrete subgroup from the males assigned to this colony. The sections of the burrow system which they inhabited had become isolated as a result of the collapse of a nest cavity. See the arrow separating these two sections in figure 22. The collapse of nest cavities is an indication of overcrowding which is more characteristic of socially disorganized groups. When there are too many rats in a nest cavity, they more rapidly scratch off the roof to the point of its collapse. The three males were the slowest growing of any aggregate. Living directly in front of Passage 4 exposed them to continual disturbance by the many rats from Areas III and IV which passed through Passage 4. This coupled with their small size, and the known indications of disturbance of male 59 strongly suggests that they were accessory males who did not participate in reproductive activities.

The most striking fact about the females of colony g was that seven of them along with their mother were born at approximately the position where they were found in May 1949, and yet none of them had surviving young. In fact, only two other of female 42's daughters lived elsewhere and they were non-reproducing members of the neighboring colony f in Area IV opposite Box 28. Whenever one of them came into estrous it was pursued all night by a pack of males from colonies f and j. Of the several females so noted, 674, happened to be marked at the time. On the basis of her frequently exhibiting lordosis during copulation, intromission probably occurred. Yet when she was killed 6 weeks later she had only six placental scars and there were no surviving young from the 3 months of the spring breeding period. All other females here had similar histories (see p. 155). These 13 females lived in 4 nest cavities. This crowding alone may well have led to the death of any litters born. In contrast to this, the 13 females of colony a, South Alley Burrow, had 10 nest cavities in which there were nests as well as 11 other cavities in which nests could readily be constructed. Thus, in colony a there was a cavity containing a nest for each female with a litter. Where there is not ample space in the burrow for a female to live in isolation at the time of parturition and following it, the normal response is to construct a new burrow during the day or two prior to parturition and to construct a nest in it. The failure of these responses to be exhibited in sufficient degree to isolate the parturient females of colony g suggests that these responses are inhibited in females under stress.

Colony h: Central Area IV (table 53).

The rats of this colony most frequently utilized Passage 1 enroute to and from the Food Pen. This exposed them to the antagonistic actions of male 49, the dominant male of the South Alley Burrow, colony a, as well as to that of the lactating females residing there. Colony h rats were most closely associated with the all-male colony k. Many of these colony k rats exhibited two loci to their home ranges. They spent the majority of their time in the area of the East Alley between the burrow by Passage 3 and Passage 6 into the Food Pen. Yet rather frequently some of these rats would leave the Food Pen in just the opposite direction and go over into Area IV by way of Passage 1. Despite separation in space colonies h and k might well be considered as a single unit. The intermingling of these two colonies is another line of evidence which leads me to believe that rats which have arrived at relatively the same social status are actually attracted to each other. There is nothing particularly noteworthy about the males of colony h, but the females require comment. Of the 35 females in colonies a to h which were examined for placental scars only four failed to have any. This suggests that these four never conceived. Three of these nonconceiving females were members of colony h. Furthermore, they were physically all very slow maturing. Of the 59 females in colonies a to h, which were born in 1948, there were only 10 whose Maturity Index was over II.5, yet 4 of these were at colony h. The comparison of the number of females with Maturity Indices over and under II.5 in colony h and elsewhere has a Chi Square of 15.081, with a probability by chance far less than 0.01. These females were exposed to more males than were any other group of females. They may be considered as having rather close associations with the 30 males of colonies h, i, and k.

Colony i: Areas I to IV Marginal Colony (table 54).

These 13 males were primarily (12 out of 13) those which maintained the closest association with their places of birth in so far as geographic position was concerned. They inhabited a burrow against the outer fence opposite Passage 1 as well as the three nearest harborage boxes in Area IV. However, they were very effectively excluded from the vicinity of the South Alley

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Rat's number	Place of birth	Maturity index	May weight	May wounds	Surviving young (0)	Placental scars
Males:						
775...............	SAB...............	I.64	528	11	....	....
777...............	SAB...............	II.17	446	10	....	....
725...............	SAB...............	I.83	466	11	....	....
669...............	NAB...............	II.00	468	24	....	....
Mean...........	....	I.91	477	13. 5	....	....
Females:						
76................	SAB...............	III.00	356	3	No...............	0
475..............	SAB...............	III.00	286	2	No...............	16
58................	Area III...........	II.67	405	12	No...............	0
60................	Area III...........	II.56	380	10	No...............	0
Mean...........	....	II.81	357	6. 8	....	4. 0

Burrow by male 49 and from Area I by male 690. Because of this situation, it is highly unlikely that they contributed much to the fertilization of females inhabiting these, the most favored localities. Although they formed an all-male colony, as was colony k, their more favored status is indicated by their higher homogeneity index (table 57) as well as by the fact that their mean number of wounds was 7.4 in contrast to 20.4 for colony k.

TABLE 54.—*Colony i: Areas I–IV marginal colony (including Boxes 31, 32, 35) April–May 1949**

Rat's Number	Place of birth	Maturity index	May weight	May wounds
Males:				
67......	SAB.......	I.17	530	9
699......	SAB.......	I.86	446	7
683......	SAB.......	II.14	386	2
909......	SAB.......	I.00	468	0
376......	SAB.......	II.40	402	19
479......	SAB.......	II.70	450	4
732......	Area I.....	II.00	490	9
735......	Area I.....	III.00	374	6
799......	Area I.....	III.00	446	9
852......	Area I.....	II.33	411	1
739......	Area I.....	I.17	500	18
760......	Area I.....	II.00	534	3
429......	Area IV....	III.00	306	9
Mean..	....	II.14	442	7. 4

*No females.

Colony k: Passage 3 Burrow and the East Alley Ladder (table 55).

The relationship of this colony to colony h has already been discussed.   The burrow by Passage 3 originally began as a way station for rats traveling between the North Alley Burrow and Area III. It soon began to attract, for overnight residence, individuals being excluded from these localities. As soon as this happened, the burrow began to decay and the tunnels and nest cavities became a stinking mire.   Nevertheless, it was inhabited by individuals who were becoming social outcasts and were forming colony k.   During late January 1949 I left a ladder lying on the ground in the East Alley opposite Passage 6.   Immediately some of the members of colony k began to utilize it as a place of harborage.   Here they remained under the paint platform with so little cover that they could readily be seen even when the temperature was near zero.   There was never any attempt by this group of males to construct a burrow or more than a padlike nest.   As in colony g, there was indication that increased stress inhibits burrow construction and nest building activities.   Other than the large number of wounds characterizing these rats the only other point of note was that five of the seven surviving males born in Area III and excluded from it became members of this group.

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TABLE 55.—*Colony k: Passage 3 Burrow and East Alley ladder, April–May 1949**

Rat's Number	Place of birth	Maturity index	May weight	May wounds
Males:				
79......	SAB.......	I.42	392	35
685.....	SAB.......	II.00	360	24
868.....	NAB	II.25	488	26
97.......	Area I.....	I.90	504	26
873.....	Area I.....	III.00	374	4
670.....	Area II....	I.67	450	27
54.......	Area III...	I.67	462	20
56.......	Area III...	II.50	444	39
57.......	Area III...	II.00	342	3
657.....	Area III...	I.50	452	27
662.....	Area III...	I.57	450	14
83.......	NAB	II.00	477	17
742.....	Area IV...	II.25	414	3
Mean..	....	I.98	429	20. 4

*No females.

J. *Stress and Reproduction.* The accounts of individual colonies amply document the reality of an intercolony gradation of characteristics. Even so an appreciation of the consistency across characteristics is difficult from these general accounts. I, therefore, arbitrarily divided the colonies into three groups (figure 128) which may be considered as having high, medium, or low social rank. These rankings reflect what I prefer to call social class (see pps. 176 to 178, 255 to 259, and 280 to 281).

Relevant characteristics of these three social classes are presented in table 56. Each of the 130 rats in this analysis was between 8 and 14 months of age. The higher ranked class contains proportionately the most females; they were larger; had grown faster; had conceived more often; reared proportionately more of the young conceived; and were less frequently wounded in combat. Medium ranked or middle class rats exhibited less favorable status on each of these six characteristics. Similarly on each characteristic the lowest ranked rats fared even less well than did the middle class rats. In a general way we are justified in concluding that the less favorable are these six characteristics the more intense has been the socially stressful experience of the rats forming the class.

Yet, social class is far from as discrete a phenomenon as table 56 seems to indicate. Had we considered a less closed population than that in the

Towson enclosure, I am sure that nearly imperceptible differences would characterize any particular ranked colony in comparison with the next lower ranked colony.

In order to gain more precise insight into the gradual transition in rank among colonies, five variables for each colony were transformed into indices. Each might vary from one to zero or near zero (table 57). The lower the index the greater had been the intensity of associated stressful conditions.

1. Weight index $= 1-(M-W/M-m)$
Where:
   $M=$ Maximum mean weight for a single of the 11 colonies.
   $m=$ Minimum mean weight for a single of the 11 colonies.
   $W=$ Mean weight of the particular colony for which the index is being calculated.

This index was calculated separately for each sex and half their sum is shown in the first column of table 57. Because of the importance of the sex ratio to stress a value of 1.0 was arbitrarily given for males in colonies lacking males, and 0.0 for females in colonies lacking females. Colonies whose weight index approached 1.0 had experienced few of the stresses which inhibit growth, whereas colonies whose weight index approached zero had experienced many stresses.

2. Proportion of the colony which were females.

The more females in a colony outnumber males the less stress the colony has experienced. This is discussed in detail under the topic of sexual behavior (pp. 152 to 158).

3. Homogeneity index.

The members of a colony may have been born mostly in the same locality. If this is so, the group has marked homogeneity of origin and similarity of social experience. On the other hand, the members of a colony may have had several different places of origin. Such colonies have little homogeneity of origin and experience considerable stress as a result of their lack of common social history. Let $0_1 \ldots 0_n$ be the places of origin of the members of a colony in an order of decreasing number of individuals per place of origin. Let $n_1 \ldots n_n$ be the number of individuals from origin $0_1 \ldots 0_n$. Then the homogeneity index $= [(1 \times n_1) + (0.5 \times n_2) + (0.25 \times n_3) \ldots n_n]/N$. N represents the number of individuals in the colony. By this arbitrary method a high homogeneity of origin approaches 1.0 and a

TABLE 56.—*Social rank and important conditions associated with it*

Rank [1]	Number		Mean May 1949 wt. gr.		Mean life-span maturity index		Mean number of wounds		Placental scars		Young [2]	
	Males	Females	Males	Females	Males	Females	Males	Females	Number of females examined	Mean per female	Total	Average female
High........	7	24	510	464	I.73	I.63	10. 4	5. 2	15	13. 1	95	3. 96
Medium.....	12	17	479	431	I.92	I.96	11. 4	5. 5	9	12. 9	37	2. 18
Low........	42	18	441	419	II.09	II.19	15. 4	6. 4	13	5. 4	0	0. 00

[1] See figure 128 for the grouping of the colonies according to high, medium, or low rank.
[2] Born March to May 1949, and still alive May 17, 1949.

TABLE 57.—*Indices of stress*

Colony	1 Weight index	2 Proportion females	3 Homogeneity index	4 Proportion of females reproducing [1]	Average number of young per female	5 Index of production of young	Composite index (mean of 1 to 5)
a......................	0. 884	0. 928	0. 90	0. 769	4. 3	1. 000	0. 896
b......................	. 698	. 666	. 91	. 750	3. 8	. 883	. 781
c+d...................	. 776	. 600	. 75	. 428	3. 4	. 790	. 669
e......................	. 648	. 642	. 72	. 555	2. 3	. 537	. 620
f......................	. 378	. 534	. 69	. 250	2. 0	. 465	. 463
g......................	. 228	. 812	. 65	. 153	0. 0	. 000	. 369
h......................	. 202	. 500	. 81	. 000	0. 0	. 000	. 302
i......................	. 056	. 000	. 71	. 000	0. 0	. 000	. 153
j......................	. 294	. 100	. 47	[2] 1. 000	0. 0	. 000	. 373
k......................	. 000	. 000	. 53	. 000	0. 0	. 000	. 106

[1] Lactating or pregnant May 1949.
[2] Only 1 female in colony. Though she was lactating when examined in May 1949 she had already lost her recently born young.

low homogeneity of origin approaches zero. Low homogeneity indices reflect forced dispersal, and lack of stable social oranization. A wider variation in this index would arise were it feasible to incorporate into it data concerning proximity to other colonies of known social rank.

4. Proportion of females reproducing.

5. Index of production of young.

The most successful colony reared on the average only 4.3 young per female. An index of 1.0 was assigned to this colony. The average number of young for the others are represented as percentages of 4.3. An arbitrary index of zero was given to those colonies lacking females since all indications were that even had females been present no young would have survived.

In the rank ordering of the colonies from a to k in a descending order of social rank, it may be seen that, with the exception of colony j, at least two out of the three indices are lower than for the preceding colony (table 57). No single one of these indices is alone adequate for judging the relative amount of stress. As the amount of stress increased, there was a decline in the reproductive performance of females. This decline is reflected both in the proportion of the females who were lactating or pregnant, and in the average number of young per female.

Reproduction is inhibited in two ways (see table 56). First, as the social instability and the resultant stress begins to increase, there is a reduced ability to rear the young which are born. This

conclusion is based upon the fact that there were only half as many young per female in colonies e and f as in colonies a to d, despite the fact that the number of conceptions, as indicated by placental scars, were approximately the same. Second, as the stress increased, there was a reduction in the ability to conceive; and such individuals reared none of their young.

These two phenomena are believed to be the most important ones through which population growth became inhibited in the presence of an abundance of food and ample space for the elaboration of new burrows.

A concomitant effect of stress is the inhibition of growth (see table 56). By May 1949 there was a decreasing mean weight associated with decreasing social rank of the adult rats born between March and October of 1948. This lower weight by members of lower ranking colonies was not merely a result of their having lost proportionately more weight during the 1949 spring breeding season. Rather, the most important interrelationship between growth and social rank was that the lower the social rank of a group of rats the slower was their mean rate of growth during their entire life spans. This is shown by the higher Maturity Index ratings for the lower ranking rats.

As a final evaluation of rank the mean of the five separate indices for each colony was calculated and designated as the "Composite Index" of stress (table 57). Now we might ask "What does this index mean?" Only an intuitive interpretation may be given. An index of nearly 1.0 means that the members of the colony encounter few difficulties in fulfilling their needs. As the index approaches zero the members of the colony have on the average found it more difficult to satisfy their needs. In fact, there is a nearly ninefold differential between the highest and lowest ranked colonies, with the intervening colonies forming a gradual transition between them.

This social ordering of degree of stress quite obviously favors survival of the species. Colonies having a Composite Index of stress less than 0.5 are destined to leave no progeny. Furthermore, the average index—calculated across all members of population—is well below 0.5. Thus, if rats failed to develop a class structured society they would not long survive as a species. One cannot help but believe that the evolution of social behavior in the Norway rat has been such as to assure the development of class-structured society.

6. *Growth, Health and Mortality*

A. *Growth of the Individual.* Measurements of weight and body length were regularly taken. Body length refers to the nose-to-anus span. Little variation in these for a particular age should have resulted from genetic variability, if the assumption of near homozygosity were actually correct. Therefore, differences in growth should mainly be attributable to environmental effects. The major environmental variables anticipated by the original experimental design were those which would arise from the interaction among rats. Social stratification, or differential social experience, such as did develop, should include the major interactions. These might well affect growth through altering the amount of food attained and consumed, or more indirectly as a result of an upset in the endocrine growth physiology of the adrenal cortex-pituitary growth hormone balance. Such imbalance might arise as a result of stresses associated with social interaction. Such was the rationale with which I looked forward to relating growth to conditions affecting the members of the developing population.

No data was obtained on how much food individual rats consume. As discussed previoulsy (pp. 99 to 105) considerable circumstantial evidence developed that all rats obtained *access* to more food than required to fulfill demands for optimum growth. There were signs of emaciation on only a few sick or old rats just prior to their death. Even stunted rats had good supplies of fat desposited through their mesenteries at autopsy. Such fat deposits in rats exhibiting stunted growth is just what might be anticipated as a result of stress. Evidences of stresses did develop in the form of altered activity cycles (pp. 117 to 126); avoidance of dominant associates (pp. 179 to 180); approach and withdrawal from places where encounters with dominant associates occurred, (pp. 194 to 196); increases in the total interindividual contacts with population growth as indicated by amount of available trails (pp. 54 to 63) in relation to the number of rats present (pp. 244 to 246); subordinate status upon direct aggression from dominant associates (pp. 180 to 183); and sibling competition (pp. 147 to 148). All following documentation of evidence supporting this contention that stress arising from social interaction was the major condition altering growth, must be viewed merely as supporting this hypothesis. The reason

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for this is that in a complex system, such as dealt with here, it is rarely possible to conclusively isolate cause and effect.

a. *Average growth curves.* For rats between 10 and 460 days of age there were 462 measurements of weight in grams and body length in millimeters for females, and 680 for males. The age range was divided into 28 class intervals so that there was a minimum of 10 records for a class interval. Three figures for each interval were derived; (1) a mean; (2) a "maximum"—this was the mean of the largest one-fifth of the measurements; (3) a "minimum"—this was the mean of the smallest one-fifth of the measurements. Average growth curves (fig. 130 to 133) were developed for these by the following procedure recommended by Professor W. G. Cochran of Johns Hopkins University.

$$K - y = 10\,[a - b(x - 40)]$$

where:

K = adult weight (This I assigned as the mean weight between 340 and 460 days of age.)

y = weight at a given age

x = age in days

a = log $(K - y_{40})$

b = a-log $(K - y_{280})$

Therefore $y = 10\,[a - b(x - 40)]$

$$= K - \text{Antilog}\,[a - b(x - 40)]$$

Since a new pattern of growth usually ensued shortly after weaning (which for the present purpose was taken as 40 days) the ordinate intercept occurs at 40 days of age. Therefore, in calculating y, $x - 40$ must be utilized instead of x. The observed data was plotted on semilog paper. The log ordinate was $K - y$ and the abscissa was age in days. For these mean data, so plotted, a straight
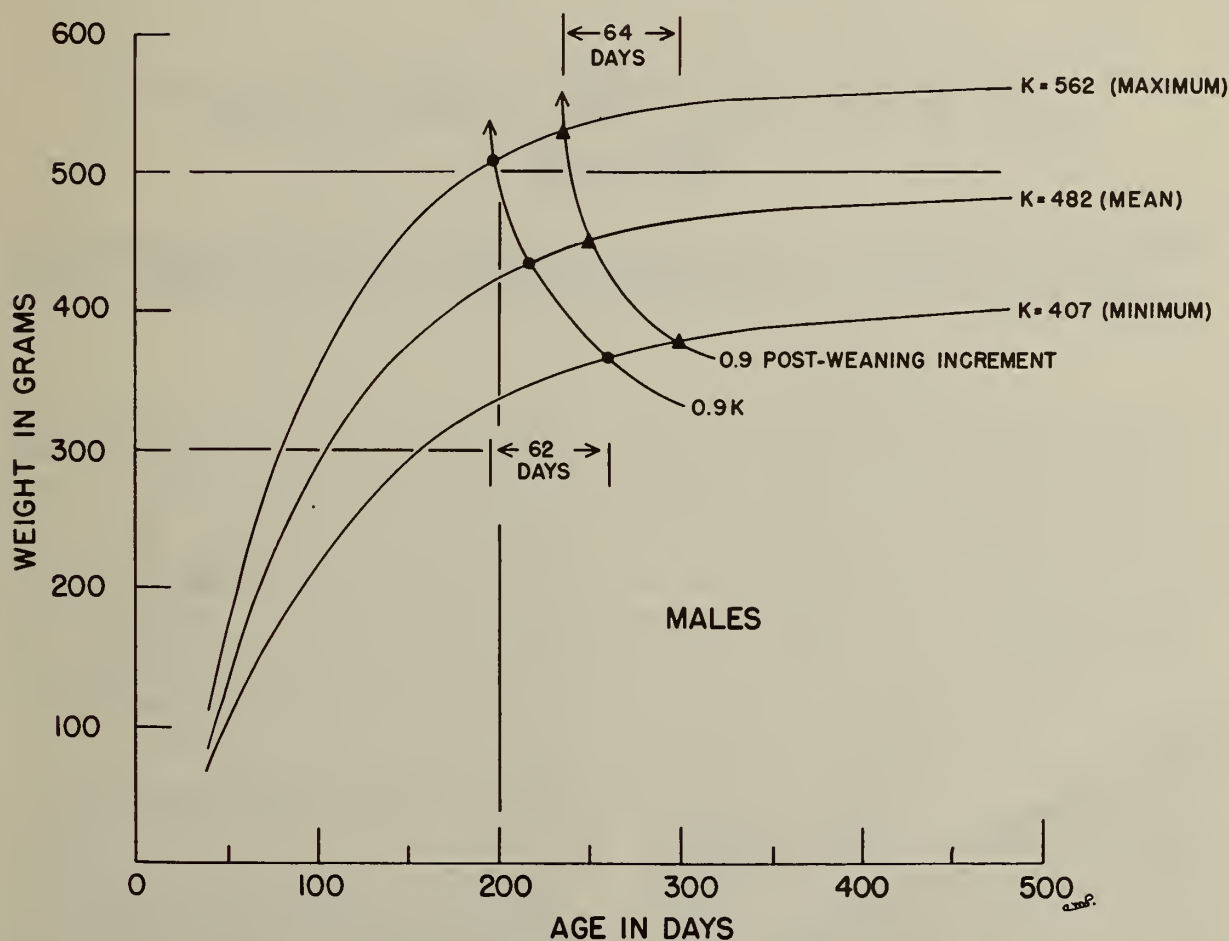
Figure 130.—Growth in weight of males. The maximum curve is that for the upper 20 percent of the records in each age class interval. The minimum curve is that for the lower 20 percent of the records in each age class interval. K's represent the mean adult weight at 391 days (i.e. all records between 340 and 450 days of age). Note that the rats with the lowest mean adult weight also grew slower as indicated by the 62-day differential between them and the heaviest rats in the age of attainment of the mean adult weight.
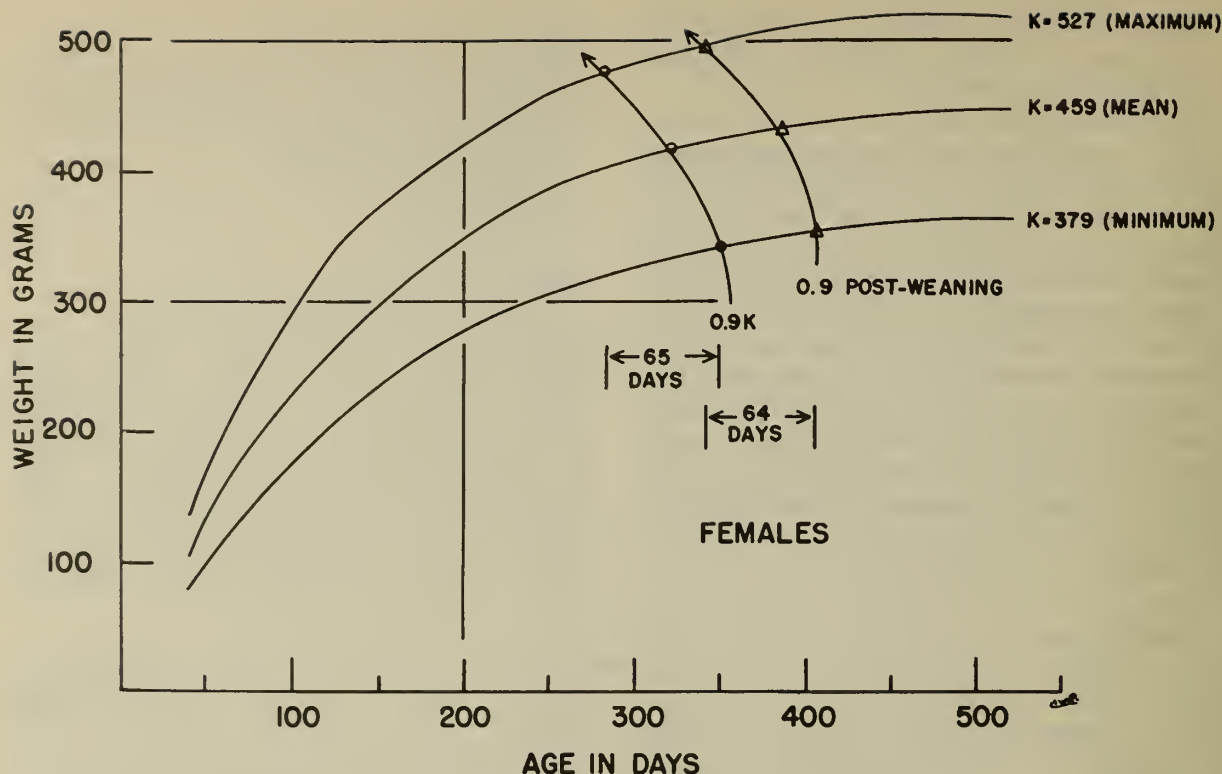
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Figure 131.—Growth in weight of females. The three curves are as described for males in figure 130. K's represent the mean adult weights at 387 days of age (i.e. all records between 340 and 450 days of age). As for the males, the smaller females were also slower growing. Note also that females not only were smaller than males but that they attained 0.9 K at a later age.

line could be drawn through them such that there was little scattering of the observed point about it. $K-y_{40}$ and $K-y_{280}$ were determined from this line. y's for 15 representative ages between 40 and 520 days were calculated as above described. In actual procedure this was a time consuming process. A close approximation of y may be made by reading $K-y$ from the fitted straight line for a particular age and subtracting this from K. This more rapid procedure was followed in the later development of growth curves for individuals or litters (fig. 136 to 141).

Rate of growth may be judged by the age at which $0.9K$ or 0.9 postweaning increment is attained.

$$\text{Age,} \quad x, \quad \text{at} \quad 0.9K = \frac{[a-\log\ (K-.9K)]}{b} + 40.$$

These x's are shown in figures 130 to 133. Both weight and body length exhibit a consistent trend

of greater age at $0.9K$ (or 0.9 postweaning increment) associated with lower K's. In other words the larger an animal the faster it grows. It must be realized that this conclusion rests upon the pooled data for many individuals. Confirmation of this conclusion from growth curves of individuals or of small groups, such as litters, could not be made because of the reduced reliability of K and because of the obscuring of any such trend by the changes in rate of growth apparent in these smaller samples (see growth charts in figs. 136 to 141).

Males not only grow larger than females but for the same K's, males grow faster than do females. That is for the same K, x at $0.9K$ is lower for males.

Growth of rats appears to be reduced from the optimum rate only at the time and to the extent that their physiology is upset due to stress. This stress interferes with maintenance of weight appropriate for a given age. Data on body length (table 58) are particularly pertinent
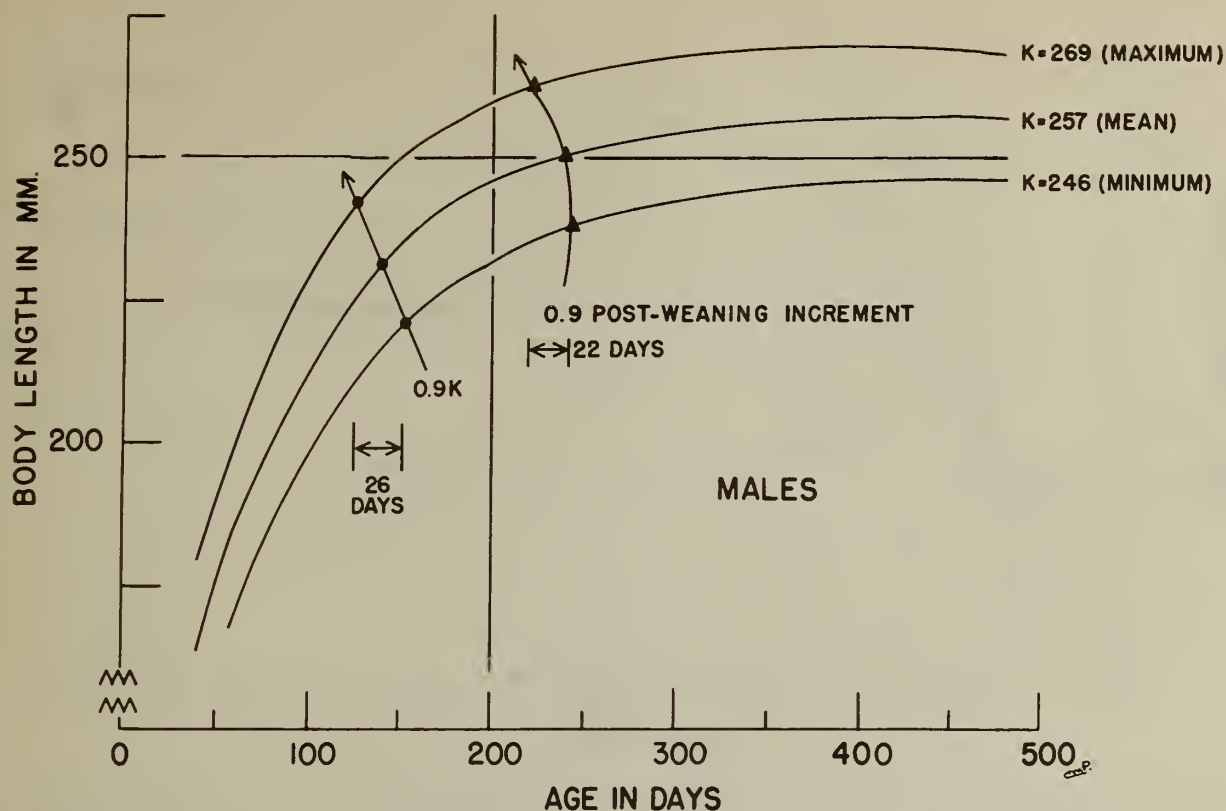
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Figure 132.—Growth in body length for males (body length was measured as the distance from the tip of the nose to the beginning of the tail). The three curves were similarly determined as for weight in figure 130.

TABLE 58.—*Variability in body length associated with changes in weight*

	Weight change		
	A Not calculated	B Decrease of 25 or more grams	C Increase of 25 to 75 grams
Days elapsing between 1st and subsequent capture..	1 to 7..............	Mean circa 30......	Mean circa 45.
Age in days...................................	100 or more........	260 or more........	260 or more.
N...	128..............	85................	71.
Mean change in body length in mm. from one record to the next.	−0.047...........	−0.141...........	+3.761.

Here the N represents all available comparisons in each category. Apparent significance of these data:

a. Column A represents the observer's error in making measurements.

b. There is an increase in body length accompanying increase in body weight (A to C comparison).

c. Increase in body length ceases following loss of body weight.

In fact, there is an indication that a slight shrinking of the body accompanies weight loss.

It may be seen that I selected the extreme category of relationship between body weight and growth as indicated by changes in body length. I am further assuming, that, during those ages when growth may actively proceed, any conditions which inhibit optimum increases in weight will also inhibit other manifestations of growth. In the charts of growth of litters born during 1948,
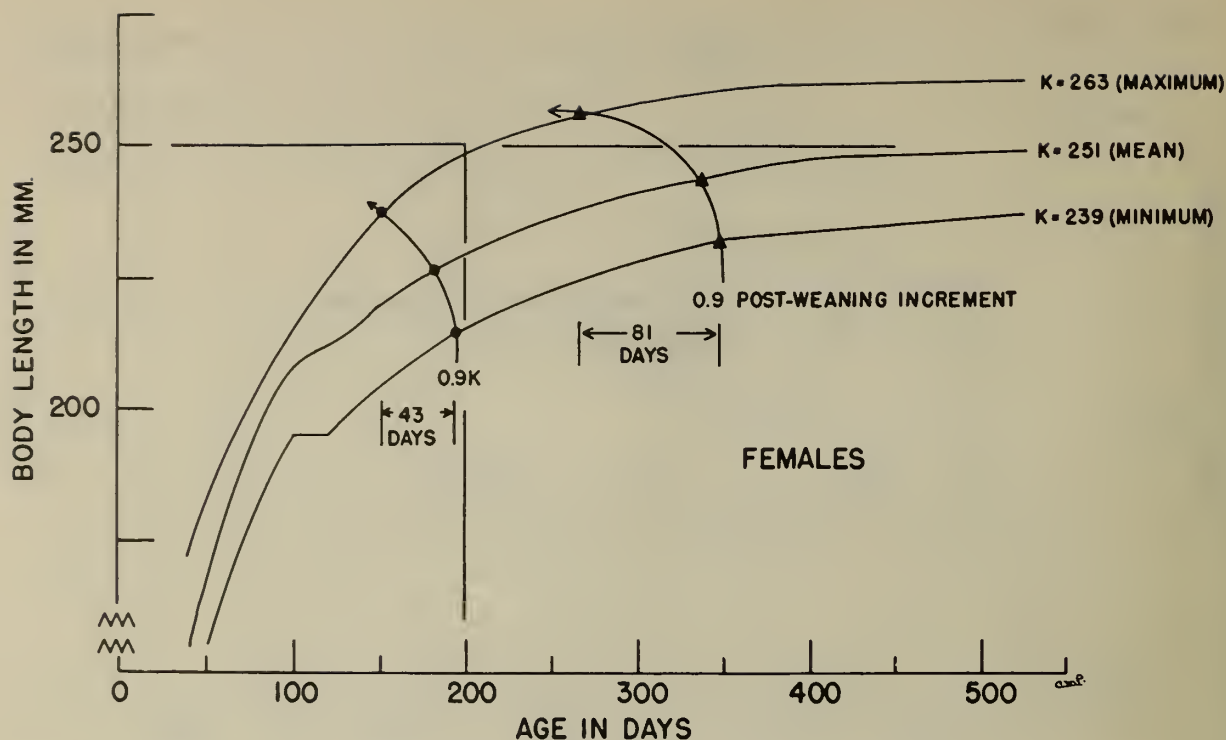
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Figure 133.—Growth in body length of females. See figures 130–132 for comments on procedures in developing these curves. Shortly after 80 days of age the mean data as well as the minimum data indicated an abrupt change toward a slower rate of growth. The maximum weights (the upper 20 percent), which presumably represents rats living under more favorable conditions did not show this depression in rate of growth.

both weight and body length are presented for a few litters. In most cases where there was a change in the rate of growth in weight there was a corresponding change for body length.

b. *The Maturity Index.* I soon noted that young rats were proportionately thinner than older ones. In other words, as rats become older the ratio, B/W, of body length (B) to weight in grams (W) became less. Furthermore, slower growing rats at any age were thinner than faster growing ones. This suggested that the B/W ratio might serve as an index to physical maturity.

Four curves of the B/W ratio were calculated:

a. Maximum B/ divided by maximum W.
b. *B* at one-third range from mean to maximum divided by *W* at one-third the range from mean to maximum.
c. *B* at one-third the range from mean to minimum divided by *W* at one third the range from mean to minimum.
d. Minimum B/ divided by minimum W.

As shown in figures 134 and 135 this resulted in three growth channels. These were designated as growth channels I, II, and III. I represents the

most favorable growth (fast-growing rats with a large adult weight), whereas III represents the least favorable growth. From the three representative rats shown in each figure it may be seen that each individual tends to follow a particular channel of this growth index.

The B/W ratio at each handling was calculated for each rat. Each B/W ratio was assigned to one of the three Maturity Index growth channels. Thus, an individual which was handled 10 times might fall in growth channel I five times, II four times, and III once. An average channel position was obtained; in this case I.6. In other words this individual fell on the average along a channel 0.6 of the way between the centers of channels I and II. Such means were calculated for each rat and are designated as its Maturity Index, or more briefly its M.I. Rats frequently lost considerable weight during a period of trapping or excavating burrows. Normally this weight loss was recovered by the next period of handling. In order not to unduly bias the Maturity Indices by these disturbances introduced by the observer, all noninitial captures in a trapping period, which revealed loss
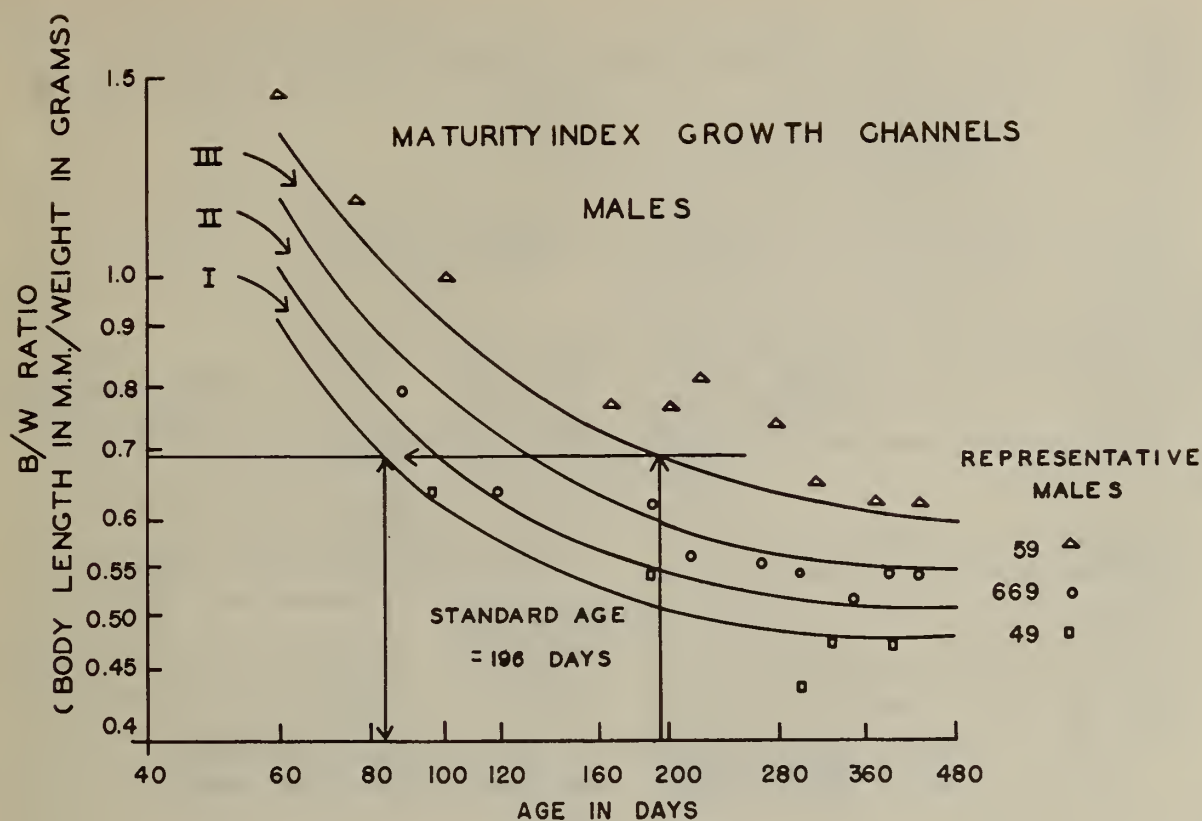
Figure 134.—Maturity Index Growth channels for males. The lower curve is the B/W ratio for the upper 20 percent of the records, while the upper curve is that for the lower 20 percent of the records. The two central curves represent the B/W ratio one-third the way toward the respective extremes from the mean. The standard age was assigned as that at which the fastest growing individuals attained 0.9 of their mature weight.

in weight, were excluded in the calculation of the lifespan Maturity Index.

This index has the advantage that it enables comparison in growth between sexes, the averaging of both sexes of the same social characteristics, or the comparison of rats who died young with those who lived to maturity. No further discussion of the Maturity Index is given at this point. In many other places in this monograph it is utilized to show the relationship between growth and other characteristics of the rats or the circumstances surrounding their life.

A standard age has been assigned as 196 days for males and 283 days for females. This is the age at which the maximum growth curve for weight attains $0.9K$ (i.e., 0.9 of the mature weight). At this age males characterized by the minumum growth curves have a B/W ratio which was attained 112 days earlier by males characterized by the maximum growth curves. A similar situation is true for females. Thus many individuals maintain

a juvenile body type far into the period which may be termed adulthood for other rats. Such evidence as reduced aggression or sexual behavior in rats who maintain a high B/W ratio suggests that slenderness of body type in some way determines or is correlated with the persistence of juvenile behavior in adulthood.

c. *Chronological order of birth.* An inspection of table 59 reveals that for 10 of the 16 comparisons of a litter with the preceding litter born in the same locality, the litter born later grew more slowly. Only two litters grew faster than the preceding one, while for four comparisons there were no appreciable differences in average growths (i.e., less than 0.1 variation in the Maturity Index).

The general magnitude of the differences in growth associated with order of birth is revealed by assembling the Maturity Indices for litters in terms of birth as early litters (Litters 7, 11, 14, 9, and 8), middle season litters, (Litters 10, 15, 17–19, 22a, 16, 25a, 13, 18, and 30), and late litters (Lit-
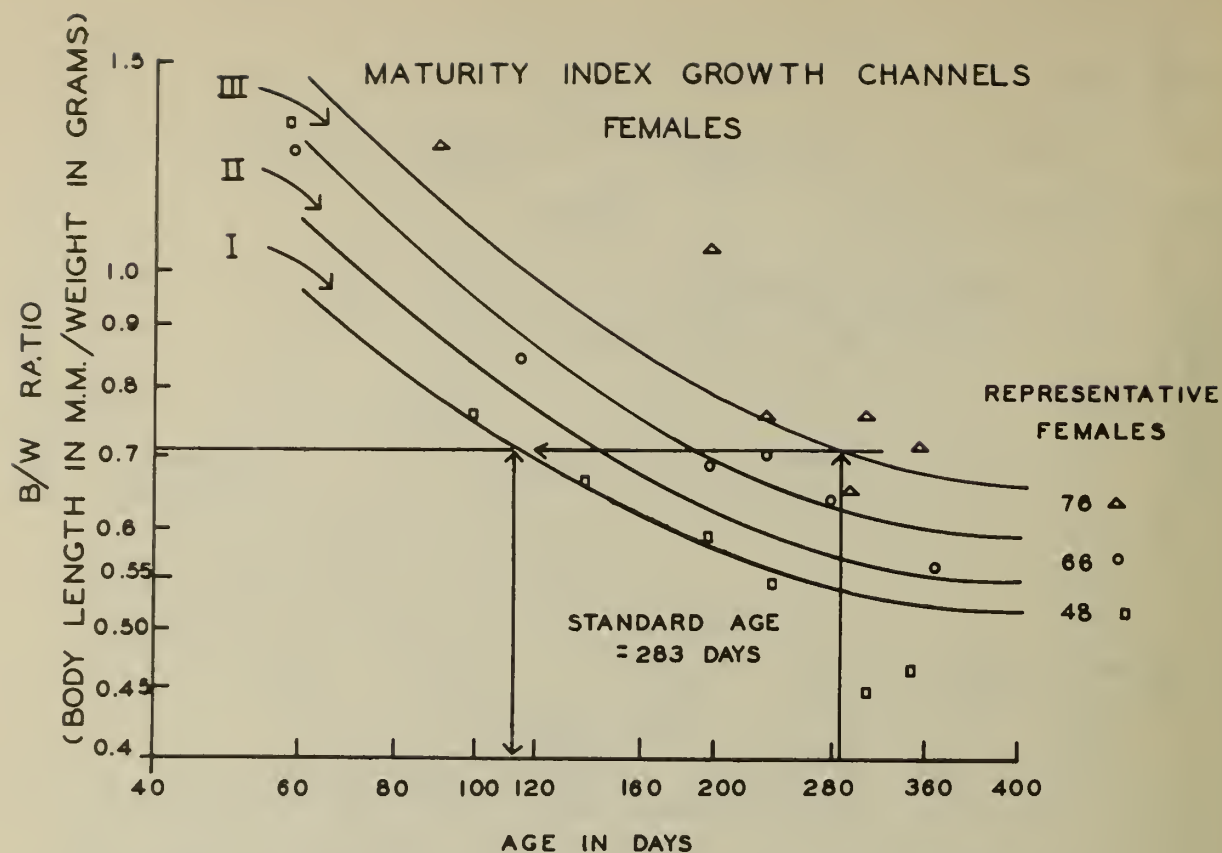
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Figure 135.—Maturity Index Growth channels for females.   See figure 134 for additional details.

TABLE 59.—*Average maturity indices for litters born during 1948*

Time of birth	Place of birth					
	SAB	NAB	Area I	Area II	Area III	Area IV
Mar. 7	L–7:I.26					
Mar. 16–27	L–10:I.77	L–11:I.43	. . . .	L–9:I.29	L–8:I.52	
Apr. 8–30	L–15:I.78	. . . .	L–14:I.51	. . . .	L–13:II.39	
May 16 to June 1	L–17, 19:I.71, L–22a:I.62	L–16:I.86	. . . .	. . . .	L–18:I.93	
July 1–20	L–25b:II.35	L–22b:II.18, L–23c:I.73	L–25a:I.75	L–30:I.92	. . . .	L–23b:II.12
August–October	L–32:II.60	. . . .	L–27a:I.72, L– 28, 29:II.83	. . . .	. . . .	L–33:II.37

ters 25b, 32, 22b, 23c, 27a, 28–29, and 33). A representative, rather than a mean Maturity Index was derived, in order that each period of time might be represented equally by each locality of birth. This representative Maturity Index was the mean of the means for each locality for the time period in question. Results are shown in table 60. These data show clearly that rats born later in the breeding season were more likely to exhibit inhibited growth.

TABLE 60.—*Representative maturity indices according to time of birth during the 1948 breeding season, and the approximate weights and measurements represented by these indices at 175 days of age*

Season Born

Maturity index	Early I.40	Middle I.92	Late II.20
Males:			
Weight...............	458	429	412
Length...............	252	247	244
Females:			
Weight...............	378	356	338
Length...............	237	231	227

In order to gain insight into why birth during a later period of the breeding season causes inhibition of growth, it is necessary to examine the growth charts (figs. 136 to 141) in the light of the circumstances surrounding the life of the litter.

Near optimum rates of growth are represented by male 690 (chart 1, fig. 136) and female 48 (chart 12, fig. 136). All other individuals, as well as litter means, exhibited less favorable growth. Inhibitions of growth, which arose at least by the time of weaning, as well as inhibitions arising later produced such depression from the optimum.

d. *Changes in rate of growth.* There is a marked sexual difference in the likelihood of a change in rate of growth. For the 25 charts of growth in weight of the litters born during 1948 (figs. 136 to 141), 13 of the 16 charts for males show one or more changes in rate of growth, whereas only 3 of the 9 charts for females exhibit such changes. The evidence that males experience more stress than do females (see data on wounds, fig. 122, migration, fig. 116 and health, table 64) suggests that the particular times when changes occur in the rates of growth are associated with changes in the intensity of stress. Males will be considered first.

Five (Nos. 1, 11, 13, 19, and 27) of the eight charts exhibiting a decrease in the rate of growth were for the first litters born in their respective localities. Litter 10 (chart 3) may for the present purposes be considered as a first litter. It was born at the South Alley Burrow 8 days after litter 7 (chart 1). The decrease in rate of growth fell between 100 and 125 days of age (mean 113) for those six litters. This is the age, based on behavioral criteria, when the rats become sexually mature. This age for these litters fell between June 17 and August 7. This was a time when many females, particularly those born in 1947, were in estrous. As a result there was competition among these males for the estrous female. Such competition was even more pronounced between them and the older males born during 1947. Prior to attaining sexual maturity, males of these litters were exposed to relatively much less stressful situations. In particular they were not forced to compete with older, but not sexually mature, juveniles. The inference is that growth rate mirrors the degree of stress currently being experienced.

Males of two other litters (charts 9 and 30) showed a decrease in growth rate later in life. The decrease by Litter 25b was associated with the initiation of the spring breeding season. However no other litter showed a decrease during this time. I can associate no events with the decrease in growth rate of Litters 28–29 which began about January 3.

There are eight clear-cut instances (see growth charts 3, 5, 10, 13, 16, and 25) where rate of growth increased. I can see no importance of the age at which changes occurred. However, seven of the eight inceptions of increase took place during the fall and winter when strife declined. One other litter deserves particular note. This is L–25b, chart 9. From 40 through 180 days of age there was a persistent increase in rate of growth. No other litter showed such a growth curve. Although one might assume that they were continually encountering more favorable conditions or making more favorable adjustments to them, there is no corroborative evidence for this.

The five changes in rate of growth for females (charts 8, 17, and 24) represent too small a sample upon which to base any inferences as to cause.

e. *Further remarks on the chronological order of birth.* As indicated previously the data on Maturity Indices show that litters born later in the breeding season tend to exhibit inhibited growth. The charts of growth in weight show this more precisely. We shall now examine a few of the sequences of litters born in specific localities.

South Alley Burrow: Males of the first two litters (charts 1 and 3) grew considerably larger than the average, and the first-born litter attained the higher adult weight. The third litter shown

Figures 136 to 141.—Growth curves for individuals or for litters. In each figure four to six curves or sets of curves are shown. Each of these separate graphs has a circled number in the upper left hand corner. These numbers designate the chart number as referred to in the text. For the sake of ready comparison the mean curve for the entire population of that sex is shown as a fine continuous line on each chart. The K's, the mean adult weight or length for each litter, was determined as the mean of the maximum measurement for each of the members of the litter. 0.9 K, and its age of attainment is indicated on each growth curve by a dot with the exact age indicated by an arrow on the abscissa. From time to time a change in rate of growth is shown on some of the charts. Had this change in rate not taken place the curve would have continued as shown by the broken line. These projected trends were ascertained by log-log plots of growth against age. Such plottings result in straight line growth curves in so long as growth rate remains unaltered. For example see figures 151 and 152. The months to which the measurements refer are shown at the tops of several of the charts.
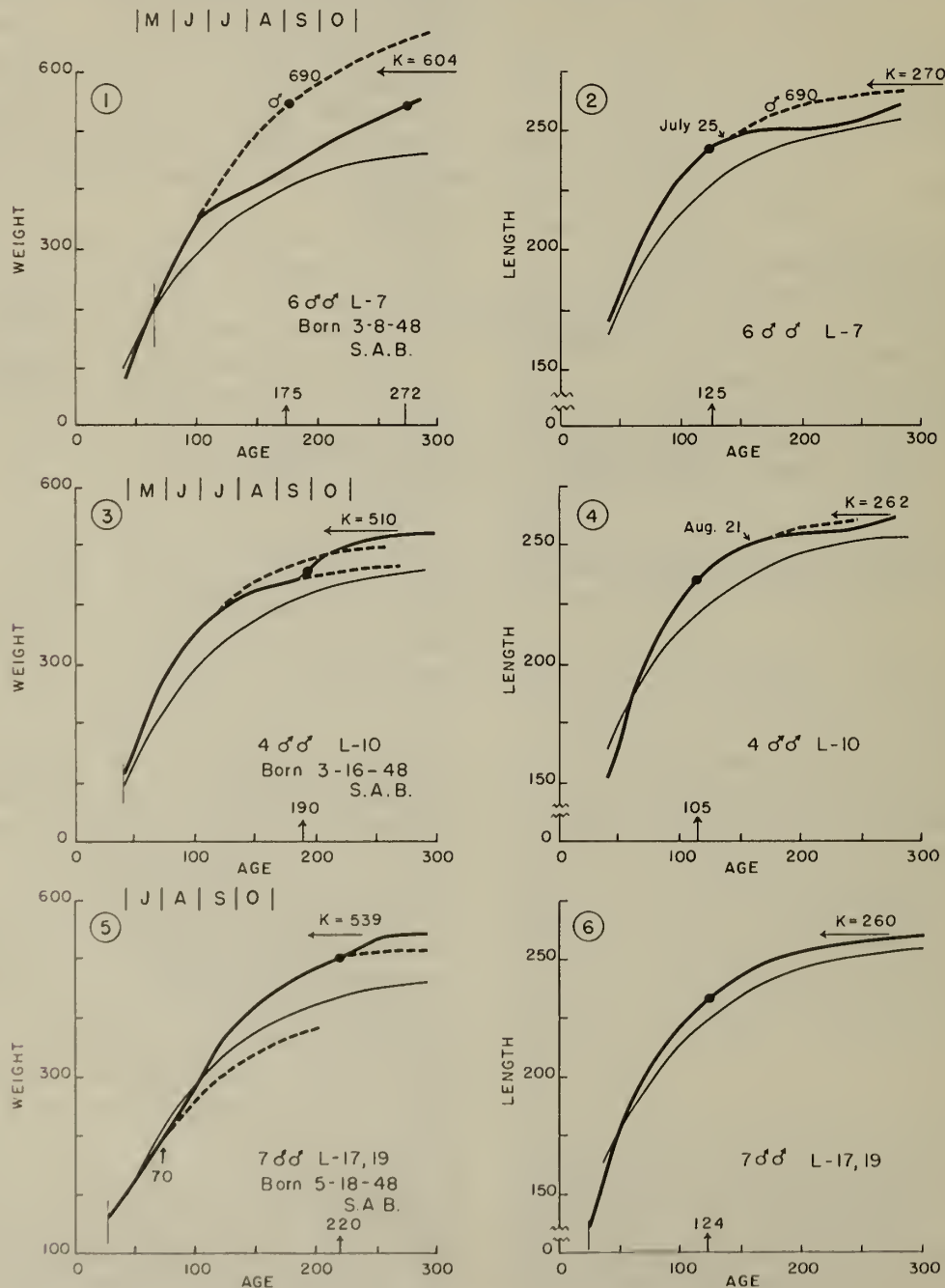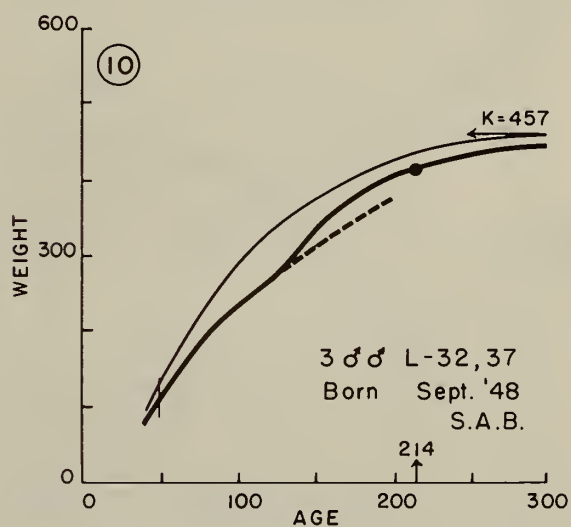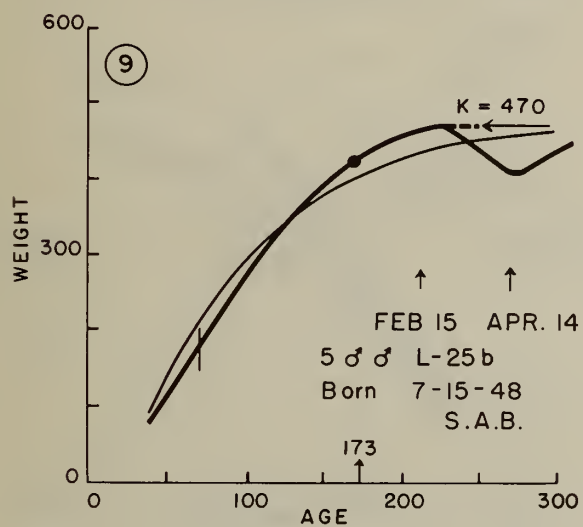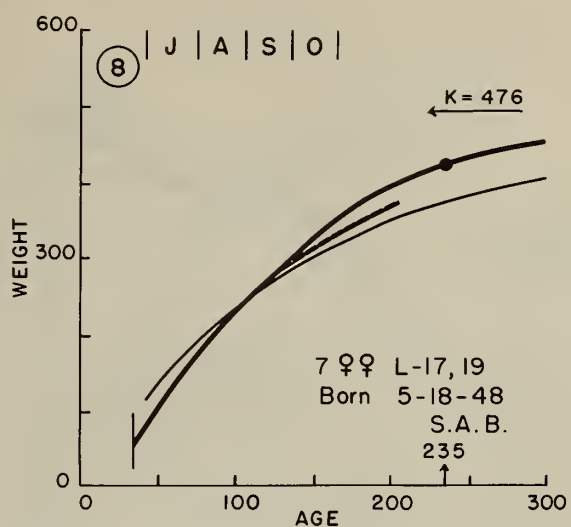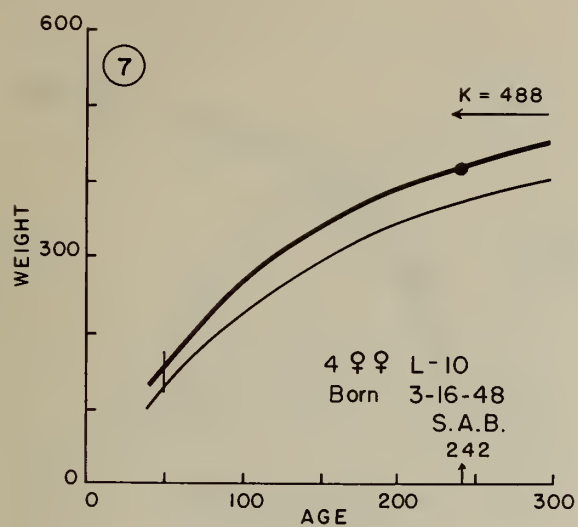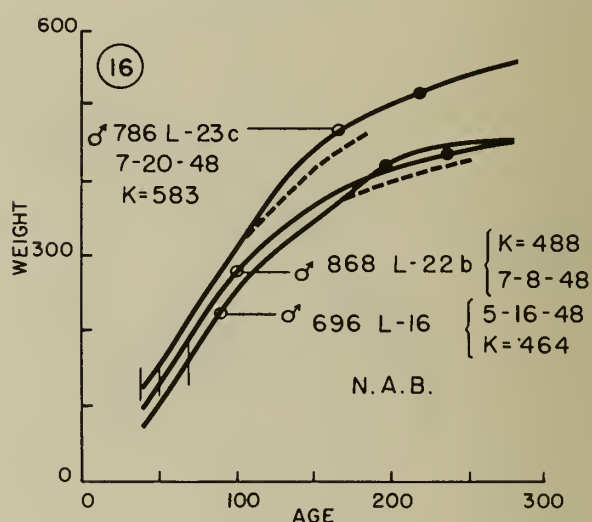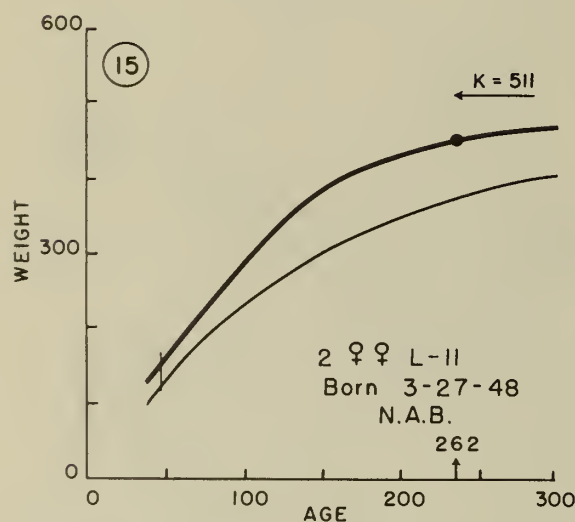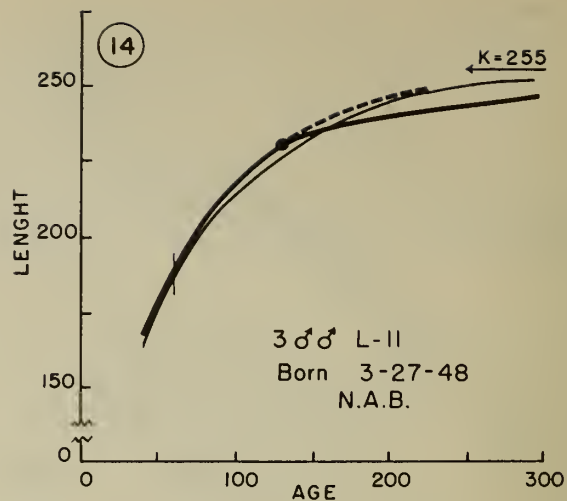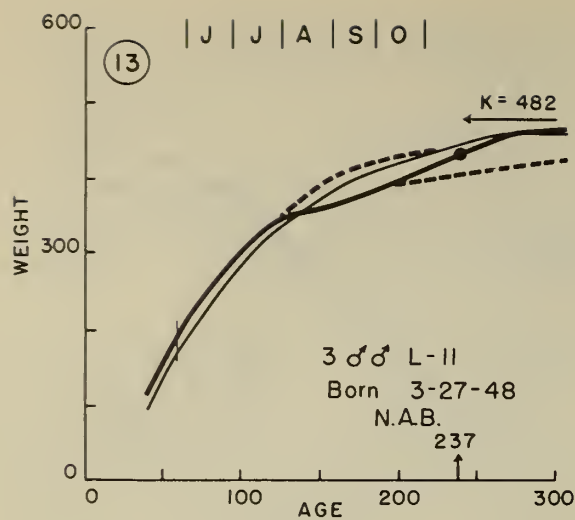

Figure 136
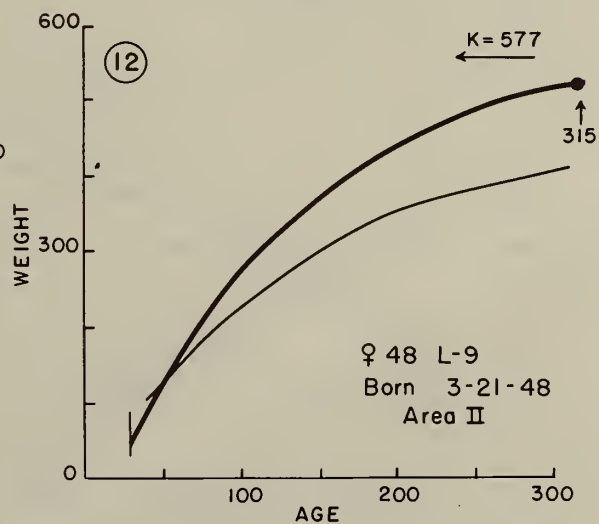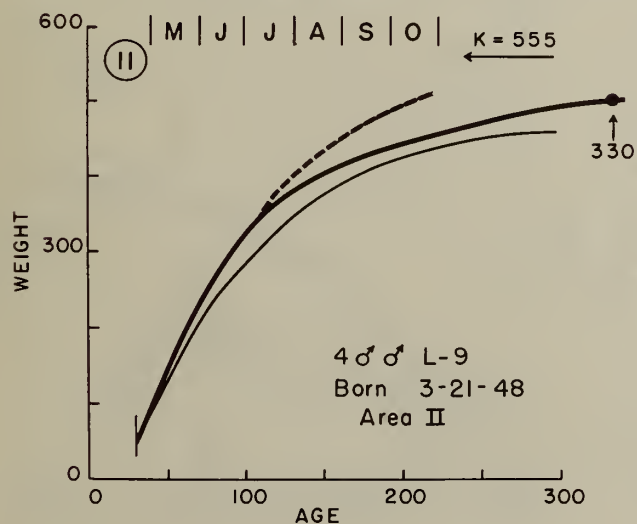
Figure 137.—See explanation on page 224.
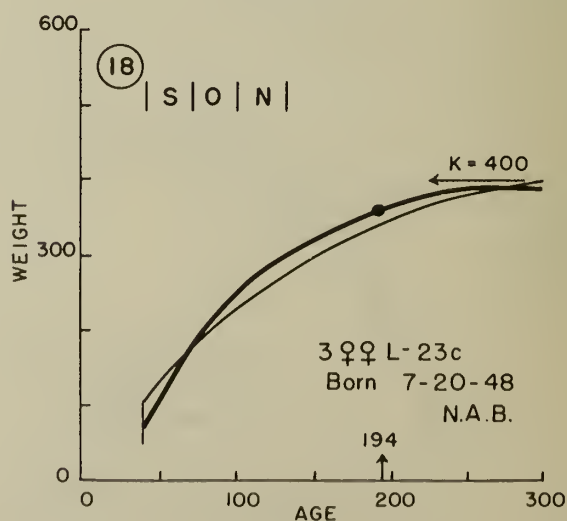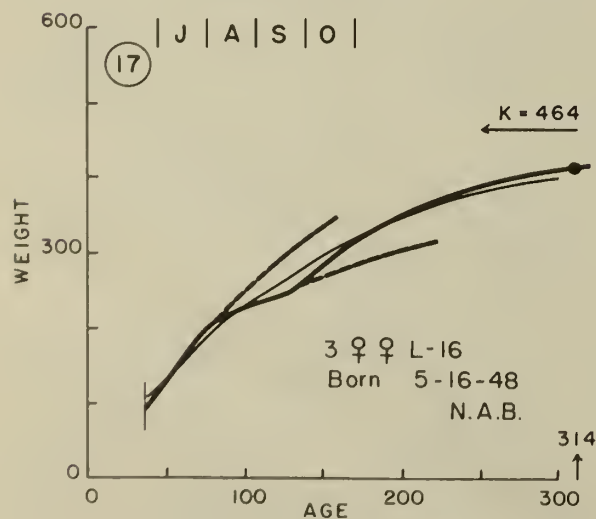
Figure 138.—See explanation page 224.
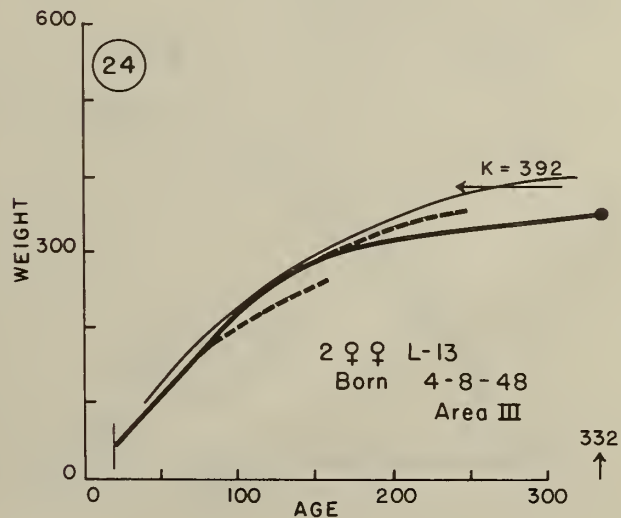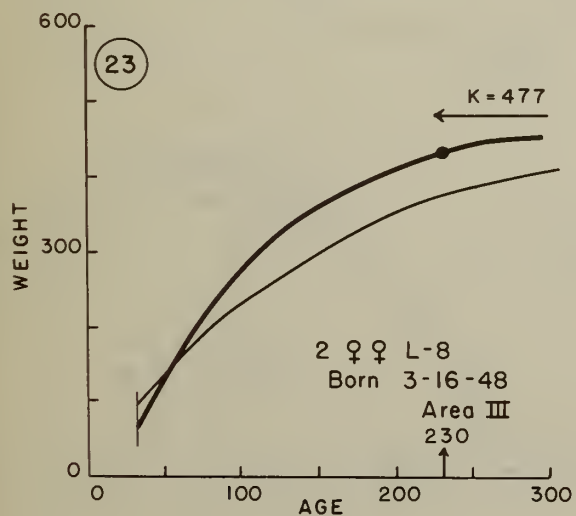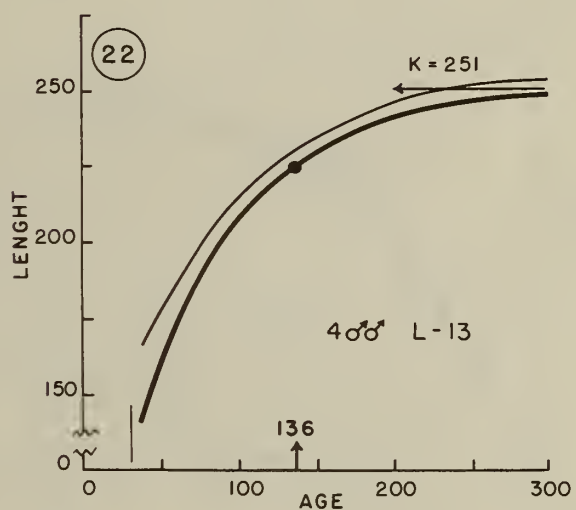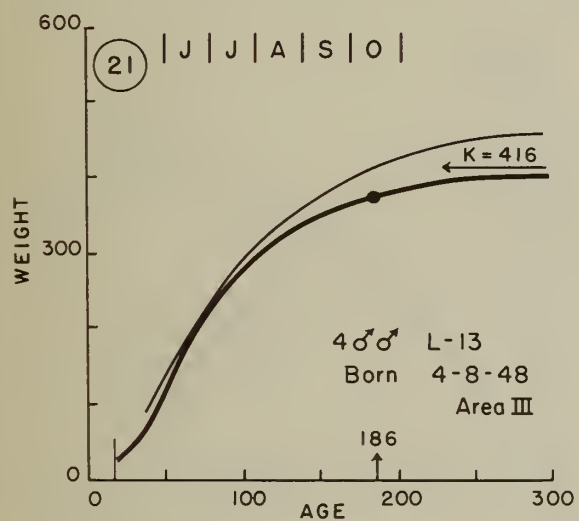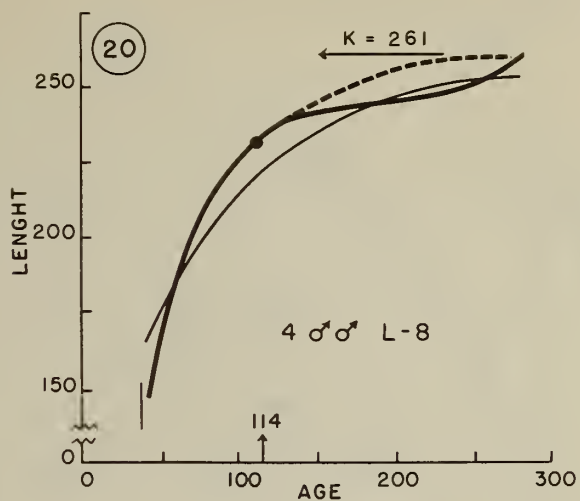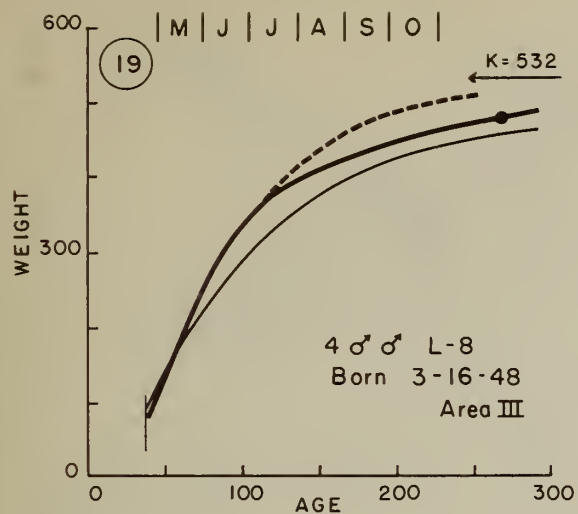
Figure 139.—See explanation on page 224.

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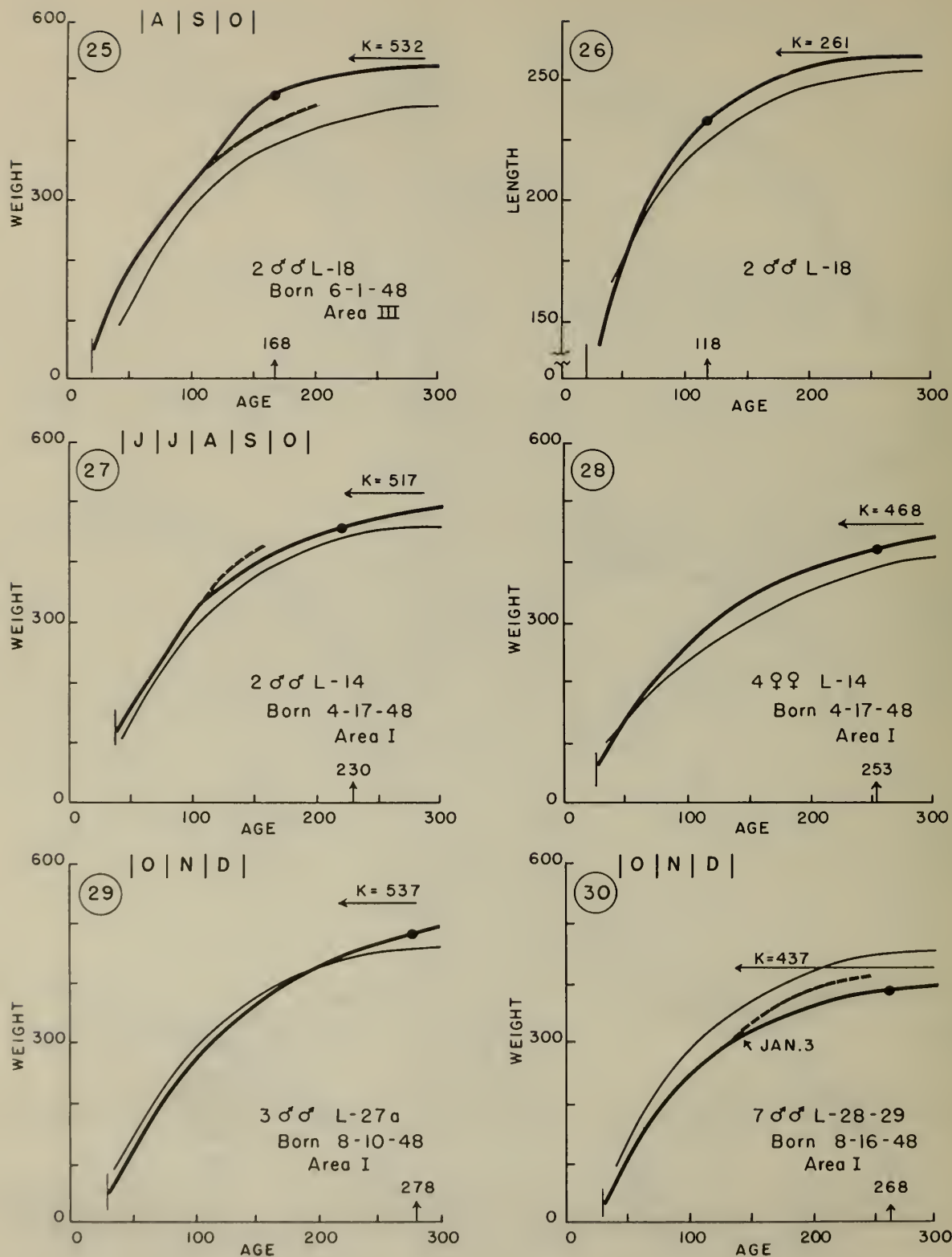
Figure 140.—See explanation on page 224.

Figure 141.—See explanation on page 224.

(chart 5) grew slower than average during the juvenile period, but because of later increases in growth rate it actually surpassed the second-born litter in adult weight. The fourth-born litter (chart 9) fluctuated about the average growth, while the last-born litter (chart 10) exhibited a growth curve considerably suppressed below the average. Adequate data for females were available for only two litters (charts 7 and 8). Here also, despite a later increase in rate of growth, the second-born litter exhibited more inhibited growth.
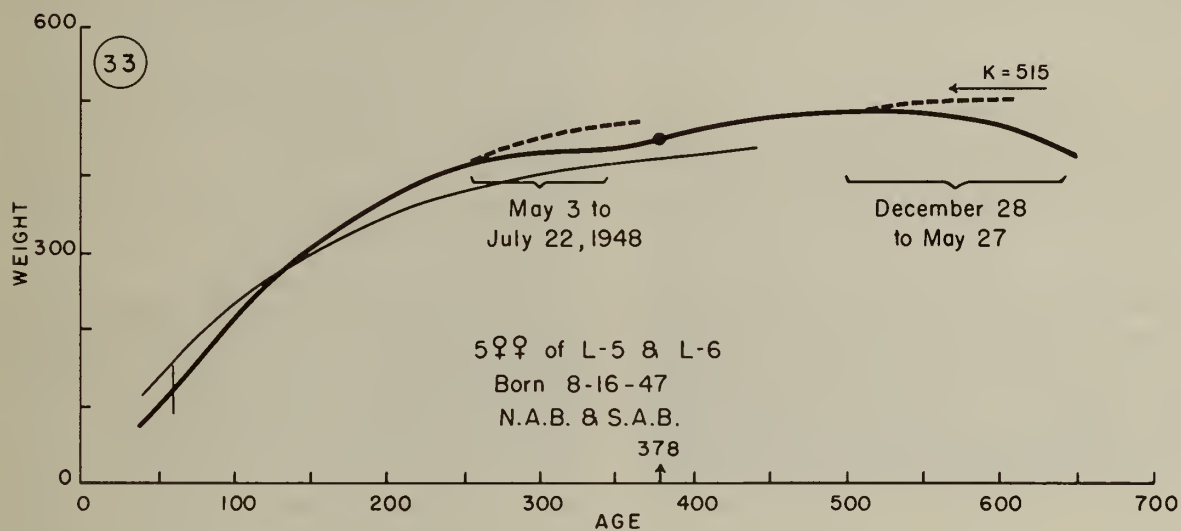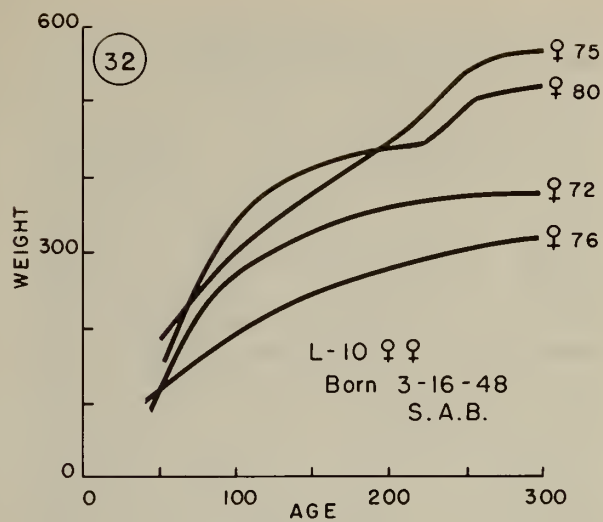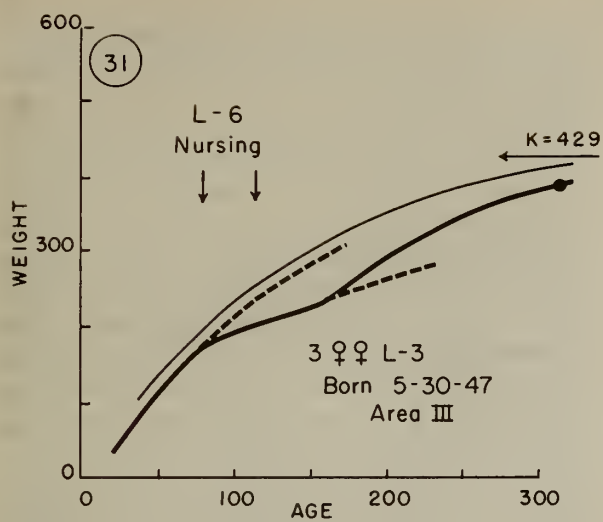
North Alley Burrow: Because only one male survived in most litters (charts 13 and 16), comparisons are not justified. For females (charts 15, 17, and 18) there were progressively more inhibited growth curves. Despite changes in rate of growth for the second litter, the mean maximum adult weights for the first to the third litter were respectively: 511, 464, and 400 grams.

Area I males (charts 27, 29, and 30): Despite a decrease in the growth rate of the first-born litter at about 110 days of age, which resulted in a lowered adult weight, this litter did exhibit a more favored growth until 200 days of age than did the second-born litter. The third-born litter (chart 30) grew much slower than did either of the two earlier born ones.

Area III: Although both the males and females (charts 21 and 24) of the second litter exhibited poorer growth than did the first litter (charts 19 and 23), the third litter males (chart 25) equalled the growth of the first litter. An understanding of why a later-born litter may have more favorable growth requires consideration of the interval of time between litters.

The later in time rats were born, the greater were the number of their associations with other rats. In order to obtain a more quantitative picture of the relationship between time of birth and growth, the population was divided into two nearly equal groups. These consisted of (1) rats born during 1947, along with the first litters born during 1948 (through April), and (2) rats born from May through October 1948. See section D of table 61 and figure 142. It may be seen that those born while the population was smaller had the most individuals in the most favorable Maturity Index class interval and continually less in those class intervals indicating more inhibited growth. Those born during the later period showed just the opposite trend. These data were grouped as favorable growth (Maturity Index I.0 to I.79 and poor growth Maturity Index II.20 to III.0). The resultant 2×2 table of the number of early and late born rats in each growth category gave a Chi Square of 14.63, which has a probability of such a difference arising by change of far less than 0.01.

From this and the previous data presented, there can be little doubt that growth is affected by the number of rats with which an individual must make adjustments. However, there is one question raised by the present data as it is revealed in figure 142. This is: Why is there an apparent exponential rate of change in the numbers of indi-

TABLE 61.—*Time and place of birth in relation to growth*

Location of place of birth	Number of rats in each maturity index class interval					N	Mean
	I.0–I.39	I.40–I.79	I.80–II.19	II.20–II.59	II.60–III.0		
A.							
a. ♂♂ alleys	15	15	12	10	9	61	I.72
b. ♂♂ areas	4	10	10	8	19	51	II.21
B.							
a. ♀♀ alleys	9	11	9	3	6	38	I.85
b. ♀♀ areas	8	3	10	9	7	37	II.04
C.							
a. Total alleys	24	26	21	13	15	99	I.77
b. Total areas	12	13	20	17	26	88	II.14
D—TIME BORN							
a. 1947–April 1948	27	21	18	14	8	88	I.79
b. May–September 1948	9	18	23	16	33	99	II.18

viduals comprising successive class intervals from low to high Maturity Index; that is from stout to thin body types? For the first group of rats there was a negative exponential indicated for the distribution; whereas for the second group there was a positive exponential.

I was puzzled as to why these data did not resemble a normal distribution, as most frequently happens with data on size. Mr. James U. Casby of the Neuropsychiatry Division, of the Army Medical Services Graduate School, suggested that the absence of an indication of normality might be due simply to the fact that the tails of the distribution of the B/W ratio were posted with more medium type data in my development of a mean life span Maturity Index from the basic B/W ratio data. Therefore, the B/W ratio was calculated for 200 days of age for all those rats which had sufficient data to plot growth curves of body and weight (see table 62). These data do indicate that the B/W ratio at this age resembles a normal distribution.

However, there is little in this table that helps in understanding the apparent exponential distribution of mean Maturity Indices shown in figure 142. I believe that the data in this figure is actually more representative of the stresses arising from social action than is the more simple data for 200 days of age. In the first place the former includes Maturity Indices for a number of individuals who died between 50 and 200 days of age. Such individuals were in general the thinner more stunted individuals. The former data also is modified by the inclusion of B/W ratios in later life when individuals subjected to stress lost weight.

That the entire life span requires evaluation, when the B/W ratio is utilized as an index of growth and stress, is indicated by the following analysis. In table 62 there are 9 males in the first group and 16 in the second whose B/W ratio at 200 days of age ranged between .452 and .529. All of these would have been assigned to Maturity Index growth channel I. Because of less favorable maintenance of weight at other times, both groups exhibited mean Maturity Indices less than I.00. Later changes in growth and maintenance of weight are shown in table 63 for those males who lived into the breeding season of the following year. The important aspect of this table is that, whereas the later-born males exhibited as nearly favorable

TRENDS IN FREQUENCY OF MATURITY INDEX WITH TIME OF BIRTH

—— Approximate Trends
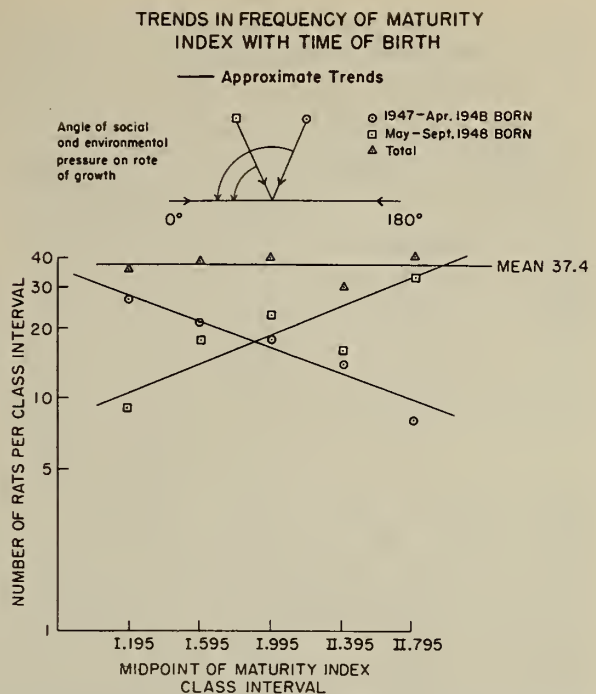
Figure 142.—Trends in the frequency of Maturity Index ratings as they are related to the time of birth, that is to the size and complexity of the population. The lower is the Maturity Index, the larger is the rat for any given age. The change in the slope of the curves from the earlier born to the later born rats suggested a manner in which they might schematically reflect the total intensity of those conditions which inhibit growth. A line drawn perpendicular from one of these curves and extending to the abscissa, will form an angle with it. The greater the angle the less the intensity of conditions inhibiting growth.

growth status at 200 days of age as did the earlier-born males, their ability to maintain weight declined with the onset of the breeding season. All these same later-born males exhibited much poorer B/W ratios prior to 200 days of age. The number of times records of these males fell into the three growth channels were as follows:

Time born	Growth channel		
	I	II	III
Early born...............	17	5	0
Later born...............	17	13	8

TABLE 62.—*Body/weight ratios at 200 days of age*

B/W ratio		Class interval	Born 1947 or March to April 1948		Born May–October 1948		Total
Male	Female		Males	Females	Males	Females	
STOUT							
.452	.471	1	3	1	1	0	5
		2	6	2	15	0	23
		3	9	8	8	2	27
		4	13	7	7	6	33
		5	3	6	5	16	30
		6	0	5	1	5	11
		7	1	0	1	3	5
		8	0	1	2	2	5
		9	1	0	1	0	2
.835	.928	10	0	0	1	1	2
			36	30	42	35	
THIN							
Mean ratio.................			.565	.628	.574	.684	

TABLE 63.—*Mean changes with age for those males which were stoutest at 200 days or age (i.e., B/W = .452 to .529)*

No.	Mean lifespan maturity index	Time born	Age in days	Length (B) in mm.	Weight (W) in gr.	B/W
9	I. 21	April 1947 through April 1948	200	254	511	0. 498
			[1]417	262	539	.486
[2]14	I. 69	May through September 1948	200	252	491	0. 511
			[1]324	258	487	.528

[1] The mean age during the April to June period of the year following their birth.
[2] Two of the 16 males listed in the first 2 class intervals of table 62 died before they were a year of age.

I therefore conclude that the Life Span Maturity Index better reflects the relationship of stress to growth than does the B/W ratio for the arbitrarily selected age of 200 days.

It was pointed out on pages 95 to 99 that the frequency of entering traps increased for rats born later in the history of the colony, and the assumption was made that frequency of entering traps was a direct reflection of the degree of stress experienced by a rat. See in particular table 14 which shows that lateness of birth, frequency of entering traps, number of wounds received, and inhibition of growth tend to be associated.

f. *The time between litters as this influences competition and growth.* Litter 13 (charts 21 and 24, fig. 139) was the only litter born in the pen which was conceived on the night of the birth of the previous litter by their mother. There was only 23 days difference in the age of these litters and both were known to nurse at the same time in the same nest cavity. Whereas any preweaning inhibition of growth of the second litter may be a direct

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result of the competition with the older sibs, I believe that the sustained poorer growth was a byproduct of the abnormal behavior developed by these rats as a result of this early experience. As already pointed out these L–13 rats developed a syndrome of abnormal behavior which reflected the stress they experienced in their relationships with their associates.

There are two other cases where nursing rats probably competed with older young ,who, however, were not their sibs. Prior to weaning, young rats do move into the nest cavities housing other young rats, if another female nearby has a younger litter. These two cases are for L–10 at the South Alley Burrow and L–28, 29 in Area I (see table 59). In each case the Maturity Index indicates a marked inhibition of growth over the prior litter.

The reason for believing that L–10 at the South Alley Burrow would have exhibited more favorable growth, had they not been in association with other young, who were 8 days older, is that the other three litters (L–8, L–9, and L–11) who were born elsewhere in the pen at about this time had much more favorable Maturity Indices.

g. *The nature of the stress associated with inhibition of growth.* I cannot offer any conclusive proof of the nature of the situations which are presumed to be stressful to the organism. However the circumstantial evidence suggests that whenever a rat develops an avoidance of its associates, as it moves about the pen, it is then under sufficient stress to cause inhibition of growth. At least on the basis of what is known of the ACTH and pituitary growth hormone relationship (17, 18) one would anticipate inhibition of growth provided this avoidance really does reflect a stressful situation (see discussions on pp. 260 to 264).

A few examples will assist in showing why I have come to the conclusion that rate of growth depends upon the degree of stress associated with social interactions.

The introduced female No. 11 (see table 28) was smaller and subordinate to the other introduced female, No. 10, who raised litters. She had her litter during May 1947 in Area III. This peripheral location reflected her lower social status. All three males of her litter (L–3) died while juveniles. The three female young showed an inhibited growth (chart 31, fig. 141) as juveniles. Why this should have been so, I can only guess. This guess is that they developed an avoidance of older rats based upon copying the avoidance behavior of their mother. When they were 77 days of age they found themselves in a situation where they had to pass by the North Alley Burrow where lactating female No. 15 was residing, This female chased them whenever they encountered her. Furthermore, she persisted in chasing them for nearly 2 months after her litter (L–6) was weaned. During this time the L–3 females showed a marked depression in rate of growth. These three females were not bitten during these encounters, which fell into the category I have designated as "psychological drubbing". After this experience these females developed the most marked avoidance of other rats that was noted, and they never achieved favorable growth.

There were only two of the introduced males who lived very long. These were males 8 and 12. At the time of their capture on February 2, 1947, male 12 weighed 316 grams and male 8, 296 grams. Following the death of the other three introduced males, male 12 became an aggressive dominant rat, while male 8 became a subordinate rat who exhibited many of the characteristics of the syndrome of the social outcast, including marked avoidance of other rats. Associated with the behavioral differences, male 12 attained a maximum weight of 517 grams, while male 8 reached only 434 grams.

The markedly suppressed growth of Litter 13, (fig. 139, charts 21, 22, and 24), which was thrown into competition with their 23-day-older sibs has already been noted. Both the males and females of this litter were characterized by the syndrome of the social outcast, which included marked avoidance of other rats.

Rats which developed avoidance of their more dominant associates were gradually forced to become members of less favored aggregates or local colonies to the extent that this avoidance behavior had developed. The more unfavorable the local colony, or as I have called it the lower the social class of the colony, the poorer had been both their growth and their reproductive success. See tables 56 and 57 and the accompanying discussion (pp. 214 to 216).

The females of Litter 10 offer relevant material. See growth chart 32 (fig. 141). There was a wider range in the growth curves among the members of this litter than for any other litter. Two (Nos. 75 and 80) became very large rats, while the other two (Nos. 72 and 76) exhibited markedly depressed growths. The former two

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reared litters, while the latter two did not. I shall only consider the extremes, Nos. 75 and 76, since the most conclusive data is for them. Female 75 was an extremely aggressive rat, and with the exception of avoiding a few older females during 1947, she moved about without being disturbed by other rats. Information concerning female 76 consisted entirely of recapture data. However, the location of her terminal capture and the rats with whom she was associated are particularly instructive (see table 53). She was a member of the socially lowest ranking colony which contained female members. There, two of her three female associates were the surviving sisters of Litter 13. Like them she was of stunted growth and never conceived. Because of the marked similarity of these three rats, and because of the general tendency of rats of similar history to aggregate, I suspect that female 76 also exhibited marked avoidance of her higher ranking associates.

The information in the above five paragraphs forms the strongest supporting evidence that growth is modified by the stress associated with the development of the behavior of avoiding more dominant associates. The conditions which apparently favor the development of avoidance behavior to the point where it exerts a deleterious effect upon growth are as follows. They are listed in the order of the chronological age at which growth may be inhibited.

1. Nursing competition with older sibs.
2. The "copying" or "mimicing" of the avoidance behavior exhibited by their mother.
3. Competition with older nonsib juveniles.
4. Adjustment to the priority rights of adults at the source of food.
5. Aggressive action of lactating females. This is particularly effective if a rat is forced to pass near the burrow of females who are not members of their own local colony.
6. Competition of recently sexually matured males with adult males over estrous females.
7. Territorial competition. These are the behaviors associated with exclusion and migration.

Once avoidance behavior is developed, the hesitant actions expressed as a result of it are more likely to elicit attack by dominant superiors, and thus the behavior is maintained, and therefore the stress associated with such interaction maintains the suppression of growth below the optimum.

In conclusion it may be remarked that fighting to the point of receiving wounds is not the prime cause of inhibition of growth, despite the fact that such encounters are probably stressful to both participants. Most of the decrease in growth rate for males began about 113 days of age. Yet from 115 to 180 days of age there was a low (mean 1.81) number of wounds received (see fig. 122).

h. *Trapping and handling rats as a source of stress inhibiting the maintenance of weight.* Any stress exerted upon the rats, particularly when mediated through social interactions, appears to inhibit growth. One such situation followed trapping rats, or handling them after excavating their burrows. In either case following release the rats tended to shift their residence to some other locality from that in which they were captured. This necessitated the formation of new social relationships. The reason for believing that the formation of such new social relationships were stressful was that whenever a rat, following release, was noted to enter the harborage of a colony other than its own, fighting ensued.

A number of records were available of weights at first and second handling during a period of capturing the rats. With few exceptions there was a decrease in weight between the first and second capture (see fig. 143). The point of particular note was that twice as much weight had been lost when 3 to 10 days had elapsed between capture than when only 1 to 2 days intervened. During the longer interval there was more opportunity for the effects of social disturbance to be realized.

A criticism of the validity of these results and conclusions was that a small portion of the second captures followed a period of withholding food at the Food Pen. Thus, one might expect that some of the loss in weight might have been as a result of the exhaustion of food caches in the burrows and harborage boxes. Fortunately one portion of the sample was unbiased by any chance of being influenced by food deprivation. These data pertain to the capture of rats between December 6, 1948, and January 6, 1949, when rats were only captured by removing them from their burrows. Food was continuously available in the Food Pen. However, the rats were exposed to extreme social disturbance since their burrows were destroyed and they were forced to join other rats in harborage boxes, or in burrows not yet excavated. Twenty-two rats were captured twice. There was an average loss
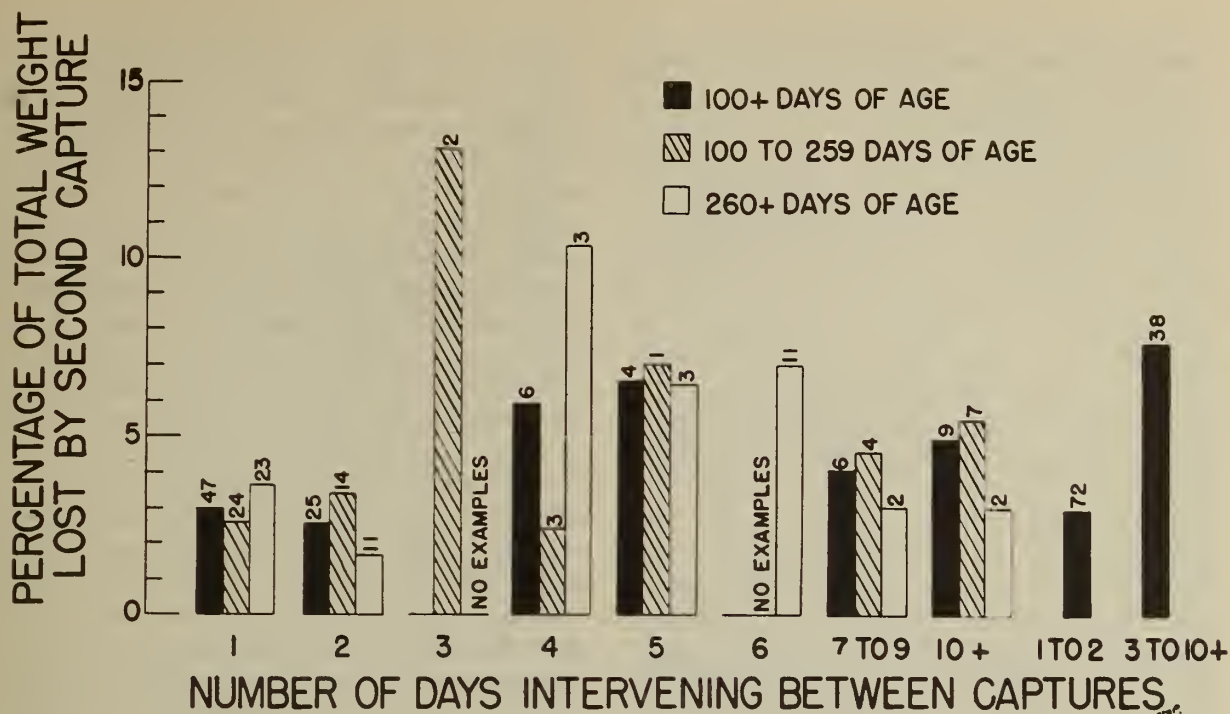
Figure 143.—Weight loss between first and second captures during periods when traps were left continuously set. The number of observations is listed at the top of each column. Mean weight loss: (1) 2.9 percent when 1 to 2 days intervene between captures; (2) 6.3 percent when 3 to 10 days intervene.

of 5.8 percent in body weight, following an average elapsed time of 8 days between captures.

i. *The question of secondary increases in the rate of growth.* As already mentioned there were no known conditions which might be definitely correlated with the observed instances of increase in rate of growth. The assumption is implicit that, if stress from social interactions inhibits growth, when growth rate increases the rats concerned must be experiencing less stressful situations. Most of the increases of growth rate for males did occur during the winter when strife was reduced. Adaptive behaviors such as migration or shifts in activity periodism may also be involved.

j. *Age and the maintenance of weight.* Few rats lived long enough to be designated as aged. For females there was a slight decrement in weight after 450 to 500 days of age (charts 33 and 34, fig. 141). The two introduced males (Nos. 8 and 12) who must have been over 600 days of age at death showed declines of 40 to 60 grams in weight during the last 100 to 150 days of life.

k. *Place of birth and growth.* Rats born in the alleys lived nearer to the source of food than did those born in the areas. This placed the alley-born rats at an advantage with reference to the energy they had to expend in going back and forth between their home and the Food Pen. A more significant difference relating to place of birth was superimposed by the social organization of the population. Rats living in the areas were forced to pass near the place of residence of others living in the alleys when they went to the Food Pen. Thus, the area-born rats were exposed more frequently to the adverse action of psychological drubbings or territorial behavior exhibited by the alley-inhabiting rats.

That a differential in growth and maintenance of weight did result, which favored the alley-born rats, is clearly shown in table 61. For the purposes of a 2×2 table Chi Square test of significance of this data the rats were assembled into those which grew larger and maintained their weight better (i.e., Maturity Index, I.0 to I.79) versus those which

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were more stunted and did less well at maintaining their weight (i.e., Maturity Index, II.2 to III.0). These two categories according to the number from each place of birth were:

Place born	Maturity Index	
	I.0 to I.79	II.2 to III.0
Alley-born................	50	28
Area-born................	25	43

This gave a Chi Square of 11.49 with a probability of such a difference arising by chance far less than 0.01.

B. *The Condition of the Pelage.* The type and thickness of the fur changes with age. Before weaning the rat acquires a covering of short pliable hair which forms a soft gray coat. This is designated as the juvenile pelage. As the rat matures, this juvenile pelage is replaced by longer darker hair. Among these are especially long, guard hairs. Color appearance during this state, which was designated as prime adult, varied from buff to brown or reddish brown. Later on in life the pelage began to thin. Thinning normally first appeared over the lumbar-sacral region. This

thinning sometimes was accentuated by the development of scar tissue, where no hair regenerated, as a result of combat. In any case the fur gradually became thinner all over. A few individuals developed such sparse hair after 400 days of age that the pelage must have been insufficient to provide adequate protection during inclement weather. Between 200 and 300 days of age the coat became suffused with white or very light hairs. This gave a grizzled gray cast to the pelage. These general characteristics denote the senescing adult.

Detailed pelage studies were not made. However, whenever a rat was handled a general remark concerning its pelage was usually made. They included the following: (1) juvenile, (2) mostly juvenile, (3) one-half juvenile, (4) mostly adult, (5) adult (good, excellent, or thick), (6) brown, buff, reddish-buff, (7) thinning over lumbar region, (8) gray-grizzled, (9) thinning all over. There were 806 such observations for which the age of the rat was known. One and 2 were grouped as juvenile, 3 and 4 as transition to adult, 5 and 6 as prime adult, 7 to 9 as senescing adult. Changes in the percentage of these categories with ages are shown in figure 144. By taking the 50 percent point of the intersection of the curves, three stages may be designated.
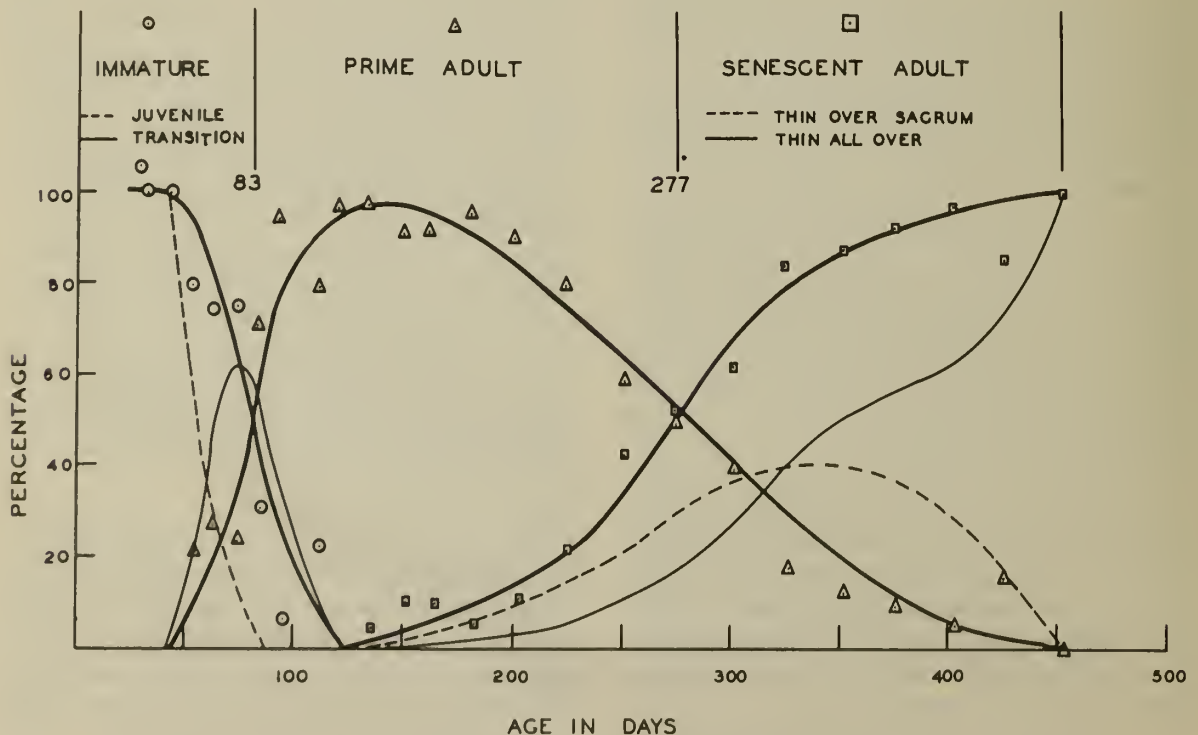

Figure 144.—Changes in the character of the pelage with age. Both males and females are included.

The immature stage of the pelage lasts to the age of 83 days. This is the age when rats are just beginning to exhibit behavior indicative of physiological sexual maturity. The prime pelage lasts from 83 to 277 days of age. At about 130 days of age all rats have developed the prime pelage. It is also interesting to note that this is the age by which most rats have also exhibited behavior indicating physiological sexual maturity. At this age the integration of the individual into adult society is usually just beginning. I am here speaking of the development of a stable adult role. Until this role is achieved the individual is behaviorally not sexually mature. This adult role becomes established between 130 and 277 days of age, and accompanying it there are progressively more signs of a loss of prime pelage. By 277 days of age physical growth has for practical purposes ceased. After this age there were progressively more and more signs of an inability to maintain a prime pelage until by 450 days of age all rats had a thin pelage all over their bodies. In the figure this period was designated as that of the senescent adult pelage. More properly it might be called the senescing adult pelage stage. The true senescent stage probably began shortly after 450 days of age. One category, *very* thin all over, is not represented in the figures. The increase in the percentage of the population so characterized are as follows with the age in parenthesis: 3(290); 10.5(340); 17(390); 31.5(440). The number of observations in each age were repecively 119, 65, 52, 29. On the basis of the last three percentages, a projection of the trend indicated that all rats surviving to 560 days of age would have a very thin pelage all over.

There is one trend in these changes of pelage which upon first inspection appeared anomalous. Prior to assemblying the data I had anticipated that prime pelage would be maintained as long as bodily growth was proceeding. However, despite the fact that growth was still quite apparent between 130 and 277 days of age, there was progressive loss of prime pelage. It occurred to me that loss of prime pelage was due to alterations in the physiology as a result of stresses experienced in making social adjustments. In order to explore this notion the population surviving to May 1949 was divided into categories of low- or high-social rank as previously discussed. Data on the pelage of these two categories were plotted as shown in fig. 145.

The data for males are particularly instructive. Initiation of loss of pelage began over 2 months earlier for the socially lower ranking group, and likewise the 50 percent point of change occurred 73 days earlier than for the higher ranking group. For females there is no such clear-cut difference between social rank and pelage changes. There is an indication that the socially low-ranking females began to lose the prime pelage sooner. On the other hand in later life they lose the prime pelage less rapidly. This latter is in conformity with an inadequately documented suspicion that many lower ranking rats develop a behavior of avoiding competitive situations. Between sexes the difference is mainly one of females maintaining their prime pelage longer. In all categories the amount of scar tissue present certainly contributes to the rapidity of loss of prime pelage. To what extent it is the determining factor, the data are inadequate to verify. However, since the thinning with many individuals also includes portions of the body not developing scar tissue, I am inclined to believe that differentials in the loss of prime pelage do represent some physiological change affecting regeneration of hair, which arises as a result of the stress experienced. Furthermore, more of the socially low-ranking rats exhibit thinning of the pelage at an early age (under 140 days for males and under 200 days for females) than can be accounted for by scar tissue (see fig. 122).

C. *Health and Mortality as Observed under the Field Conditions of the Experimental Colony.*

a. *Rats found dead or dying.* During the course of the regular rounds of inspection of the pen several rats were found which were dying or recently dead.

Thirteen rats (males 6, 8, 45, 53, 79, 651, 685, 768, 868 and females 7, 17, 27, 78) were characterized by the following conditions. They were very emaciated; they had difficulty in breathing—as they attempted to do so they wheezed quite audibly; locomotion was difficult—they wobbled as they walked or just made jerky hops on all 4 feet; the pelage was in poor condition—the fur was sparse, matted, and not recently groomed; usually the back was so permanently arched that I could not force it back into its normal curvature; the gut was bloated; and most of these rats had been excluded from reentry to the burrows by their more healthy companions. Two of these rats were found dead in a hunched position with their noses thrust in a slight depression, which had been scratched out of the grass and soil immediately
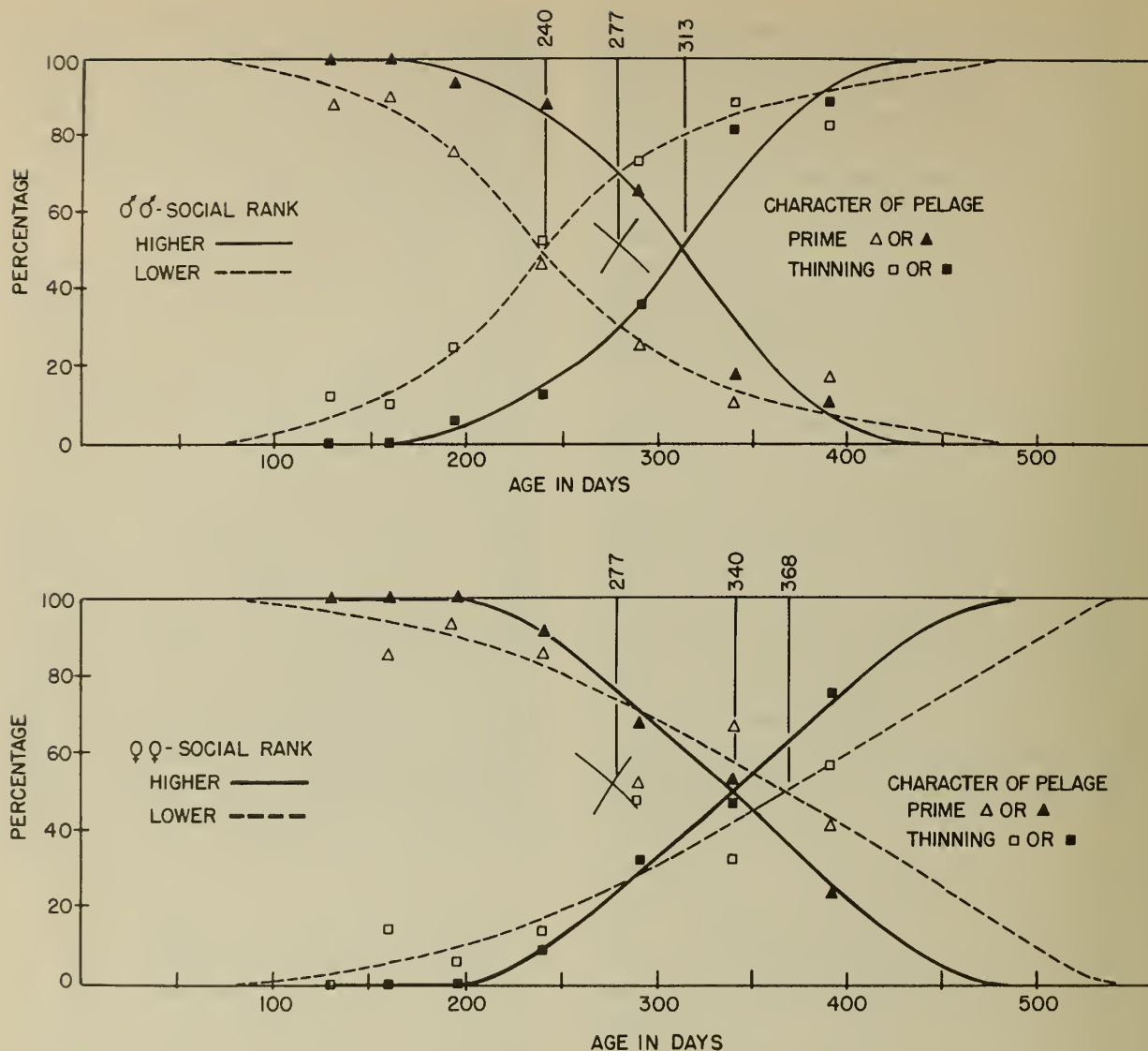
Figure 145.—The influence of sex ond sociol ronk on the tronsition of the prime pelage into the thinning or senescent stote. These figures are bosed upon 250 observations for males ond 217 for femoles. The intersection of lines ot 277 doys is the 50 percent point in the tronsition of prime to senescent stote for the lorger somple shown in figure 144.

preceding death. Most of these rats were over 300 days of age. Some had no recent wounds while others had many.

Several recently dead rats were found which were of normal weight and which were without external pathology.

b. *Internal strife and cannibalism.* Among mature rats there was considerable fighting. Males received more wounds than females (fig. 122). Three male rats, two of which had received extensive head wounds, were known to have died as a result of fights with other rats. The third

was found in the Food Pen on a spot of bloody soil; all the flesh had been eaten by other rats and the skin was turned wrongside out. Two factors are important in this case of cannibalism. The rat killed had large infected wounds over the lumbar sacral region for the previous 2 months. This indicated either prior low-social rank, or at least marked contention with its immediate superiors for social status. The raw exposed area may also have served as an additional incentive for other rats to attack it. Also, during the night of its death the food in the hopper became exhausted;

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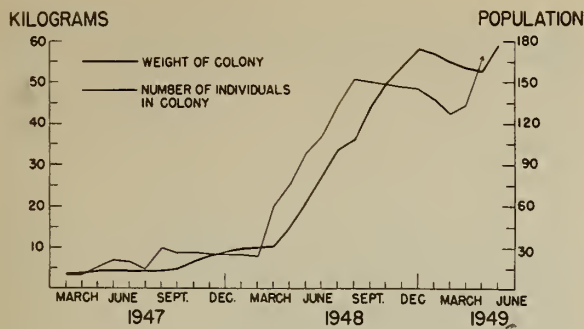Figure 146.—Growth of the population in biomass and number of individuals.

thus it might be assumed that hunger was a factor. At this time, however, there were two other rats lying on the ground that had died from unknown causes. These two rats were not eaten by other rats until several days after the previously mentioned overt incident of cannibalism. During the early months of this study, dead rats were ignored by their surviving companions, and left to be decomposed by bacterial and maggot action. This led to doubt concerning those statements which attributed a role to the act of cannibalism in the transmission of disease. Accompanying the increase in population density, however, there was an increase in social tension and in the frequency of cannibalism. Ten rats whose identity was known were eaten by other rats. Usually the dead rats were dragged into harborage boxes or burrows, the skin turned wrong side out and the flesh stripped from the bones. Other similar acts of cannibalism must have been overlooked, since burrows were rarely excavated by the investigator. Dead rats, which were partially decomposed by bacteria or maggots, were sometimes eaten by their companions.

c. *The relationship of flies to health and mortality.* Fly larvae occasionally contributed to both morbidity and mortality. Unfortunately identification was not made of the species involved. Warbles most likely were of the genus *Cuterebra*. Larvae of the genus *Chrysomya* were identified from carcasses. This genus is known to be involved in cases of accidental myiasis in man and domestic animals. However, it was not known whether it was involved in the observed cases of myiasis of rats. *Callitroga americana*, the common screwworm of domestic animals, is involved in myiasis of a semiobligate type but other genera have been observed in accidental myiasis. The following are the relationships of flies to rats in the colony:

Rats removed from traps occasionally had masses of fly eggs deposited in their fur. These were usually the soft pelaged juvenile rats, although rarely adults were involved. The eggs were always combed from the fur before release. That flies lay eggs on free-ranging juveniles is evinced by the following field observation:

"6–19–48: A young rat was seen to be wandering about the open pen. It entered harborage Box 21 which was then opened and the rat caught. It was a male about 34 days old that had not previously been captured. Fly eggs were scattered through its fur. It was rather weak." This rat was never caught again.

The most significant effect of screw flies upon rats is when they lay their eggs in the extensive purulent wounds exhibited by some of the males. During fights males may receive a single gash or several smaller nicks in a single location. These frequently become infected and developed into extensive shallow festering wounds which may last for weeks or even months before healing. The lumbar sacral region is the most common site for these infections, usually just above the base of the tail, although occasionally they occur on the shoulders. During the colder months the flies are not a factor, but with the advent of warm weather open wounds predispose the rats to death by myiasis. The following three field notes describe the maggot-rat relationship:

(1) Male 99 "April 13, 1949: Two large infected wounds; one above base of tail (20 x 20 mm.), the other extends from left hip around anus. These are all wounds that have not healed". May 28, 1949: "I noticed large green flies buzzing about the top of harborage Box 29, which was lying on the ground. On turning it over I found a rat that was a walking mass of maggots. He ran actively under a nearby board and finally escaped into tile 4 burrow." "May 29, 1949: Rat in Passage 4 burrow tail protruding out, and green flies buzzing about. I tried to catch it by the tail but it ran further down the burrow."

This rat was not found in this burrow on June 1, 1949, or elsewhere in the pen the following and terminal week of this study. If a rat is not found within a day or two after death by myiasis only the bones and a few patches of skin may be left solely as a result of the maggots' consumption of tissues.

(2) Male 69 "February 15, 1949: 22 body nicks". It was not recorded again until:

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"May 26, 1949: Found freshly dead and full of adult maggots along the trail from the Food Pen to the North Alley Burrow. The presence of adult maggots and the indications that the rat died last night, must mean that flies laid eggs on an extensive wound area, and finally as the maggots matured and invaded more of the rat, they killed it. In the evening when food was placed in the Food Pen other rats running out of the Food Pen to the North Alley Burrow ran over it stepping on it". "May 27, 1949: Remains of this rat found on Path 4. The bones were stripped of all fresh flesh by other rats, even though plenty of food was present in the Food Pen.

(3) Male 677: "May 26, 1949: This rat died shortly after it entered the gathering sack from an entry to Area IV Burrow, which was being excavated. Flies presumably had laid eggs in wounds which must have been on the left cheek and right shoulders. Maggots have eaten all muscular, and other tissue about scapulae, humerus, entire throat region, left cheek, and thoracic vertebrae between the scapulae. Fur shows no sign of having been groomed in a long time."

Under the conditions in which this colony existed maggot infestation was certainly one of the prime mortality factors. This is probably not generally true for rats living eleswhere unless the conditions are such as to foster social strife and the resultant fighting. Those rats which receive extensive wounds and are thus more subject to screw fly attack are those larger, rapidly maturing rats who contend unsuccessfully for high-social rank. Several hundred rats were examined from city blocks in Baltimore where garbage occurred widely distributed in open containers. None of these rats was extensively wounded, and few had over two to three small nicks on their bodies. Wherever availability of food or haborage is limited it is likely that the competition will be increased and that during the warmer months infestation by screw fly maggots will be an important mortality factor. In his discussion of screw fly infestation of livestock Bishop (19) makes no mention of rats or other wild animals serving as reservoir hosts.

Warbles (Cuterebra) represented another avenue of dipteran contribution toward ill health among rats. Sites of infestation included: body (8 rats), forelegs (2 rats), genital or anal region (12 rats),

head (1 rat). The sites of infestation frequently became infected following the emergence of the larvae. Among males one or both testes might become free of the scrotum and eventually lost, or the penis become free of its sheath and point posteriorly.

d. *The relationship of sex to health and mortality.* The prior comments and other aspects of ill health and mortality are summarized in table 64. These will be discussed row by row. Rows A and B refer mainly to wounds received in combat. In table 56 are additional data regarding wounds received in combat. Both sets of data give evidence of the grater frequency and severity of wounds received by males (also see remarks on pp. 95 to 96). Most of the body injuries were open wounds, although a few were purulent sealed nodules.

Row C, *Tail Injuries:* Included here are the following categories: (a) enlarged knob or swollen along whole length: male (1), female (4); (b) part of tail missing: male (6), female (2); (c) tail vertebrae rigid as if fused: male (3), female (2).

Row D, *Foot Injuries:* The general picture of conditions here is that a foot (never more than one on the same animal) becomes swollen, small purulent areas develop on the surface, the swelling may or may not subside, toes may drop off, and the foot may become stiff as if the bones had fused. Seven of the nine males were 300 or more days of age before an infected foot was observed.

Row F, *Bronchiectasis:* Rats which were found to be sneezing, coughing, wheezing or otherwise seemed to have difficulty in breathing were placed in this category. The age distribution was under 200 days (14), 200–300 days (2), over 300 days (5). Although there is no direct evidence for this, it is probable that colds are a very important debilitating factor contributing to the mortality of those individuals who for other reasons are not in good health. Four of the individuals having colds were also emaciated and weak.

Row G, *Ill Health—General:* Grouped here are such varied items as emaciation, arthritis, fly eggs in fur, and difficulty in reviving after anesthetization. The four rats which were especially arthritic had their vertebral columns permanently arched, and they walked with an awkward lumbering gait.

Rows H and I, *External Parasites:* Each rat handled was usually examined for external parasites by blowing the pelage forward. Only one flea was observed. Four of the five ticks were the

TABLE 64.—*Summary of health and mortality*

Row	Item	Number of males	Number of females	Total
A	Extensive body injuries....................................	21	5	26
B	Blind (26) and face cut (4)...............................	21	9	30
C	Tail injuries..	6	7	13
D	Feet injuries...	9	0	9
E	Total body injuries—Total A to D....................	57	21	78
F	Had a cold...	16	5	21
G	Ill health—general.....................................	13	7	20
H	Ticks and fleas..	6	0	6
I	Lice (common to abundant).............................	19	7	26
J	Warbles-infections.....................................	13	10	23
K	Tilt-headed..	2	2	4
L	Total F to K...	69	31	100
M	Mortality-(found dead).................................	20	8	28
N	Anesthesia or exposure in traps.........................	9	3	12
O	Disappeared...	44	12	56
P	Total mortality total M to O.........................	73	23	96
Q	Surviving to May 1949..................................	50	53	103
R	Total rats weaned 1947 and 1948.........................	123	76	199
S	Total recaptures (7+ days)..............................	490	400	890
T	Times handled...	970	723	1693
E + L + P	....	199	75	284

dog tick, *Dermacentor.* The state of lice infestation was not always recorded, but, on many records it was noted that no nits or lice were present. Presumably, self-grooming and possibly also mutual-grooming was responsible for the low prevalence of lice.

Row K, *Tilt-headed Rats:* Presumably the four rats who walked about with their heads permanently twisted to one side had arrived at this state as a result of a middle ear infection, *Streptobacillus.* Despite this condition, one of these rats was the most dominant individual about his burrow.

Row N, *Dead from Anesthesia or Exposure in Traps:* Included here are those rats dying from exposure to cold or heat while in traps or those given too much anesthesia. The preponderance of males possibly indicates their lowered resistance.

Row O, *Disappearance:* Fifty-six rats disappeared sometime between the time of their last capture and the period during May and June 1949, when all rats still living were captured by excavating all burrows. Probably no more than 10 or 12 rats became the prey of owls, cats, and opossums which managed to circumvent the various barriers surrounding the quarter-acre pen. All the remainder are presumed to have died from various causes and to have disintegrated without ever being found. Several were found so decomposed, and their remains so scattered, that their metal ear tags could not be found. It is believed that no rats escaped from the pen. The preponderance of males in this category again indicates their greater susceptibility to mortality factors.

These 13 categories of ill health or mortality were recorded primarily at times when the rats were captured and handled. Therefore, the probability of observing some condition characterizing a rat should be approximately proportional to the frequency with which it was captured. Rows R and S in table 64 show that there were 613 handlings of males and 476 of females. These instances

refer to one or more captures of an individual rat during separated periods of capturing. The total times handled (row T) is not as accurate an index for judging the probability of observing the conditions, since these conditions rarely changed in a given rat during a single period of trapping, and since males reentered traps (repeated) more frequently than did females. It is quite apparent from table 65 that males are much more predisposed to conditions terminating in ill health or mortality. Also refer to figure 147.

TABLE 65.—*The sexual differential in susceptibility to ill health and in probability of mortality*

Comparison from table 64	Chi square	Probability of chi square
Row E to Rows R + S......	7. 72	Less than 0.01.
Row L to Rows R + S......	5. 54	Less than 0.02.
Row P to Row Q...........	14. 77	Less than 0.01.

e. *Relationship of growth (Maturity Index) to health and mortality.* The question arises: "Do those conditions which alter growth also alter the likelihood of the individual's experiencing those conditions of ill health and mortality which were observed in the experimental population?" In order to answer this question related groups of data presented in table 64 were lumped together. All duplications were eliminated, so that each rat is represented only once

in each major category. Littermates not characterized by each condition were compared with those so characterized. A summary of this is given in table 66.

Combat Injuries: The difference of 0.30 in the Maturity Indices for males is believed to be biologically significant. It represents an average difference of 26 grams at 196 days of age. The important point here is that the rapidly maturing males are more likely to engage in competition with similar males for priority of action. Less rapidly maturing males are in early life conditioned to avoid competitive situations, and are thus less likely to receive extensive wounds. See table 67 for additional information.

Having a "cold": From table 66 it is quite apparent that rats which are subject to having colds are not only members of litters with an inhibited maturational pattern, but they themselves have the poorest maturational pattern. It is presumably the inhibited pattern of maturation which predisposes the rats to contract colds, rather than the possession of colds which produces an inhibited pattern of maturation. This is shown by the fact that most of the rats having colds were recorded as having a Maturity Index in the Class III range just prior to contracting the cold.

Rats having ectoparasites: The data in table 66 indicates that there is no correlation between pattern of growth and likelihood of having those ectoparasites which were present in this population.

TABLE 66.—*Maturity index in relation to health and mortality*

Health and mortality categories	Males		Females	
	Number	Mean maturity index	Number	Mean maturity index
Combat injuries (mostly), Rows A to D of table 64...................	42	I.82	17	I.97
Negative littermates..............................	34	II.12	24	I.82
Rats which had a cold, Row F of table 64..........................	13	II.53	4	II.29
Negative littermates.............	14	II.19	10	I.93
Rats having ectoparasites, Rows H to J of table 64....................	29	I.85	10	I.92
Negative littermates................	44	I.98	12	I.92
Rats born in 1948:				
Lived over 150 days but died before May 1949...................	16	I.95	6	I.95
Lived to May 1949...............	49	II.05	46	I.93
Rats which died between 50 and 150 days of age....................	29	II.25	6	II.31

TABLE 67.—*Prevalence of mortality or extensive injuries among male rats in relationship to the level of their maturity index*

Maturity index range	Mortality of rats born in 1948		Extensive injuries	
	Died before May 1949	Lived to May 1949	Injured	Uninjured littermate
I.00 to I.39.	0	7	9	3
I.40 to I.79.	8	11	13	10
I.80 to II.19. . . .	3	11	10	4
II.20 to II.59. . . .	3	8	5	9
II.60 to III.0. . . .	2	12	5	8
Total. . . .	16	49	42	34

Mortality: It appears from table 66 that rats living to 150 days of age but dying before they are a year old have an average maturational pattern which does not differ from the average maturational pattern of those rats surviving to approximately a year of age. However, the distribution of the Maturity Indices which makes up the mean for the males is interesting. It is shown in table 67 that all males in the top 20 percent of the Maturity Index range survived. These were those individuals who had made a successful adjustment in the contention for social position. On the other hand, 50 percent of those who died were included in the second most favorable range of Maturity Indices, I.40 to I.79. Six of these eight males were etiher born at the South Alley Burrow or were members of a litter born in a neighboring favorable location and whose mother moved to the South Alley Burrow at the time they were being weaned. All were born during the first half, the more favorable half, of the 1948 breeding season. Probably their growth had been inhibited just sufficiently to prevent their successful competition, yet they had matured under conditions which predisposed them to contend for priority. Five of these rats were noted to be social outcasts just prior to their death. They had become emaciated, failed to groom their fur, and were prevented by other rats from entering the burrow systems. Two of the other three died as a result of screw fly infestation of extensive wounds. The last rat was also extensively wounded and was killed and eaten by other rats. Rats of a similar or lower Maturity Index, who survive, are generally those which adjust by not initiating combats or who flee when challenged. However, mortality among adolescent rats, 50 to 150 days, is certainly associated with the degree of inhibition of maturation (table 66).

f. *Infestation of the rats by microorganisms.* This section is concerned with the autopsies performed at the termination of the experiment in March 1949 by the Johns Hopkins School of Hygiene and Public Health, and by the National Microbiological Institute of the U.S. Public Health Service. These data refer to 31 males examined by Hung-Ying Li of Johns Hopkins; and to 77 females and 23 males examined by Drs. Chester W. Emmons, Robert T. Habbermann, Carl Larson, and W. T. S. Thorpe of the National Microbiological Institute. Of the adult females in this latter group there were 53 whose identity was known.

Negative Results: None of the rats examined at Hopkins or the NIH had *Salmonella*; nor did any of the 31 males examined at Hopkins have *Leptospira*. Emmons (20) found no *Histoplasma* in any of the rats. The absence of these three organisms in the experimental population is noteworthy since the original members of this population were secured from Parsons Island, an isolated 150 acre island, which lies across the Chesapeake Bay from Annapolis, Md.

Positive results: *Streptobacillus moniliformis* was isolated from the middle ears from 15 of 33 necropsied rats. This organism when transmitted to man produces one of the conditions termed rat-bite fever. It was also probably involved in damage to the lung tissue, associated with the infection of the lung, termed bronchiectasis. Many of the older rats showed extensive lesions of the lungs. *Bartonella muris* was found in the only two rats examined for this bacterium. Helminth parasites and the percentage of rats examined that were infected were as follows:

> *Trichosomoides crassicauda* (6.5); *Capillaria hepatica* (53.3); *Strongyloides ratti* (16.4); *Heterakis spumosa* (60.9); *Syphacia obvelata* (2.2); *Tricuris muris* (2.2); *Hymenolepis* spp. (42.6); *Cysticercus fasciolaris* (3.3).

Infestation with this latter tape worm probably arose as a result of the invasion of the pen by a cat on two or three occasions before an adequate electric fence barrier was established. The above summary is given in detail by Habermann et al, (27).

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g. *Social rank and growth as factors influencing the prevalence of infections with microorganisms.* It has already been shown that the probability of ill health and mortality, as given in table 64, is greater for males, who are also more likely to be exposed to fighting and other stressful conditions. The sample of autopsied females was examined to determine if prevalence of infection was associated with such indicators of stress as social rank and growth.

Capillaria and *Streptobacillus* were grouped together as organisms causing "social contact" diseases since their transmission is facilitated by one rat biting or eating another. *Heterakis*, *Hymenolepsis* and the condition of bronchiectasis were grouped together as "random contact" diseases, since all rats came more nearly having the same probability of exposure through water, food, or soil contaminated with the eggs or the bacteria. Fifty-three females were included in the total sample. An individual rat might have none or all of the infections. All of the rats were not examined for all five conditions. The total examinations were 197. Most of the records supplied by the Microbiological Institute were in terms of intensity of infection as well as presence and absence. For the purposes of this examination mild infections were listed in the "absent" category along with those individuals for whom no infections was detected.

Several comparisons showed no statistical significance between the "present" and "absent" categories. These included: (1) Random contact diseases with social rank; (2) social or random contact diseases with the Maturity Index classifications of growth; (3) social and random contact diseases among those rats who were in the lower one third of the rank ordering of the 53 females in both social rank and growth. These latter females were presumably the ones which had experienced the most stress.

Two comparisons resulted in significant differences: (1) Social contact diseases: (a) present according to social rank: high—21, medium—9, low—7; (b) absent according to social rank: high—6, medium—7, low—10. Chi square, 6.17; p of Chi square less than 0.05. See table 56 for related data. (2) Disease prevalence among the more favored rats: The 53 females were rank ordered according to both social rank and growth (Maturity Indices). The more favored rats were designated as those who fell in the upper third of the rank ordering in both categories. There were

90 examinations which gave none, one, or more of the diseases for each of these rats. Social contact diseases: present—19, absent—9; random contact diseases: present—22, absent—40. Chi square. 6.90; p of Chi square was less than 0.01.

From the significant and nonsignificant comparisons certain tentative inferences are suggested. Rats who have high social status, and who are more likely to bite (and probably also eat) other rats are more likely to contract infections of *Capillaria* and *Streptobacillus*, whose transmission is facilitated by such action. Such rats appear to be more resistant to the condition of bronchiectasis and to infections of *Hymenolepsis* and *Heterakis*. However, increased size alone does not necessarily contribute to resistence. Many of the larger rats must experience more stress than some of their smaller associates as a result of their unsuccessful competition for favorable status. Among the smaller rats, or those of lower social rank, there is an equal probability of getting or avoiding the diseases. No conclusions concerning this are warranted. These results point to the desirability of planning studies on population ecology to accurately determine the effect of social organization and growth upon the prevalence and incidence of disease.

D. *Population Growth.* During the 27 months of observation, the colony of Norway rats increased from 10 individuals weighing 3.5 kilo to 171 weighing 60 kilo (fig. 146). It is quite unlikely that the number of adult rats, alive at the beginning of later spring breeding seasons, would have ever exceeded 200. See the previous discussion (pp. 54 to 63) on the growth of trails as an indicator of population level.

The 10 adult females alive from March through May 17, 1948, weaned on the averge 9.2 rats. During the same period in 1949, there were 59 adult females surviving from 1948 which produced only an average of 2.2 young which were still alive on May 17. Many of these latter were not yet weaned, so that the average number surviving through weaning would probably have been 2.0 or less. All the evidence is that this trend in decrease of number of weaned young per female would have continued at least into the next year. Although projection of trends is a poor tool, the best estimate that might be made is that by 1950 there would have been 77 breeding females during the spring breeding season. These would have produced on the average only 0.55 weaned young from March through May. Probably not more than 72 rats

would have been weaned during the entire 1950 breeding season. Despite the crudeness of this estimate, it is certainly unlikely that there would ever be over 200 adults at the beginning of any future breeding season.

Furthermore, as the colony aged there was a changing sex ratio toward a greater proportion of females as a result of the higher mortality of males (fig. 147). During 1947 16 males and 12 females were weaned. Half of these females but none of the males survived to May 1949. During 1948 104 males and 65 females were weaned. Sex ratio prior to weaning was unknown. Why there were so many more males than females weaned is also unknown. Rats born in 1949 which had been weaned or were near weaning age by May 17 were sexed; there were 57 males and 63 females. By 1950 there should have been both an actual and relative preponderance of females.

The number, 200 rats, is particularly instructive when we compare it with the number of rats that might have been raised in the available space had each individual been isolated as a juvenile into 2 square feet of cage space, as is customarily done in the laboratory. Under such laboratory conditions 5,000 healthy rats might have been reared in 10,000 square feet of space instead of the 200 which utilized such space under free-ranging conditions. This figure of 5,000 rats is actually a conservative one in regard to representing the biotic potential expected from this free-ranging colony. The studies of Emlen and Davis (22) and Davis (23),

supplemented by my own observations, indicate the following conditions for determining the potential reproduction, were other limiting factors not in operation: (1) eight per weaned litter with equal sex ratio; (2) first litter by 5 months of age; (3) one litter every 2 months; (4) no beeding during the 4 midwinter months; (5) all rats born the first breeding season should be dead by the end of the third; (6) it is within the potential lifespan of a rat for all which were born in the pen to have been alive at the end of the experiment; (7) the study lasted from March 1947 to June 1949.

With these conditions as a basis for judgment, 50,000 descendants from the original 5 females might have been alive in June 1949. Nevertheless in the comparison above, it is believed that the figure 5,000 is a more realistic one in indicating the potential density of 10,000 square feet, although it is conceivable that 50,000 healthy rats could be maintained in a similar space by confining each to a cage somewhat less than 8 inches square. What, then, was the cause of this 25-fold decrease in utilization of space under naturalistic conditions? The obvious explanation is that under free-ranging conditions the rats expressed genetically determined and culturally modified behaviorial potentialities which would be impossible under caged conditions. This explanation has broad implications. Whenever the density of a population becomes increased beyond that level to which the heredity-to-enviroment relationship provides optimum adjustment, then the individual and the group must forfeit some
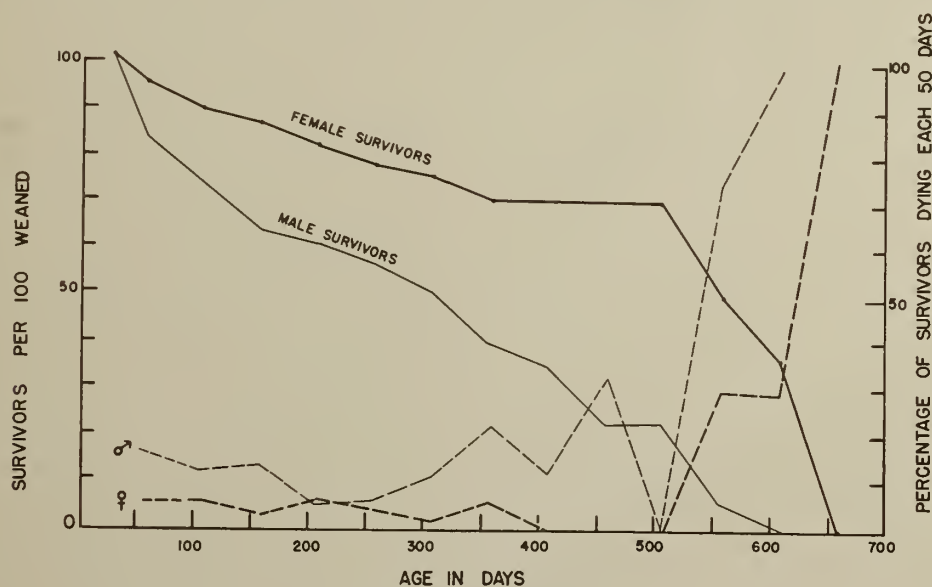

Figure 147.—Survivorship curves.

of their potentials of behavior if all members are to maintain an adequate state of health.

It was quite apparent that the behavior of most rats did become inhibited or modified as a result of the interaction with other rats. Whatever the nature of the alteration in behavior it ultimately entailed avoidance of more dominant individuals. Whereas the forfeiture of behavioral potentiality enabled the individual to live longer, there were concommitant negative effects upon the individual which reduced both conception and the survival of newborn rats.

This appears to be the process involved whereby a population of Norway rats may limit its own growth in the absence of predation, and where food harborage, and space for construction of burrows were always in excess. It suggests certain general procedures that will facilitate reduction of population density in this and similar deleterious species which serve as reservoirs of diseases transmittable to man, or cause property damage. These are: (1) Restrict the space available for habitation. Irrespective of other conditions, territoriality will immediately decelerate population growth. (2) Concentrate the locations of sources of food or harborage. This serves to increase competition and thus to cause stress to the rat's physiology. (3)

Increase the probability of one individual contacting another, particularly in proximity to goals. For example, where there is a single place of access to a source of food, contacts near the food will increase, and it will also be easier for a single individual to prevent the accesss of others. (4) Disrupt social organization through migration and the restructuring of groups (5, 24). These four procedures need not reduce the total amount of food or harborage. Instead, their action is exclusion from access to goals or production of physiological stress—both as a result of social interaction.

Restriction of the amount of goals such as food and harborage, when their distribution is unaltered may be anticipated to reduce density or prevent growth of a population only when the requirements of the existing population are no longer fulfilled. In urban areas of Baltimore inhabited by rats, removal of board fences, trash, and food (either separately or together) have usually been followed by reduction in the population of rats (25, 26). These reductions were no doubt due to: (1) Decreased amounts of environmentally supplied requirements, and (2) social interaction stressors operating through (a) migration, (b) restriction of available space, (c) spatial concentration of goals, or (d) restricted routes of access to goals.

IMPLICATIONS OF THE STUDY

This study was undertaken in order to obtain more insight into the biology of the Norway rat under natural conditions as well as to explore the specific hypothesis that the growth of rat populations may be inhibited through social interactions. The manner in which social interactions inhibit population growth provides an understanding of how alterations in the environment operate as an effective means of reducing rat populations.

Furthermore, these findings open up a field of research in which animals subjects may be of value in elucidating some of the social problems which confront man today. This field is the relationship of the physical structure of the environment to social behavior and to social organization of groups.

ABSTRACT

Five males and five female wild Norway rats, *Rattus norvegicus* were introduced into a 100-foot-square enclosure. Food and water were almost continuously and abundantly available. Predators were excluded. The history of these rats and their descendants was followed for a period of 27 months, the primary objective of the study being to determine in what way social interaction might inhibit population growth.

Early in the history of the colony there was a space-social class stratification in which the more dominant individuals inhabited the southeast half of the enclosure. This division was maintained throughout the entire study.

Individuals tended to remain near their place of birth. As the population increased, local competition forced rats from the socially higher ranking colonies in the southeast half of the pen to invade the northwest half. This migration was primarily by males. There was no reverse migration from socially lower ranking colonies into higher ranking ones. All changes in social status were downward. These migrations led to an increased number of social interactions among members of the socially lower ranking colonies.

Females were quite aggressive when lactating. At these times they excluded most other rats from the vicinity of their burrow, with the exception of other reproducing females of the same local colony.

In a few instances a highly dominant male established a territory about a burrow containing several reproducing females. He usually excluded all other males from the vicinity of the burrow. The most important consequence of such male territorial behavior was that it reduced the frequency with which other males were able to invade the area and make advances on a female when she was in estrous. Females in such situations were characterized by marked success in conceiving and rearing young. Effective male territorial behavior developed only about colonies of females which historically were of high rank.

In the northwest half of the pen there developed an excess of males as a result of the migration to it of those excluded from the southeast half. Membership in local groups was here less stable as evinced by the greater number of places of origin represented by the members of a local group at a particular time. There was never any clear-cut expression of territoriality by any individual in such groups, although occasionally one male dominated others. A female member of such a group, when in estrous, was continually followed by a pack of males. In rapid succession she would be mounted for a total of several hundred times during a single night. The behavior of such females indicated they experienced considerable stress. Conceptions were reduced and few young were raised. The normal preparturient behavior patterns of self-isolation, burrow construction, and nest building, which are requisite to successful rearing of young, were reduced or entirely inhibited.

As the population increased a larger proportion of the colonies were characterized by this low social rank and instability, with the concomitant reduction in reproduction. This is basically the process by which a population of rats limits its numbers in the absence of other controlling factors. All evidence indicated that no more than 200 adult rats would ever have existed in the quarter acre pen at any one time. At one end of the social spectrum there was a colony consisting of a single dominant male and a harem of 13 females, most of whom were reproducing successfully. At the opposite extreme there were all male aggregates

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whose members rarely engaged in any sexual activity.

A behavioral complex which contributed to the accentuation of social interaction was that relating to the construction and use of trails. Each pair of major goals, such as a burrow or a site for procuring food became connected by trails. These trails also interconnected with each other. However, expansion of the meshwork of trails was limited by some response which precluded the minimum diameter of the polygon enclosed by a group of trails becoming less than 5 feet. Once the pen became filled to this extent further increase in the number of rats merely increased the frequency of contacts between rats inhabiting the same locality. The opportunity for increased contacts with other individuals became greater among the socially lower ranking groups of rats inhabiting the northwest half of the pen. This resulted from the greater number of rats inhabiting this half of the pen following its invasion by rats forced to emigrate from the higher ranking colonies inhabiting the southeast half of the pen.

In addition to spatial isolation of colonies according to their social rank, there was isolation in time. All rats visited the single central source of food and water. Members of higher ranking colonies tended to maintain the bimodal nocturnal rhythm of visiting this source that was characteristic of the early history of the colony when the population density was low. In contrast to this, members of lower ranking colonies tended to visit this source at times when most members of higher ranking colonies had retired to their burrows. Thus, they were more active in the dusk and dawn hours and between the two peaks of activity exhibited by their higher ranking associates.

One of the impacts of social interaction was the alteration of growth. Inhibition of growth was greater among individuals born into socially low-ranking groups. Regardless of the relative rank of the group into which an individual was born, growth was inhibited in proportion to the number of other rats with which the individual associated following weaning. Thus, as the population increased more individuals were characterized by inhibited growth.

Social rank was judged on the basis of success in combat, growth, place of birth, migration, reproductive success, and associates. Some of these served as both cause and effect of social rank. The best criterion for judging social rank was the overall picture presented by the group of adults with which an individual associated during the breeding season.

The secondary objective of this study was to describe how rats interact with their physical environment in fulfilling their needs for food, shelter, and reproduction. Fulfillment of these needs was considered from the viewpoint of how the behaviors contributed to the survival of the individual and the species.

Most rats stored food. This behavior was accentuated in lactating females and in some socially low-ranking rats. Dispersal of food through the environment was enhanced by caches serving as secondary foci from which other rats transported food to neighboring localities. The value of stored food was not recognized. Caches were frequently covered over while enlarging the burrow, or they were excavated to the surface and allowed to deteriorate by the action of rain, etc.

The frequency of responses from a point of orientation declines roughly exponentially with distance. In the construction of nests, this leads to the utilization of materials close to the nest site. In the construction of burrows this leads to a diminution in frequency of longer tunnel segments.

Orientation in space is initially governed by the presence of goals such as sources of food or places of retreat. Shortest routes are generally not traveled exactly. Instead orientations are from one vertical object to another or along a continuous vertical object or narrow smooth plane. Repetition of traversing the same routes leads to the formation of trails. These trails are kept clear of vegetation. Once this happens, tactile responses to the sides of the trail facilitate orientation. Such tactile responses appear to be innate or are learned very early. Young rats on their first independent excursion rapidly move along established trails. Thus in a very few hours they have found sources of food and water as well as other burrows which may serve as places of retreat. Alternate routes between goals are learned. When an introduced physical barrier, or the presence of an aggressive rat, bars travel, the individual immediately resorts to an alternate route toward its goal.

This biological modification of the environment as well as the social structure of the existing group forms a cultural mold which guides the development of the young rat. Overt aggression of adults against the juveniles is infrequent. Aggression

toward juveniles takes the form of threats. The frequency of these are important in determining adult behavior since they lead to the conditioned behavior of avoiding the approaches of other rats. This avoidance of a more dominant rat is the major characteristic of a subordinate individual. Young rats gain their initial sexual experience with adults. In many other ways the behavior and fate of a maturing rat is determined by the actions and activities of its adult associates.

DISCUSSION

1. *The Writer's Attitude Toward the Study of Behavior*

A proper perspective to the study reported in this publication requires an appreciation of the philosophic position I have in its formulation and pursuit. I hold that if one is to pose questions concerning social behavior or is to formulate meaningful hypothesis that are subject to experimental verification, one must first develop a broad understanding of behaviors, their consequences, and the situations which elicit or modify them. This must be done for each species to be studied. Observation and analysis form the first step. In this process one notes that under certain conditions behaviors become modified so that the consequences are inappropriate or that the individual or the group are deleteriously affected. On the basis of such miscarriages of behavior one then has a logical basis for the formulation of hypotheses, whose testing requires experimental manipulation of the animal's physiology or of the situation which modifies the elicitation and expression of the behavior. This philosophical approach to the study of behavior has been elaborated by Lorenz (27).

Most studies of physiology and behavior, in which the wild Norway rat or its various domesticated breeds have been used as subjects, have completely ignored this point of view. Experimentation has been based upon hypotheses primarily formulated on the basis of clinical studies on man. I am not implying that one cannot derive insight into biological problems which also has relevance to human problems from the study of rats. What I am saying is that without a knowledge of the biology of the experimental subject in its native haunts, one cannot hope to achieve maxi-

mum effectiveness in experimental design or even to rephrase the hypothesis appropriate to the experimental subject. Furthermore, familiarity with ecological approach to animal behavior engenders cognizance of the fact that one frequently is able to recognize a behavioral phenomenon in one species, which may be experimentally studied in a second species, even though conditions pertaining to the second species reduce the probability of initially recognizing it there. Thus, even when our interest in animal experimentation is to seek answers of relevance to human experience, we can expect to strike pay dirt as often from hypotheses derived from a knowledge of the experimental animal, as those derived from man. Utilization of both sources of hypotheses offers the most promising path to successful experimentation.

The above serves as a background to my selection of material in the literature for comment. This selection will be devoted (1) to providing further understanding of the behavior and ecology of rats living in organized groups, and (2) to suggesting likely causes or implications of some of the observed phenomena. No attempt will be made to duplicate the reviews of various aspects of the biology of the Norway rat. The following are some of the major sources of material reviewed by others:

Population ecology: Davis (28), Barnett (29).
Rodent control: Storer (30), Chitty and Southern (31).
Epidemiology: Hirst (32).
Domestication: Castle (33), Richter (34, 35).
Psychology: Munn (36).
Sex Behavior and Physiology: Beach (37).
Use in Laboratory Studies: Farris and Griffith (38).
Fighting: Scott and Fredericson (39).

2. Steiniger's Study of Group Behavior of Rats

During approximately the same years I made my studies of Norway rats in an enclosure near Baltimore, Steiniger (40) conducted quite similar studies. Since his study and mine are the only ones to date which have attempted observation of group behavior under simulated natural conditions, it will be well to mention those areas in which his observations corroborated mine, as well as those conclusions which are additional or contrary to mine.

His enclosed pen was only one-sixteenth (i.e., 64 square meters) of mine. This much smaller area must have accounted in part for the more marked antagonism he noted among his rats. Another contributing factor was that groups of strange rats were periodically added to the pens. Furthermore, the surface of the pen was unstructured by any barriers which would permit evasion and retreat of subordinate rats from their superiors. Except for occasional peculiarities due to size or wounds, individuals were not identified, and thus observations relate only to those having obvious differences in size or sex. He presents much additional information concerning behavior of rats based upon his observations of feral colonies.

When entire groups of new rats were introduced in the absence of prior residents marked fighting ensued. Usually only one male and one female survived this ordeal which might last 2 weeks. In this process males usually killed males, and females killed females. A much more stable group developed from such a pair in which second and third generation members formed a closed group. Among these there was considerable tolerance. Younger members were permitted to take food from their elders with only mild, if any, rebuff. However, introduced alien rats were usually attacked and killed. At these times of heightened emotional state, members of the previously peaceful ingroup would attack each other. [I have noted the same phenomenon among house mice (16)]. However, these latter attacks usually terminated in more peaceful interactions such as mutual nuzzling. When a member of an ingroup (Rudle) was removed to the laboratory for several days it was usually attacked upon its replacement—just as if it were an alien rat.

Steiniger cites two escape behaviors which I never observed in my larger pen. The rat being pursued either attempted scaling the wall or it would stop suddenly with its head against the earth and its posterior elevated with its tail trembling. I suspect that both of these behaviors are abnormal concomitants of confinement in a space too small to permit escape.

The process whereby only a single pair survive from an original 10–15 introduced rats is designated as territory or precinct (Revier) formation. The concept of territoriality is hardly appropriate to these confined quarters (circa 26 by 26 feet), since exclusion of subordinates could only occur by their death.

However, Steiniger's concept of the development of a peaceful Rudle or ingroup is probably sound, even though outgroup members were only present in the sense of introduced aliens until they were killed off by the ingroup members. Amicability persisted between parents and progeny even through the time when the latter were in turn rearing young. Likewise, amicability usually persisted between adult sibs. The importance of these observations is that rats reared together are more tolerant of each other than they are toward introduced aliens, or than are rats unfamiliar to each other when introduced into a strange situation. Steiniger is quite vague as to the duration of his studies, number of rats in groups, their age, etc. Yet it is quite apparent that tolerance among ingroup adults did involve development and acceptance of hierarchial roles. He cites an instance of a fight between two 7-month-old brothers which terminated in one receiving a deep laceration. The latter always avoided his brother in competitive situations. Sham battles, that is boxing followed first by one rat being forced over on its back and second by both rolling over and over while holding on to each other, was observed among both juveniles and adults of the ingroups. Such interactions not involving gross wounds, as well as those involving the kicking of one rat by another, are classified as "play" by Steiniger. Had Steiniger marked his rats for visual identification I suspect that he would have found that one of two such interacting adults usually assumed the subordinate role.

Steiniger's account of sexual behavior duplicates in nearly every detail my own account, except that he makes no mention of the preliminary phase of sexual rolling and rubbing at female scent spots. He says that the male scratches the female's back as he mounts. Perhaps this is so, but even in my

examination of frame by frame movie strips the male's mount appears to involve more of a developing grasp than an actual scratch. Another interesting observation was that when the stem mother came into heat when her sons were 4–6 months old, most copulations were with these males, and very rarely with the original stem male, although he was the most aggressive rat toward alien males introduced at such times.

As to storage of food, Steiniger in general confirms my observations of storage by all ages from 4 weeks, of temporary storage at sites closer to the food source then the burrow, of excess storage, and of periodic cleaning out of food caches.

3. *The Rat as a Social Animal From a Comparative Point of View*

Three questions are relevant to the present discussion. To what extent do rats have culture? Why have many studies by animal psychologists contributed so little to the understanding of interactions between or among rats? In what way are studies on rats and other animals germane to the broad problem of sociality, including that of man?

Man has been the principal subject concerning whom concepts of social behavior and culture have been derived. However, in what follows I have attempted a formulation of social phenomena, relationships, and consequences, which permits a comparative evaluation of the rat and other animals including man. This formulation was prepared after the completion of the account of the rats inhabiting the Towson quarter acre pen. It was actually the organization of this account which focused my attention on the inadequacies of theory applicable to comparative sociology. Advancing the theoretical base for more logically planning future studies comprised the intent of this formulation of comparative sociology. I have made no attempt to fit into this formulation all my observations and conclusions regarding the biology of the Norway rat. To do so requires much additional information not included in the present study.

The *societal plexus* involves all conditions which may affect the consequences of an actual or anticipated performance by one individual, which in turn affects another individual or reacts back on the original performer. *Social behavior* is then any performance with such effects. A *society* is an aggregation of two or more individuals among which there is a greater than chance expectancy of social behaviors. *Culture* represents any and all processes and conditions whereby the performance of members of one generation alter the way of life or success of members of succeeding generations.

Consequences of social behavior include alterations of (1) physiology, (2) the probability of an event with an effect, or (3) the gratification-denial parameter of experience. The last of these three concerns the extent to which social behavior facilitates or interferes with the satisfaction of a need. These three consequences of social behavior may have either *adaptive* or *adjustive* significance. Adaptive implies attainment and maintenance of physiology conducive to growth, survival, and reproduction. Adjustive merely implies ability to accommodate to the exigencies of an existing situation sufficient for temporary survival irrespective of deleterious impact upon growth or reproduction. At the lower phylogenetic levels the premium is on reproduction and on adaptive behaviors culminating in its realization. However, as we go up the phylogenetic scale certain trends are noted: (1) greater longevity, (2) fewer young per female, and (3) a smaller proportion of the population which reproduces. Although such trends are apparent in lower phylogenetic categories, the climax has been attained in the Western technological society of man. This trend produces a situation in which adaptive behavior relates less and less to culmination in successful reproduction, but merely to maintenance or restoration of a well-balanced physiology. Allee *et al* (*41*) have emphasized that, as we proceed up the phylogenetic scale into more completely integrated groups, natural selection operates more on the group with regard to its structured characteristics than it does on the individual as a survival unit. With the deemphasis of natural selection on the procreating individual per se there arises the opportunity of a greater prevalence of adjustive behaviors. Adaptive behaviors in a highly integrated social group primarily relate to maintenance of a well balanced physiology. This raises an interesting question: Does the development of complexly integrated groups demand that many of their members develop adjustive but nonadaptive behaviors, which are of themselves of value to the group?

Perhaps an example will clarify the intent of this question. Western technological society demands a high mobility by its members as well as a continually increasing concentration of individ-

uals in areas where existing residents already are characterized by marked propinquity to other individuals. The physics of this situation has been discussed in detail by Stewart (42, 43, 44). Stewart designates this propinquity among individuals as the population potential. An inherent assumption of his formulation is that population potential is positively correlated with the incidence of interactions. A favorable byproduct is the more effective production of material goods. My own studies (45a) of the correlation between population potential and rates of mortality or admission to mental hospitals shows that the latter exhibits a positive correlation with population potential, as also does the former after 35 years of age when proneness to metabolic breakdown diseases becomes accentuated. Greater susceptibility of the mobile portion of the population to mental illness is confirmed by Malzberg and Lee (45b). Thus, conformity to the demands of Western technological society is certainly adjustive in that it assures greater material rewards, but the evidence of disruption of physiological homeostasis strongly indicates that such behavior is not adaptive.

If this insight approximates reality we can anticipate a positive correlation between the complexity of society and the prevalence of psychosomatic symptoms and behavioral deviates. If not, the observed prevalence of these conditions merely reflect some malfunction of social organization.

Consequences of social behavior may arise from either direct or indirect social behaviors. In *indirect* social behavior two individuals need not be present at the same time for one to exert an influence on the other. The only requisite is that the activities of one individual produce changes in the environment which alter the behavior of some other individual. *Direct* social behavior involves the simultaneous presence of a symbol denoting some quality of the absent individual that is relevant to the present one. In this case the qualities of the symbol are equivalent to performance by the absent individual.

Neither the social behavior of the performer or its effect on another individual necessarily involve any learning process. Where physiological alterations occur in the direction of prevention of homeostatic imbalance or return toward balance, and if the animal is endowed with an adequate nervous system, learning may take place. Thus, even in the absence of innate social behaviors or of innate responses to them, learned behavior leads to

codification of the performance-effect system. Furthermore, where learning is possible certain aspects or qualities of the performance-effect system, of the individuals themselves, or of the environment in which the system operates, may become associated with the operation and thus they become goals in and of themselves with respect to the gratification-denial parameter of experience. Such transformations become *attitudes* or *value systems*.

At any point in time each individual is characterized by a specific predisposition to respond in a particular way to impinging stimuli. Such predisposition constitutes the individual's *personality* which functions as a determinant of social behavior. Thus, personality is here considered as the complex of genetically limited and environmentally modified states of physiology, or capacities for perception and action which modify responses. All responses reflect the influence of personality variables, regardless of whether or not the response has social implication. Attitudes or value systems constitute the most complex aspects of personality.

Physical determinants of social behavior form an important, and conceptually a much neglected, aspect of the social plexus. These include physical objects as such, their spatial distribution or function as barriers, and their motivational or symbolic implication. The distribution and shape of objects or characteristics of the environment modify the frequency and pattern of contacts between individuals, which in turn are important variables in determining the size and stability of groups, as well as the stress experienced in relation to the frequency of making adjustments following contact. In addition, some objects, such as a piece of food at which two individuals may arrive simultaneously, are related to specific motivational states, such that encounters here are quite different from elsewhere. A special case is that of *cultural artifacts*, in which certain aspects of the environment are restructured by certain individuals, and this restructuring alters the behavior of other members of the same generation or even of later generations.

Quality and configuration of routes of communication, of places of abode, of the amount of foodstuffs, or of the aggregates of individuals themselves, form pertinent examples. Response to these changed conditions may be either innate or learned. At higher phylogenetic levels, particularly with man, cultural artifacts assume *symbolic connotations*

which facilitate maintenance and transfer of attitudes and value systems. Functionally, although of an ephemeral nature themselves, attitudes and value systems, are just a special case of cultural artifacts.

Societal determinants of social behavior are constituted of organizational characteristics of the group as well as secondary attributes of the group arising from its functioning as an organized group. Thus, societal determinants represent a supra-organismic level of influence in contradistinction to the individual level of influence represented by personality. Group attributes include such phenomena as (1) conservation of moisture or body heat in aggregates, (2) more effective repelling of predators, or (3) development of group norms which bias the individual's attitudes.

In their formulation of "A general theory of action" with reference to human social behavior Parsons and Shils (46) are only concerned with adjustive behavior and the process through which attitudes or value systems held by one individual are internalized by another individual, in which they then become an integral component of his personality. As I see it, Parsons and Shils overlook a large area of the social plexus which is relevant to human experience and which is requisite to a formulation of comparative sociology. They ignore the three types of consequences of social behavior listed above, except for attitudes or value systems related to satisfaction of needs.

Sprott (47) in his review of Parsons (48) and Parsons and Shils (46) concurs with my critique at least to the extent that he recognizes the need for proceeding with the evaluation of those variables affecting social behavior, other than those involving only direct social interaction, without awaiting completion of a fully adequate theory of social action. In fairness to Parsons one must recognize his awareness of the restrictions to his theories for he writes: "But quite clearly *we have advanced no theory* of the interdependence of social action processes and the biological and physical factors of their determination" [(48), p. 488]. Even though he recognized the existence of such factors he prefers to ignore them. In contrast, my own emphasis is that development of a comparative sociology requires initial consideration of the origins and consequences of those social behaviors least involved with values or attitudes.

Detailed observation of lower forms raises doubts as to the frequently implied absence of symbolic communication, attitudes, and value systems in forms other than man. For example, there is the ethic of honor your father and mother. Operationally rats exhibit behaviors indicating conformance to such a tenet. For example, one of the 21-month-old stem mothers, No. 39, of colony a (table 44) still maintained her residence with her daughters, nieces, grandchildren, etc. at the home burrow, even though she was no longer capable of reproduction. This old female, as was also true for other old females who had successfully reared a number of young, was "honored" to the extent that her presence was tolerated within a group to whose welfare she appeared to contribute no longer. I shall not attempt speculation on the origin of this relationship. Suffice it to say— comparative examination of social behaviors without artificial restrictions of scope should provide more meaningful insight.

In dealing with man Parsons and Shils focus entirely on adjustive behavior, and ignore any implication of adaptive behavior. That is they are concerned with what a particular species, *Homo sapiens*, strives for or is motivated toward, not what does he have to strive for in order to survive as an organism. In so doing they intentionally or inadvertently ignore a large segment of the *social plexus* which affects both man and other species to varying extents. Their restriction of point of view is a logical derivative of their failure to consider social phenomena from a comparative point of view.

We may also put the shoe on the other foot and ask: "Why have experimental studies with Norway rats failed to advance very far our understanding of social phenomena?" By taking into consideration the complexities of social behavior or Norway rats in a naturalistic environment observed by me and by Steiniger, and by taking into consideration the formulation of the social plexis as presented above it becomes apparent why studies by experimental psychologists [See reviews by Crawford (49) and Munn, (36).] have contributed so little to the understanding of social phenomena of the rat as a social animal. Those conducting these studies exhibit a nearly total ignorance of the nature of the normal social behavior of this species. This has posed great barriers to stating properly questions to be tested, to structuring the experimental situation, or to evaluating results. Development of social behavior in the rat, other than for the rudiments of sexual intercourse, maternal behavior,

or interindividual relations, demands space, structured by goals, within which groups may form with integrity from other groups with whom they still have the opportunity of developing interrelationships, and demands time through which the activities by members of one generation can affect the activities and fate of members of the same or later generation. To the extent that these criteria are not met, full social behavior will not develop.

Let us first examine the usual background of rats used in experimental studies of social behavior. The young gain their first experiences in the cramped quarters of a small cage structured only by a nest, a water bottle and a food hopper, and in association with an emotionally and behaviorally deprived mother. They are prematurely and abruptly weaned at 21 to 30 days and left in a cage made still more barren by the removal of nesting material. Here the rat is left alone or in company with a few others of his own age and sex for the relatively long period of weaning to adolescence. Sleeping, eating, and drinking require the barest minimum of demand on the rat's potentials of behavior. Even where antoagonistic behaviors develop, only poorly defined stable interrelationships can develop between any two rats, because in the confined quarters, more likely than not, the other members become involved in a general melee. Cooperative behavior is confined to huddling, and then only if perchance the cage is cold and drafty. Before passing judgment on the propensities of the rat for social life, reflect, if you will, on the extent of social behavior you might anticipate for human subjects reared in comparably sterile environments to adolescence. Some time during adolescence, roughly 60 to 100 days in most domestic rats, the rats are exposed to the experimental situation. These studies rarely extend into the prime adult period, roughly 210 to 270 days of age, much less beyond this into later life.

Social facilitation, in terms of the speed or frequency of an activity, the attraction of one individual to another, and fighting, have been three of the principal areas of research. In general these results have been "disappointing". Such social facilitation as has been demonstrated primarily involves unlearned behavior where each rat interferes with the activity of its associate. This interference apparently restricts the attention to the task at hand so that increased speed of action ensues. Other than attraction to a female in heat by males or to young by a lactating female, there

has been little evidence in such studies of social attraction. The general lack of success probably stems from failure to provide a situation in which one rat learns to regard a specific other individual either favorably or unfavorably. Furthermore, there should be reciprocity of regard. Were such training provided throughout the period of development, the chances of eliciting social behavior would be greatly augmented. There is little reason to believe that the mere housing of two rats in a small bare cage would later cause one to be attracted or repulsed by the other.

Certain behaviors, for example hoarding, have been studied extensively by experimental psychologists. Furthermore, ignorance of rats in their native haunts leads to erroneous statements such as Beach's [p. 123, (50)] that it is not surprising that some rats never learn to hoard food "since Norway rats rarely hoard food under natural conditions". In the context of these experimental studies the hoarding is unsocial. However, in a socially structured population, a behavior such as hoarding has several social implications. The basic function of hoarding, of which the rat is not cognizant, is the dispersal of food through space such that a larger proportion of the population benefits from any given source. One could never have arrived at this conclusion from laboratory studies, which have given rise to the conclusions that hoarding is increased by such factors as early deprivation of food, decreased temperature, or familarity with the surroundings. My present studies showed that there was ample opportunity for some deprivation, particularly among the progeny of socially lower ranking rats, both during the period of nursing and following weaning. Thus, the origin of intensity of hoarding (see example of female 43 and her young, pp. 147 to 148) has social implication. Furthermore, once hoarding behavior is initiated, it demands more trips between the rat's home and the source of food than would otherwise occur. This increases the probability of contacting and interacting with other rats. Thus, the socially low-ranking rat is more likely to hoard because of early deprivations, but the increased contacts accompanying hoarding increase the frequency with which such a rat is attacked by higher ranking associates. That is, the rat increases its probability of being punished for hoarding. Two consequences have already been detailed. These are that non-harborage storing develops and that activity, including food transport, tends to become more

diurnal. Hoarding, more appropriately designated simply as storage, is a behavior with many nuances, to whose origin many conditions contribute, when it develops in the context of a socially structured population. Likewise, experimental studies of the rat, covering such areas as perception, motivation, learning, and emotion, all of which have been intensely pursued in the laboratory, promise to become much more fruitful when further pursued with respect to the conditions which foster social interaction and development of culture. Only after completion of such complex studies can we hope to arrive at an approximate evaluation of the rat as a social organism.

The remaining portion of the discussion section of this monograph will suggest, or fill in, some of the obvious gaps required to describe the sociology of the Norway rat.

4. The Learning of Social Adjustments as a Factor in Determining Physiological Disturbance and Social Mobility

Barnett (51) has investigated competition among wild Norway rats in 1-cubic-meter enclosures in which the inhabitants were marked for visual identification. Several males which were simultaneously introduced might live together for as long as 22 months without mortality or rarely ever any injury to one another. However, the introduction of another male leads to his attack by the resident males. Barnett concludes that this latter is evidence of territorialism. Such a conclusion is probably not warranted. The study cage was much smaller than the normal range of a rat, nor was there the opportunity of sustained exclusion from a given space. When these two conditions are not fulfilled we are not justified in speaking of territoriality but merely interindividual antagonism. From this latter viewpoint Barnett's observations become important.

The stranger introduced into the group frequently died, not from wounds, but from an undetermined physiological breakdown. This raises a very interesting question: Why do several rats who are strangers to each other make a satisfactory adjustment when simultaneously placed in a confined space in contrast to the inability of another strange rat to make a similar adjustment when introduced into the group at a later date? Contact rate cannot be the cause. There is only a 25 percent increase in contact rate per rat from a group of 5

to one of 6. No substantiated explanation of this important question may be made. However, I wish to suggest a plausible hypothesis, which is amenable to experimental verification.

It has been shown by Marx (52) that rats who have learned a maze exhibit a declining ability to retain this learned behavior as more and more different types of mazes have to be learned between acquisition of the learning of the first maze and the later date at which they are tested for its retention. In other words, interpolation of different but similar learning tasks mutually interfere with each other. Development of a hierarchy or similar system of social adjustment among a group of rats who are strangers to each other requires learning. Furthermore, one would suspect that the rate of acquisition of a learned adjustment between any two rats is inhibited by the interference of learning adjustments with other rats. In the early stages of this slowed down social learning each rat should serve as a relatively unconditioned stimulus for the other rats. Therefore, contact between any two rats should produce only a mild emotional response and physiological disturbance. Physiological adjustment, such as increase in adrenal size, should be able to keep pace with the gradual increase in intensity of interaction as social learning proceeds. Thus, at the termination of hierarchy formation each rat's physiology should have achieved a state capable of coping with the intensities of interaction then existing. Barnett showed that such physiological accommodation actually took place. During the initial contacts of the first 2 days among members of the group being formed there was depletion of the sudanophilic material of the adrenal cortex (Selye's alarm reaction), following which there developed a stage of increase in adrenal size with maintenance of sudanophilic content (Selye's stage of resistance). At the time of the introduction of another rat each of the resident members of the group are involved in only one learning situation, that directed toward the stranger. Thus, the intensity of action of each group member toward the stranger might be designated as 1, or a total intensity of N, in contrast to the relative intensity of $1/N-1$ characteristic of each interaction while developing the hierarchy. This means that a strange rat introduced into an established group of N rats receives N times the intensity of action that characterized the group during its formation. If this formulation approaches correctness, it is small wonder that Barnett

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observed the strange rat dying from physiological exhaustion within a day or two. According to Selye's formulations, the terminal stage of exhaustion must have been reached, without the opportunity for the intermediate stage of resistance intervening after the initial stages of alarm reaction.

At the time of introduction of a stranger even the members of the established group should be under a heightened emotional state. Dr. Allan Dittmann of the National Institute of Mental Health informs me that a similar situation is characteristic of groups of delinquent children which he is studying. The group is composed of six boys. From time to time one boy is released to go home and a replacement added. Not only does this new boy have a hard time at first, but also the group as a whole is set into turmoil for a day or two following his admission.

With this background we are in a better position to appreciate the origin of the stress existing in many of the local colonies of rats in my Towson population. Most males and a few females are ejected or at least depart from the more stable socially higher ranking colonies. These individuals are attracted to and join some other, but socially lower ranking group. As a consequence this whole group is upset and the intruder in particular must receive particularly intense interactions. The intruder is sometimes able to join the group. But this increases the size of the group. And since groups tend not to exceed 12 individuals pressure builds up to exclude some member. When this happens there is a drifting rat which usually attempts to join another group. Since groups attempt to exclude intruders, a drifter should find easiest access to those groups which have the most recent additions of other drifters, because they will have the less crystalized social structure. This process predicts a gradient among the colonies in a population such that at one extreme membership is highly prolonged and relatively unchanging, while at the other extreme membership is temporary, and the individuals represent many places of birth. A reexamination of table 57 supports this formulation.

Mobility, in the sense of frequency of change of residence and group membership, is negatively correlated with attainment and maintenance of body weight and with reproductive performance. All evidence indicates that resultant changes in social status are downward.

5. *Events and Conditions Relating to the Maternal Period of Life*

In the following seven sections there are presented results of several lines of investigation, as well as formulations derived from them. These provide insight into the field studies and indicate some problems toward which future study of the maternal period of life may be directed with profit.

A. *Stress Induced by Electroconvulsive Shock in Relation to Adrenal Function, Growth, and Maternal Behavior.* The studies of Rosvold and his associates on rats (53 to 58) provide valuable insight into how stressful experiences may have produced some of the physiological and behavioral aberrations apparent in the present study. Electroconvulsive shock (ECS) was the stressor. Chronic ECS produced adrenal hypertrophy, and an increased output of ascorbic acid. These effects on the adrenal were apparently mediated by way of the hypothalmus and the anterior pituitary. Futhermore, these effects on the adrenal by ECS were produced only when behavioral changes simultaneously occured. Thus, adrenal and behavioral changes accompany ECS alone but not ECS plus anesthesia. On the behavioral side learning and retention of a learning is impaired in the ECS stressed rats; nest building is impaired or even inhibited for at least 10 days post ECS treatment in males and for a much longer time in lactating females. Females who received ECS treatment for 15 days beginning within 84 hours following conception resorb many embryos. In these females nest building and retrieving of young is usually impaired throughout lactation although the young reared equaled controls at weaning. These maternal behaviors show residual impairment even with a second litter born 47 days after shock treatment. If the mother received ECS treatment during the first 15 days following parturition, growth of the young was inhibited both during this and the following 15 days during which weight data were recorded. Furthermore, rats who received 10 days of ECS beginning at 170 days of age exhibited an inhibited growth during the 23 post ECS days. To the extent that the ECS stressor and the social interaction stressors are equivalent it is logical to believe that the inhibition of growth, conception, burrow building, nest building, and maternal behavior recorded for the wild rats in my 100-foot square

Towson pen may also be attributed to effects mediated through the pituitary-adrenal system.

B. *Effect of Litter Size on Growth and Later Behavior.* Seitz (*59*) has demonstrated some important effects of litter size. Fischer strain albino domesticated rats of the F_{50} generation of inbreeding were used as subjects. Litter size was artificially determined. The experiment included 5 litters of size 12 and 10 litters of size 6. Mothers of the smaller litters were more maternal in the sense that when disturbed they were more reluctant to leave the litter following disturbance, they were more diligent in searching for removed young, and upon finding them were more effective in retrieving them, and they built better nests. No observations were made on the interactions among siblings prior to weaning, although it was the initial assumption that the greater competition among sibs of litter size 12 for the opportunity of nursing would be the major cause of any postweaning differnces in physiology or behavior. At 21 days of age each of the 120 rats was placed in an individual cage where it remained in isolation except for those short tests, such as mating, that involved another individual. The following are typical of the types of results obtained having statistical significance at the 0.05 level or below. Males but not females, of the smaller litters grew more rapidly. Members of the smaller litters hoarded less, ate more following 23 hours of fasting, defacated less and traveled more when in a strange open field, and had a shorter latency in entering a strange field. In addition, there was the qualitative difference that members of smaller litters were more docile and never bit the handlers as did the members of larger litters. Although the exact effect of maternal behavior and preweaning sibling competition in producing the observed changes among Seitz's rats cannot be stated, it is quite apparent that these variables were in operation in my free-ranging colony of wild Norway rats. Litters did vary in size and there was an indication in the case of females 43 and her litter, L–18, that some control of litter size may be exercised. It will be recalled that 6 of the 12 young born disappeared during the first 24 hours. There was also considerable indirect evidence that the socially lower ranking females exhibited reduced maternal behavior. At least they more frequently failed to rear litters, and failed to exhibit the normal pattern of nest and burrow building associated with paturition. Females who reared their progeny successfully did differ in nonmaternal behavior as well as in that constellation of characteristics which I have termed social rank. It is difficult to believe that such differences were not mirrored in maternal behavior as well, and that one of the major origins of differences in postweaning behavior and physiology of rats resulted from the behavior of their mother.

Following 16 months of isolation each of Seitz's males was placed with a female in heat. In general mounting failed to occur. "Courting" in the form of grooming the female or licking her genitals did take place. Although members of large litters exhibited a longer latency in approaching the female (i.e. she was a strange object), they spent more time courting her. This courting involved oral behavior upon the part of the males. It was Seitz's inference that the members of larger litters experienced more frustration in the early behavior of nursing, and the increased later hoarding of food pellets tends to confirm this inference. Grooming and genital licking are similar in their motor aspects to early behavior of nursing. Since nursing frustration augments even the more divergent oral behavior of hoarding, it is logical to expect an increase in the prevalence of grooming and genital inspection by the more frustrated males from large litters. This is my interpretation, whose origin is based on the previously cited observation for the wild Norway rats which showed that genital inspection of the mother who is coming into heat at the termination of lactation is a direct transfer of the behavior of inspecting the teats by young who at weaning still trail their mother.

C. *Size of Group.* Several lines of evidence from my experimental population were cited which indicated that as a general rule the ingroup rarely exceeded 10 or 12 rats. That is, the number of rats which lived in the same burrow or in closely neighboring burrows and had more frequent associations with each other than with other members of the population roughly approximated the usual litter size. This was so even though each group as finally constituted was composed of members of several different litters. From this I infer that tolerance of group size is determined by the number of individuals, mostly sibs, with which each individual had associations up to the time of weaning. It is presumed that whenever the group exceeds 10 individuals, antagonism between individuals increases to the point that some individuals are excluded. Elton and Laurie [in (*31*)] provide a large group of data which supports this belief.

Four-thousand seven hundred and five infested hay ricks examined between January and June gave a total of 46,126 rats, weanlings or older, or an average of 9.8 rats per rick. Unfortunately, they do not provide statistics on the variability of number of rats per rick. However, in 32 subsamples, each of which contained 50 or more ricks, the average varied between 6.7 and 15.2 rats per rick. The 15 densest populations averaged about 100 rats per rick. This indicates a skewness of the distribution such that the more typical density was probably nine or less. Since these unthreshed ricks represented a concentrated source of both food and harborage, it is apparent that rats do exercise control of group size toward an optimum level which approximates that of the preweaning litter size. For these rick-inhabiting rats Leslie, et al (60) list the mean number of embryos found in 225 pregnant females as 8.65 and the mean number per litter in the nest as 7.31 for 85 nests. A similar number of young per litter was found by Emlen and Davis (22) from a rowhouse residential area in Baltimore. They found an average of 9.0 embryos during the latter one-fourth of pregnancy.

D. *Reinterpretation of the Wistar Institute Studies on Captive Gray Norway Rats.* Beginning in 1919 the Wistar Institute initiated a colony of gray Norway rats stemming from a small group of wild caught individuals. Certain of the papers (*61, 62, 63, 64*) concerning the first 25 generations are of particular import to the present discussion. Knowledge of the biology of free ranging rats revealed by my present study, and the increase in knowledge of the interrelationships between stress, endocrine function, growth, and reproduction arising since King's publications provide the basis for gaining further insight into the biology of the Norway rat through examining the data presented by King.

a. *Methods of rearing and selection:* Only 6 of the 20 wild caught females bore litters in captivity. Their young were reared by domesticated albino mothers, since the change to captivity so disturbed the wild females that they destroyed their young when left with them. During the 2d to 25th generation the grays reared their own young even though considerable mortality took place during the suckling period through the first few generations. Those rats selected for breeding and further studies on growth, etc. had to meet the criteria of membership in medium sized litters (4 to 7 per litter) in which no members died from birth to 60 days of age. Males from one litter were placed in a large

cage (10 by 10 by 57 inches) with females from a nonclosely related litter. Sometimes males from at least two litters were placed with females from at least two other litters. Nesting material was placed in the cage, which the rats used to build nests. These groups were left intact throughout their life span. Litters were conceived, born, and reared in the presence of these several adults of both sexes. This pattern of breeding was maintained through generations 2 to 20. Brother-sister inbreeding was practiced through generations 21 to 25. We shall primarily be concerned with what hereditary selection was taking place during generations 2 to 20. It is quite apparent that the program of breeding minimized random gene drift. Selection, though this was not apparent to King and Donaldson, was directed toward greater tolerance to the disturbances accompanying confinement.

For initial generations the behavior upon approach of a worker was for the rats to become highly excited, dash about the cage, dig down and hide in the nesting material, and even to jump out at the observer when the cage door was opened. If the rat escaped, it ran violently about the cage upon capture and return, and sometimes died very shortly after return to the cage (see p. 259 for another type of traumatic death). Within the cage considerable fighting occurred. The largest males frequently bit and sometimes killed his smaller brothers and other younger males approaching adulthood. Some fighting also occurred among females. The suboridnates were frequently forced to cower together at one end of the cage. Because of the inability to escape, I believe that gray Norway rats housed under these conditions are under much greater stress from social interaction, than those living under the feral state. One would therefore anticipate much more variability due to environmental causes among those caged gray rats. The young during foetal, or neonatal life, as well as during adolescence, were subjected to the strife engendered among their elders. Death prior to weaning, according to King, resulted from (a) the disturbed mother eating the young or (b) other adults crowding in the nest and smothering the young when the approach of workers disturbed these adults.

Members of such litters, a part of whom died from this and other causes prior to 60 days of age, were never used for further breeding. Therefore, one would anticipate that selection toward greater tolerance to crowded group life and to the dis-

turbance associated with handling would ensue, as in fact it did. Females less frequently ate their young, and cages could be opened without rats running about, hiding, or jumping out. Social stratification continued through succeeding generations, but one would assume that social strife was reduced among cage mates, although King makes no precise statements in this connection. The only change in litter size was toward a slight increase in the frequency of litters under four or over seven [table 9, (63)]. Therefore, using only litters of size 4 to 7 for breeding did not reduce variability, nor was average size of the litter significantly altered. Therefore, it will be my contention that all changes observed by King and Donaldson were byproducts of selection for greater tolerance to disturbance.

The major changes were as follows:

1. Reduced sterility. Percent sterility for generations 2 to 9: 70, 37, 30, 19, 11, 9, 6, 19. In all later generations all females were fertile.

2. There was a gradual reduction in the frequency with which suckling young were killed by being eaten by the mother, or by being suffocated by other adult associates who lost their trait of crowding into the nest.

3. From generations 1 through 10 there was a progressive decrease in size of the thyroid but no change in gonads, hypophysis, or adrenals.

4. There was no change (at least for generations 1 to 10) of mean length of either sex at approximately 600 days of age.

5. For any given length the rat became fatter.

6. There was a progressive increase in average weight and a progressive decrease in variability in weight at any age.

7. The average length of the reproductive span of females increased from 190 days in the 2d generation to 440 days in the 25th.

8. There was a reduced mortality between 12 and 20 months of age.

King (63) concludes tentatively that these changes in weight were due to heredity rather than to environment. Although she never states this precisely, she implies at several points that there had been selections for genes which favor growth to a larger size, much as corn and many domestic animals have been selected for larger size by using the larger individuals of each generation for breeding stock. Since there was no evidence from the method of selecting breeding stock that larger animals were used, it is more logical to assume that selection was for temperament or emotionality, particularly toward a phlegmatic hypothyroid type. This assumption appears adequate for explaining the increase in average weight, the decrease in variability in weight, reduction in sterility, and prolongation of the span of reproduction.

The maximum weight achieved by any rat in a sample may be assumed to represent the optimum results of both heredity and environment. Six-hundred and fifty grams for males was attained by King's rats, mine housed in the 100-foot square pen, as well as feral rats in Baltimore (23). This suggests that all three groups possessed quite similar heredity in relation to size. Extremes of weight for any age are more revealing than are means. Such data for my rats and King's are shown as log-log plots in figures 148 and 149. Straight lines were fitted by eye to those sections of the data having close approximations to a straight line. Certain conclusions may be drawn from these figures.
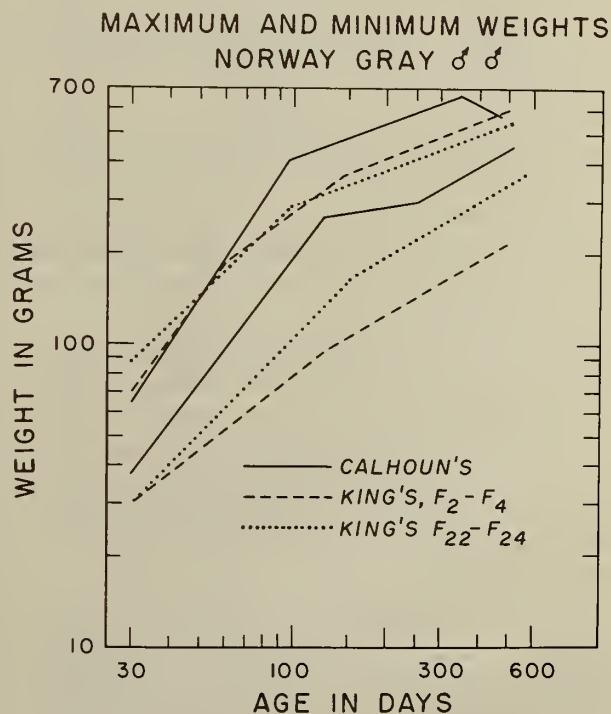

Figure 148.—Maximum and minimum weights of feral (Calhoun's) and captive (King's) male Norway rats. Here maximum and minimum refer to the actual extremes at each age.

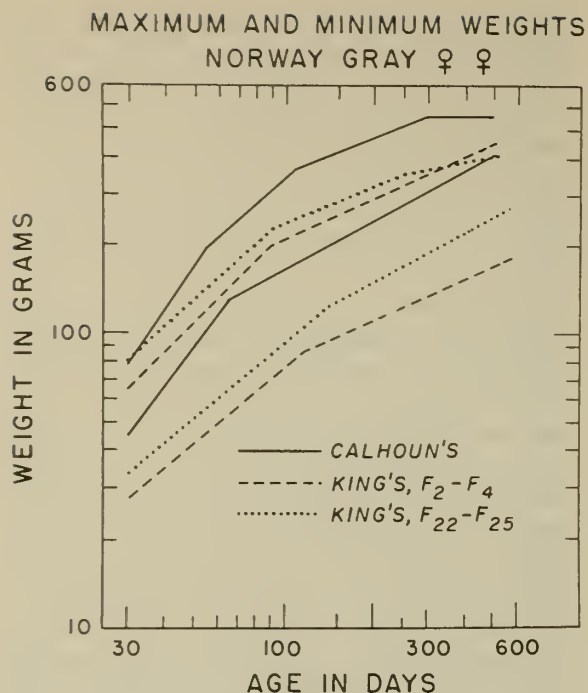## MAXIMUM AND MINIMUM WEIGHTS
NORWAY GRAY ♀ ♀

Figure 149.—Maximum and minimum weights of feral (Calhoun's) and captive (King's) female gray Norway rats.

1. My rats grew faster, although only the females attained greater maximum weights than King's.

2. My rats were less variable.

3. The maximum weights of King's rats of both sexes were heavier at 30 days of age for the later generations.

4. Only King's males of the later generations attained greater weight at 30 days of age than did my rats.

5. Minimum weights of all generations of King's rats were less than mine for all ages.

6. Where changes in rate of growth are evident near the age of sexual maturity, the point of inflection arises at a later date for the minimum weights than it does for the corresponding maximum weights. This applies to both my rats and to King's.

The slower growth rate, the greater variability in weight, and the lower maximum and minimum weights of King's rats are logical consequence of the crowded conditions of caging in which subordinate or younger rats could not avoid the undue stress exerted upon them by dominant and larger individuals. Under such conditions one would anticipate the following sequence of events: In-creased emotionality, increased firing of the hypo-thalamus, increased secretion of ACTH by the anterior pituitary, increased output of adrenal cortical hormones, and as a consequence decreased secretion of growth hormone by the anterior pituitary. Even the most favored rats felt the impact of this crowded social setting more than did my wild rats, who though dominant, less frequently found the necessity of engaging in interpersonal conflicts. The lowered minimum weights of King's rats at weaning shows that the opportunity for stressful experiences were greater than for wild young. More favorable growth for the later generations of King's rats may be attrib-utable solely to their more phlegmatic tempera-ment, which enabled them to respond less emotionally to stimuli within and without the cage.

b. *Other relevant data from King's studies. Birth weight:* Birth weights were significantly lower for rats conceived during July and August when temperatures in the animal rooms sometimes exceeded 90° F. King found adult weights to be positively correlated with birth weights. There-fore, higher summer temperature, as well as in-creased social interaction, may have contributed to the lower weights of rats born in my colony during the summer of 1948, as a result of both the hotter summer weather and the increase in number of rats over that of 1947.

Survival: It is a general rule that females live longer than males. This was true for my rats (figs. 153 and 154) as well as for feral rats on a farm (28), and for domestic rats (65). King's data is an outstanding exception to this rule. Of 1,353 males studied 27.1 percent had died by 20 months of age and 28.8 percent of the 1,384 females. The sexual difference in the number dead or alive at the end of 20 months is not significant ($X^2 = 1.137$). However, it may be recalled that King used a highly select group of rats of which no member of the litter died before 60 days of age. This suggests that some portion of the span of life from conception to 60 days of age (the age of loss of juvenile pelage) is critical to the determination of survival time for males, and that all later experiences produce an equivalent effect upon the survival time for the two sexes.

E. *Maturation, Maintenance, and Decline of Repro-ductive Performance in Female Rats.* Biologists dealing with animals in their native habitat have been concerned primarily with reproduction as the

counter balance to mortality in preserving a population. Davis (28) has treated thoroughly this concern with reproduction as it pertains to Norway and roof rats.

My studies of the Towson population of Norway rats made me realize that phenomena relating to reproduction can be given an entirely different focus. This focus concerns the conditions surrounding the maturation of the individual as these conditions modify physiology and behavior, which in turn alter reproductive performance. In other words, reproductive performance becomes a criterion for judging the approach to the optimum by environmental and social conditions.

High reproductive performance should indicate favorable conditions in so long as the species does not exercise conscious control of the frequency of conception. If we know the environmental, social, and cultural conditions which foster high reproductive states in lower mammals such as the rat, we can examine them for general principles applicable to producing less stressful conditions of living by man, irrespective of the associated human reproductive performance. In other words, the general kinds of conditions which assure a high reproductive rate for rats should be indicative of the type of environment providing the minimum of stress for humans.

The Towson data (pp. 152 to 160; 203 to 216) provide an insight into some of the conditions associated with reproductive success. Such success involves appropriate interaction with males, culminating in insemination; fertilization of ova, nonresorbtion of embryos; and appropriate maternal behavior terminating in weaning of the young. However, the Towson data (pp. 158 to 160) are too few to provide complete insight into the maturation of reproductive performance.

Several sources of such quantitative data are available in the literature. These will be examined for the light they throw on maturation of reproductive performances and its modification by environmental conditions.

In the study of wild populations, it is customary to trap large samples throughout the year. In lieu of exact knowledge of age, characteristics of the sample are usually listed according to length or weight classes. However, insight into the maturation of reproductive processes demands a knowledge of approximate age. It is obvious from figures 130 to 133 that equal intervals of length or weight do not correspond to equal intervals of age.

Therefore, in order to assign approximate ages to the midpoints of class intervals of length in millimeters for data in the literature, the 426 measurements of Towson females falling between 170 and and 270 mm. were reexamined. For each 10 mm. interval of length I calculated the mean and standard deviation of the age in days. Approximate ages and their standard deviations as read from a smoothed curve drawn through these points are shown in columns 2 and 3 of table 68.

One-hundred and four measurements of nose-to-anus length were available for the Towson colony rats for which there was another measurement within seven days or less. Differences between these two measures represent variability in the measurement rather than changes due to growth. The midpoint difference, or error, was 4 mm. Thus 0.4 of the readings in any 10 mm. class interval should actually have been in the next smaller or larger class interval. For this reason the actual range in age for each class interval of lengths must be more nearly approximated by $\pm^\sigma$ rather than $\pm 2^\sigma$

Two kinds of data on reproductive performance are available from samples of populations of wild rats: (a) the proportion which are parous, that is they are able to bear litters (i.e. as judged by the fact that they are visibly pregnant or have placental scars from prior litters), and (b) the proportion which are visibly pregnant with the naked eye upon external examination of the exposed uterus.

Davis and Emlen (66) present data on parity of out-of-doors, urban rats in Baltimore. Estimates of the proportion parous are given in column 4 of table 68. These estimates are based upon a smoothed curve drawn through their data on 430 females. Some females first conceive while quite young, whereas for others this event is delayed for many months. At 165 days of age 0.5 of the rats have still not conceived, despite the fact that all have probably been ovulating for a long time. Davis (28) shows that 0.5 of the rats are ovulating at a length comparable to 40 days of age. Therefore, for the average female conception is delayed for 125 days beyond first ovulation or 80 days beyond the youngest rats to conceive. Conception seemed to be inversely proportional to stressful social conditions in the Towson population. Therefore, I suspect that variability in the social experience and effectiveness of other behavioral adjustments to environmental conditions operated in the urban populations of Baltimore rats to pro-

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TABLE 68.—*Maturation of the reproductive performance of female rats*

Body length in mm. (midpoint of 10 mm. interval)	Age in days at midpoint of length class interval	Standard deviation in days	Proportion macroscopically parous	Proportion macroscopically pregnant	Span, S, in days between conceptions	Incidence, I_1, of pregnancies by parous rats (No. per year)	Incidence, I_2, of successfully weaned litters (No. per year)	Success, P_1, at rearing litters	Proportion, P_2, of females exhibiting mature complex of reproductive behavior
			r	p	$S = t_{27}/p$	$I_1 = T/S$	$\dfrac{T - t_1 I_1}{t_9}$	I_2/I_1	$P_1\, r$
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
175	64	10	0.000	0.000	....	....	....	0.000	0.000
185	74	17	.015	.011	23.0	15.87	0.00	.079	.004
195	88	23	.051	.035	25.2	14.50	1.14	.206	.031
205	111	32	.151	.089	28.8	12.68	2.61	.368	.129
215	144	42	.351	.179	33.3	10.98	4.04	.564	.332
225	186	53	.588	.257	38.8	9.40	5.30	.740	.542
235	238	62	.732	.285	43.7	8.36	6.19	.892	.755
245	298	68	.845	.308	46.6	7.61	6.79	.985	.916
255	366	73	.930	.322	49.2	7.22	7.11	1.000	1.000
265	438	77	1.000	.333	51.0	7.17	7.17		

duce delay in conceptions. Genetic variability of physiology, which is independent of the environment and which produces delays in capability of conceiving, cannot be ruled out. However, the possibility of genetic variability alone causing a year's difference in ability to conceive appears remote.

The second reproductive statistic is the proportion of females pregnant. I chose data on 2,202 Georgia rats (*67*) for this purpose. These rats were smaller than the Baltimore rats. The median length was 11 mm less, and a pregnancy rate of rate of 0.01 was reached at a 10 mm. smaller size. Therefore, I have assumed that the ages of these rats are equivalent to that of the next higher length class interval of the Baltimore rats. The pregnancy rates listed in column 5 of table 68 were taken from a smoothed curve drawn through these age adjusted values.

Based upon the Towson study duration of pregnancy is 23 days and the minimum time between parturition and a following conception, when the first litter is successfully reared, is 28 days. Therefore, 51 days represents the minimim span between conceptions of successfully reared litters. I shall assume that no conceptions occur on the first post partum day if the litter survives, although in fact the first-day post partum conceptions do occur rather rarely. Pregnant individuals can be recognized by external examination of the exposed uterus after the first 6 days following insemination (*22*), that is during the last 17 days of pregnancy.

Thus, we have several reproductive characteristics whose typical values may be considered as "knowns". They are:

$r=$ Proportion of females parous by macroscopic examination. Column 4, table 68. These are the females which are either visibly pregnant or have placental scars on the uterus from prior pregnancies. It must be pointed out that the observed r is an underestimate because primiparous females cannot be recognized as pregnant during the first 6 of their 23 days of pregnancy. This amounts to an underestimate of 26 percent in the 74-day-old age class. This error rapidly diminishes in older rats for whom parity can be judged in the majority of cases by placental scars alone. For the present purpose of gaining insight into the maturation of repro-

ductive performance this error has been ignored.

$p=$ Proportion of females in entire sample, including parous and nonparous rats, that are pregnant by macroscopic examination.

$t_1=$ Duration of pregnancy, 23 days.

$t_2=$ The number of days, 17, of the 23 days of pregnancy during which pregnancy can be determined by macroscopic examination of the uterus.

$t_3=$ Normal minimal number of days, 28, of lactation for successful rearing of litters before another conception can occur.

$t_4=$ Normal minimal span, 51 days, between successfully reared litters. Here the apparently rare event among wild rats of conception on the day of parturition is ignored.

Let:

$T=$ Duration of time, 365 days, for which the incidence of reproductive events will be calculated.

$S=$ Average span in days between conceptions of parous females.

$I_1=$ Incidence of pregnancies among parous rats only. This refers to the number of pregnancies per 365 days for particular age classes. It is an instantaneous rate.

$I_2=$ Incidence among parous rats only of pregnancies where the litters are weaned successfully.

$P_1=$ Proportion of conceptions by the r parous females where the litters are weaned successfully. In other words this P_1 defines success at rearing litters.

$P_2=$ Proportion of females in the entire population who are characterized by the mature complex of behavior and physiology which enables them not only to conceive, but also to give birth and rear their young to the age of weaning.

Then:

$t_2/S=$ The proportion of time parous rats are detectably pregnant by macroscopic examination of the uterus.

Since: A sample of N rats at a particular mean age is equivalent to N days at that age.

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It follows that:

> p is also equivalent to the proportion of "rat-days" at a particular age on which rats are pregnant by macroscopic observation.

But:

> Except for the oldest age class considered (438 mean days of age, $\pm 1\sigma$ of 77 days), only a portion of the rats are parous.

It follows that:

$$p = t_2 r / S$$

Therefore:

$S = t_2 r / p$, column 6, table 68

and

$I_1 = T / S$, column 7, table 68.

Davis (28) calculates I_1 from the equation: $I_1 = pT/17$ [Emlen and Davis, (22)]. This equation assumes $r = 1.0$, which is not true except for samples of older rats, and therefore most of the estimates of incidence of pregnancy listed in his table 3A [Davis, (28) p. 381] are too small when we consider only rats which have attained reproductive parity. Davis' calculations are perfectly valid as a general incidence among all females of a particular age class. For example, using the r and p values in table 68, the $I_1 r$ by Davis' equation for 74 and 144 days are respectively 0.24 and 3.85. The shortcoming of such a pregnancy incidence is that it enables us to gain no further insight into the rat's reproductive biology. Now let us proceed with the present line of reasoning to see what insights follow from it.

Since:

$t_1 I_1 =$ Number of days during the year rats are pregnant

Then:

$T - t_1 I_1 =$ Number of days available for nursing

and since:

$t_3 =$ Normal minimal number of days for nursing a litter

Then:

$$I_2 = \frac{T - t_1 I_1}{t_3}, \text{ column 8, table 68}$$

It follows that:

$P_1 = I_2 / I_1$ column 9, table 68

Since:

> r reflects the physiological and behavioral capacity to mate and conceive, and
> P_1 reflects the adequacy of maternal behavior in providing protection and nutrition to the preweaning young.

Therefore:

$P_2 = P_1 r$, column 10, table 68; figure 150.

The youngest age groups (74 days) of rats which become pregnant conceive at a rate which during a year's time would produce 15.87 litters per rat for those able to conceive. This means they conceive every 23 days, or immediately after each delivery. This leaves no time over for nursing. Thus, for all practical purposes primiparous wild rats never rear their first litter.

Most rats are ovulating before 74 days of age. Failure to conceive at this early age most probably depends upon: 1. Disturbed reproductive physiology related to stress associated with learning the complexities of this environment. 2. Failure to have learned all the appropriate responses required to conclude mating with a male. This latter includes not only the learning of courtship and copulatory behavior, but also the expansion of home range at estrous which insured encountering males.

r as a function of age increases in a sigmoid fashion much as does a learning curve. However, r defines not how much an individual has learned but rather how many individuals have learned the required task. It is difficult to believe that hereditary differences alone can produce a year's difference in the ability to learn the task. Much more likely is it that complexities of the rats' physical environment, and complexities of the hierarchical and class structure of rat society make it more difficult for some rats to learn adequate relations with males. All females are able to compensate for these difficulties and acquire behaviors essential to mating and conceiving provided enough time transpires. At least the conclusion applies to the Davis and Emlen (66) data on parity shown in column 4 of table 68.

Achieving the ability to conceive is only a preliminary phase of the struggle for survival of the species. For even if the young are born they need to be properly taken care of or they will perish. *Prior* to parturition a well-built nest needs to be built in a place uninhabited by other rats. This means that the prospective mother must either seek a place unfrequented by her associates and
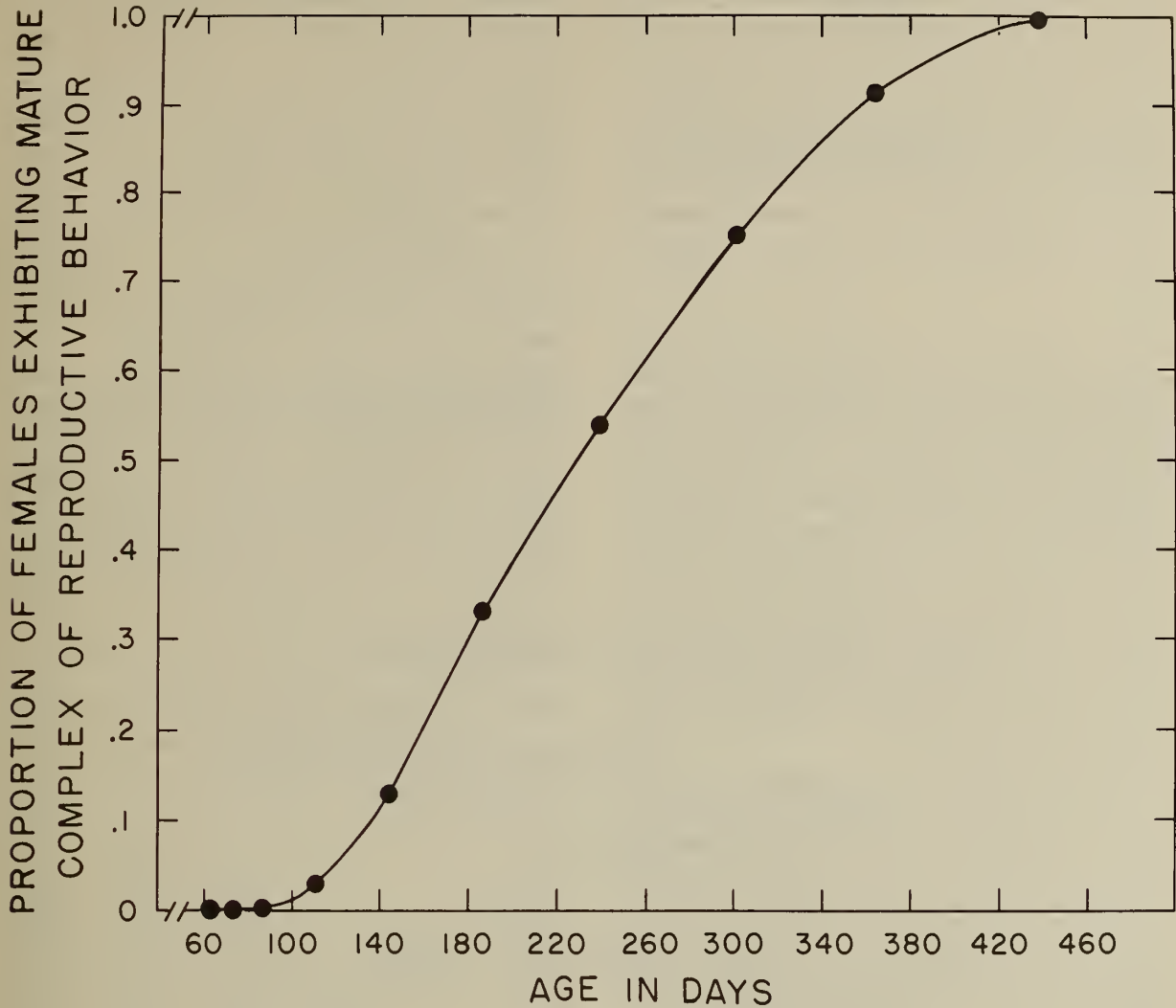
Figure 150.—Maturation of reproductive behavior. This index, P_2, as defined in the text, is the product of the proportion of parous females times the proportion of these which successfully rear litters. It assumes that the failure to reach 1.0 at earlier ages relates to environmental disruptions of learning or innate behaviors in the realms of relationships between the sexes, or of maternal behavior.

there dig a new burrow, or if she chooses to remain at an established burrow she must be able to express sufficient territoral behavior to exclude her associates from the cavity where she will have her young. Then during the critical first 4 days after parturition she must not only nurse her young but refrain from eating them. During their first 2 weeks of age the young have a better chance of survival if the mother inhibits entrance by other adults, and if she plugs neighboring entrances providing access to her section of the burrow. From birth through at least the third week of life

the mother must express adequate retrieving behavior. This enables her to change residence when danger threatens her young. And if they should wander outside the nest, as they certainly can from 12 to 21 days of age, before they are able to acquire their own food other than from nursing, the mother's failure to retrieve would certainly lead to the death of the young. Lastly, the mother must provide a cache of food adjacent to the nest so that weaning to solid food may proceed during the fourth week of life without the young having to go exploring prematurely.

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Examples of failure of each of these eight behaviors were noted in my Towson colony. Similar failures must characterize other populations of wild rats as evinced by the gradual increase of success at rearing litters revealed in column 9, table 68. How much of this failure results from inadequate learning of the appropriate behaviors, and how much is a consequence of stressful conditions which so disturb physiology as to prevent expressing "innate" behaviors cannot be stated. Suffice it to say, the maturation of maternal behaviors is slow.

Thus, environmental conditions retard the expression of both mating and maternal behaviors. The gradual attainment of full expression of both of these essential categories of behavior is even slower than either separately, column 10, table 68. Not until the fully mature age of 438 days are all rats parous and the frequency of conception has been reduced to the point where all litters conceived have the opportunity of being reared successfully. Remarkably enough, at this age, the span between litters comes out to be 51 days, which is exactly the sum of the 23 days of pregnancy and 28 minimal days of lactation determined independently from my Towson population.

Whenever p exceeds .333, regardless of the value of r, one is justified in concluding incomplete expression of maternal behavior. A p greater than .333 means that litters are lost before weaning and conception occurs less than 28 days after parturition. Similarly if p is less than .333 and r is less than 1.0 one is justified in concluding incomplete expression of both mating and maternal behavior. In either of the above cases S will be less than 51 days and I_1 greater than 7.17 per year due to recurrent conceptions closely following loss of litters.

Further insight into this general question may be derived from data on captive wild gray Norway rats presented by King (63). Nine-hundred and seventy-four of the 1,323 females alive at 3 months of age survived to 20 months of age. King lists the number of litters born to those rats surviving during each month of age.

Let L = proportion of females having litters each 30 days. Then $\hat{p}$, the proportion of females visibly pregnant, can be estimated to be: = 17L/30 or .567L

See figure 151 and table 69. Note the decline in pregnant females beginning at 9 months of age. This is in marked contrast with the pregnancy rate of rats in their native habitat, which continues to increase to 450 days of age at least (fig. 151). Inferences drawn from this difference should provide further insight into the biology of rats.

As the rate of pregnancy (p) declines, the span (S) between conceptions must increase. King probably had exact, but unpublished, data on S, and also on r, the proporiton of parous females. However, we can make a crude estimate of both r and S which shall be designated as $\hat{r}$ and $\hat{S}$. Because of reduced fertility in generations 2 to 9 only approximately 0.92 of the 1,323 females in the total sample reached parity by 20 months of age. This fixes the upper limit of $\hat{r}$ at 0.92 at 600 days. Under 240 days of age the King rats had a higher p and therefore probably had a higher $\hat{r}$ than the Davis-Emlen rats. I therefore assumed $\hat{r} = \dfrac{r_4 \times \hat{p}}{p_5}$, when r_4 and p_5 refer to the r and p values in columns 4 and 5 of table 68. These $\hat{r}$'s when plotted against age and connected to the $\hat{r}$ of 0.92 at 600 days enabled an estimate of the intervening $\hat{r}$'s. $\hat{S}$ was then calculated (table 69; fig. 152). The age of maxi-

TABLE 69.—*Estimated reproductive statistics applicable to King's (1939) captive gray Norway rats*

Age in days	$\hat{p}$	$\hat{r}$	$\hat{S}$
74	0.034	0.051	25.6
88	.096	.151	26.8
111	.158	.268	28.6
144	.210	.411	33.3
186	.249	.572	39.1
238	.269	.690	43.6
298	.254	.720	48.1
366	.245	.767	53.2
450	.225	.830	62.7
580	.140	.905	140.0

mum reproductive performance was reached at least four months earlier by the King rats than by the Davis-Emlen rats. Beyond the age of maximum reproductive performance $\hat{S}$ continued to lengthen. Thus, whether or not all litters were reared, it is quite apparent that some change in the psychology or physiology prolonged the time of conception beyond the 28th day of lactation. This period of declining reproductive performance must represent the climacteric. The life cycle of reproduction from the viewpoint of the average female in the population consists of three specific ages and two intervening periods of change:

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Developmental age or period	Age in days	Remarks
1. First ovulation................	Circa 40.............	After Davis (*28*).
2. Maturation of reproductive behavior.	60 to 328.............	a. Average interval between conceptions increases from 23 to 51 days. b. Increasing frequency of successfully reared litters.
3. Maximum reproductive performance.	328..................	Most litters reared successfully.
4. Climacteric....................	328 to circa 580.......	Average interval between conceptions greater than 51 days.
5. Menopause....................	Circa 580............	

Ages listed in the last four categories are for King's data as shown in figure 152. The developmental age designated as maximum reproductive performance, when $S=51$ days, represents the most important age for judging the relative inhibitory effect exerted by environmental conditions.

This follows if the inception of the climacteric indicates a suboptimum physiological state. To the extent that the logic of my argument to this point is correct, the earlier origin of the climacteric in King's rats strongly suggests that the cage habitat at the Wistar Institute represented a less
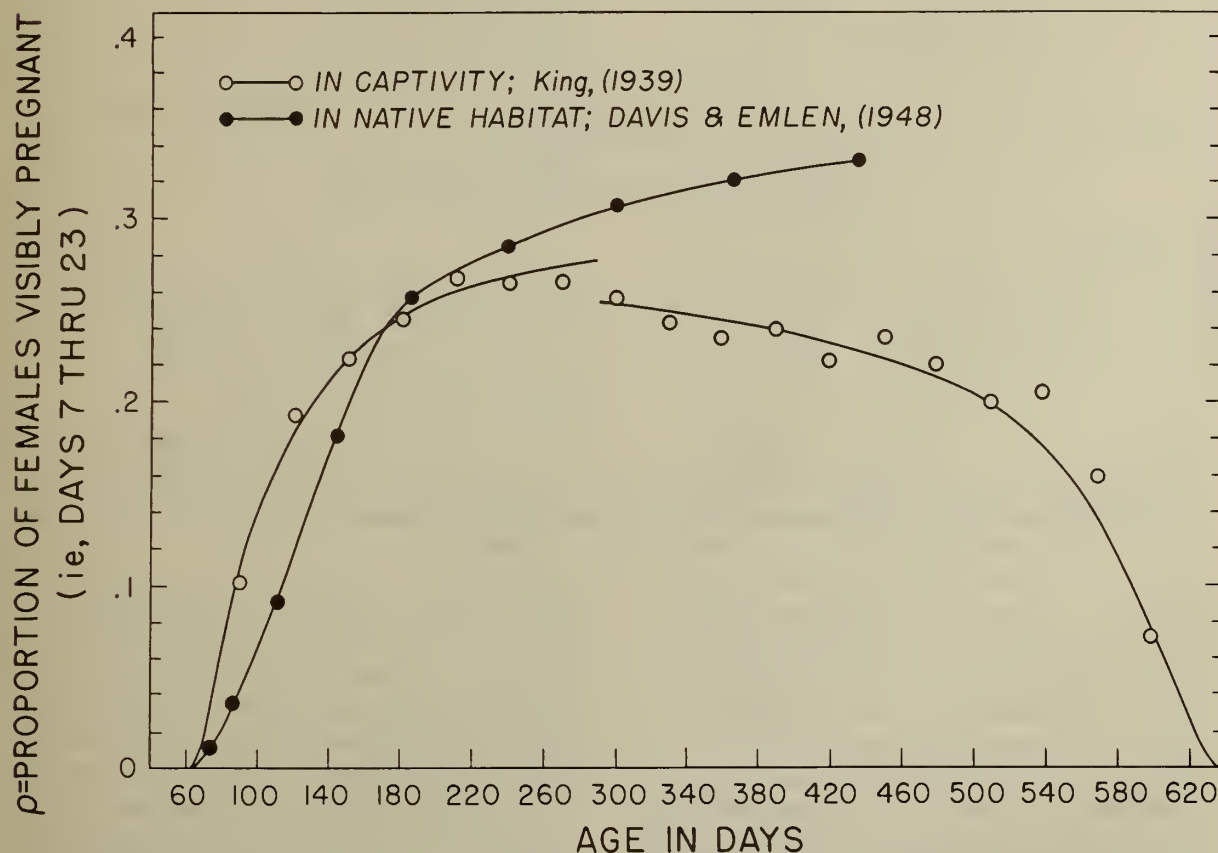
PREGNANCY IN NORWAY GRAY RATS

Figure 151.—Pregnancy in gray Norway rats. An inference from these data is that the stressful conditions of captivity cause an earlier origin of the climacteric and menopause.

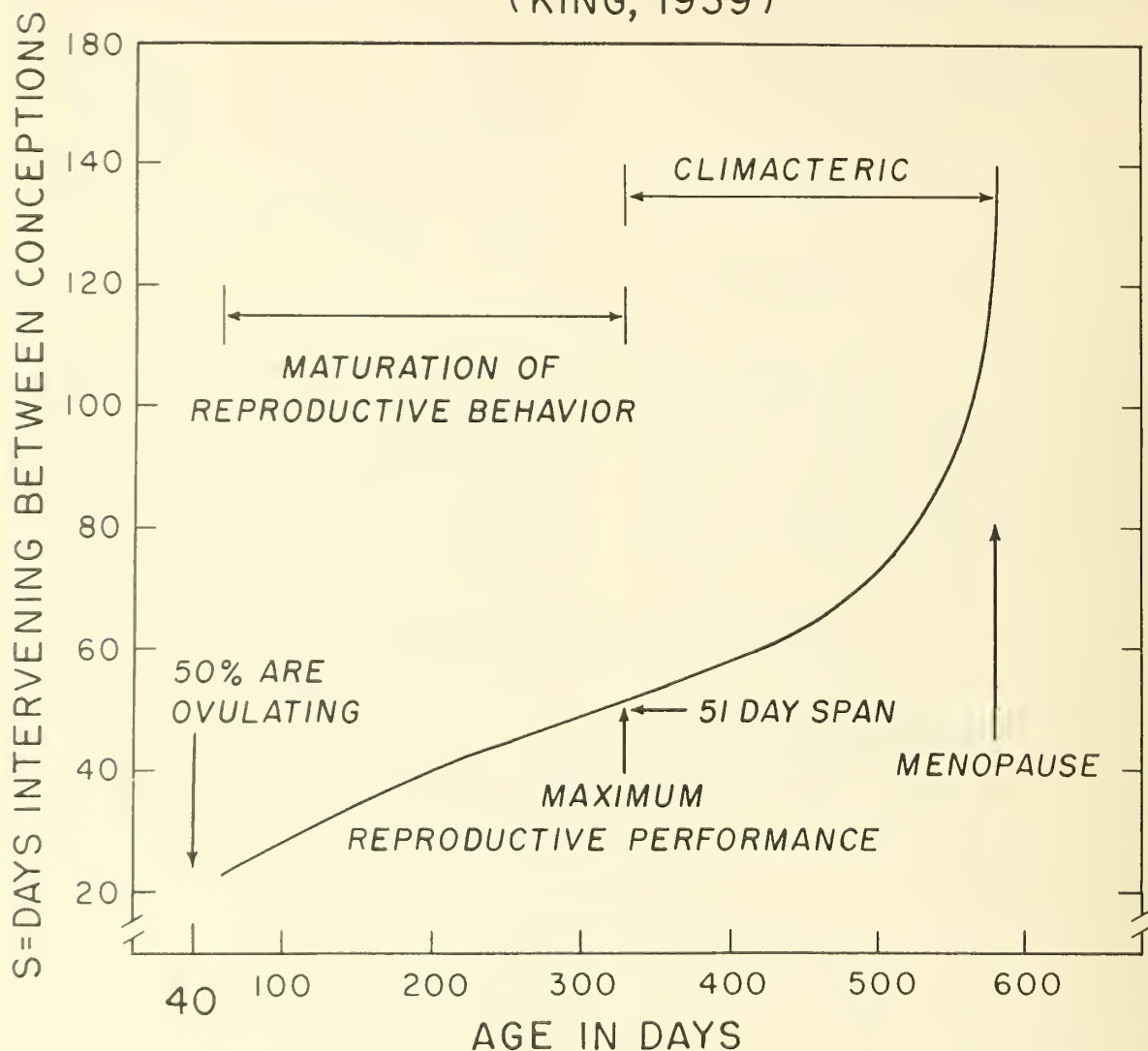# LIFE CYCLE OF REPRODUCTION IN CAPTIVE GRAYS
(KING, 1939)

Figure 152.—Life cycle of reproduction. Maturation and decline of reproductive performance result in an ever increasing average span between conceptions in so long as the proportion of visibly pregnant females increases to not more than 0.333 and then declines. S=51 days at maximum performance. When the proportion of rats visibly pregnant exceeds 0.333, an intervening decline in the span between conceptions will result.

optimum environment than that experienced by urban out-door rats in Baltimore. This conclusion corroborates a similar one (pp. 262 to 264) derived from the slower growth of these caged rats than those in the Towson study.

Size of litters of King's captive grays followed a similar pattern of change with age as did pregnancy rates (fig. 151). Litter size increased from 3 to 8 months, with the maximum at 8 months; a gradual decline characterized the 8- to 17-month age range, which was followed by a rapid decline in size of litters between 17 and 20 months of age.

There exists one additional change in the pattern of the life cycle of reproduction as revealed by data presented by Davis and Hall (68) for rats living in warehouses in Baltimore. Judging by the fact that the median size of the 409 females was 20 mm. less than those living out of doors (66). I suspect that their 155 mm. rats were actually about 64 days old; the 165 mm. rats were 74 days old, etc.

Such adjustments were made in assigning an age to the rats in each of their 10 mm. class intervals The proportion of females visibly pregnant rose from zero at 64 days of age to about 0.434 at 245 days of age then dropped to about 0.33 at 438 days of age. If we assume that $\hat{r}$ bears the same proportion to $\hat{p}$ in this Davis-Hall data as is shown for r and p in columns 4 and 5 of table 68, then S attained the optimum value of 51 days between conceptions at approximately 150 and 450 days of age. Intervening between these two ages there is an increase in $\hat{p}$ beyond 0.33 and a corresponding decrease of $\hat{S}$ below 51. Since a second maximum reproductive performance occurred at about 450 days of age, the inception of the climacteric must have begun here, or possibly somewhat earlier. Between 150 and 450 days of age one must conclude that these females were physiologically and behaviorally quite capable of achieving conception, but that some stressful conditions in the environment upset the normal course of maternal behaviors so that litters were lost shortly after parturition.

During the climacteric when $r = 1.0$, or at least is no longer increasing and p is below 0.33 and decreasing, it is only possible to derive maximum estimates of S if some of the litters are not reared to weaning. Where loss of litters, arising from incomplete expression of maternal behavior, occurs throughout the lifespan, one cannot calculate accurately the age of maximum reproductive performance or the inception of the climacteric when these are derived soley from estimates of r and p. Since S beyond this age will always be greater than 51 days, P_1 the success of rearing litters, will have an unreal value of greater than 1.0 and one cannot gain any insight, based only upon r and p, as to whether the females are partially or entirely successful at rearing litters.

In the above discussion I have taken considerable liberty with published data in estimating age from measurements and in arriving at estimates of pregnancy and parity rates from smoothed curves through observed data. Such approximations have enabled development of formulations of reproductive performance, as well as possible conditions influencing it. Though far from exact, I believe that these formulations approximate reality.

If we are to approximate the reality of reproductive performance more closely, S and I_2 as well as r and p must be determined directly for the population studied. This can only be done where the individuals composing the population are followed

even in more detail than I did for my Towson colony. Patently this is impossible in extensive studies of populations in their native habitat. However, the minimum effort demands simultaneous determinations of p and r. Age can be approximated by assigning 74 days of age to the midpoint of the 10 mm. body length class interval when p first exceeds 0.01; and than assigning the ages shown in column 2 of table 68 to the other class intervals.

The above discussions in conjuction with results from my Towson colony lead to the following generalizations.

1. Norway rats attain anatomical sexual maturity by 85 days of age.
2. The first conception may be delayed as much as 8 months. Why this is so is not entirely clear. The only rats in my Towson colony which did not conceive by nearly a year of age (tables 51 and 53) were members of socially low-ranking colonies. This suggests that amount of delay in conception is positively correlated with amount of social disturbance or stress experienced by the rats.
3. Once the ability to conceive has been attained, recurrent conceptions take place at a high rate. A threshold phenomenon is indicated. The extent to which hormones and maturation of behavior contribute to the threshold is not known.
4. The effectiveness of maternal behaviors as judged by successful rearing of litters gradually increases. This increase is of the order of tenfold between 3 and 12 months of age.
5. Even during the mature adult span of 8 to 12 months of age disturbing experiences may greatly decrease the effectiveness of maternal behavior.
6. Somewhere between 8 and 14 months of age an increasing delay arises between termination of lactation and conceiving again. This is the climacteric which terminates at menopause somewhere around 2 years of age.
7. The rate of maturation of reproductive performance as well as the duration of maintenance of successful reproduction in rats may be taken as indices of the extent to which the environment provides stressful conditions.

F. *Manipulation of the Bond between Mother and Young.* A general outline of maturational changes in relationships of young rats to their mother and adults in the naturalistic setting has been given on

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pages 143 to 152 and on figure 103. Seitz (*59*) summarizes the present state of our concepts of the importance of experiences during infancy, particularly with the mother, on adult behavior. Wiesner and Sheard (*69*) have presented extensive experimental studies of the mother-young bond as reflected in the behavior of retrieving by the mother. Wistar albino rats served as subjects. Their results will be reviewed for their bearing on the question of early experience.

Retrieving of her own young by the mother declines to about day 19–20 following parturition, beyond which time she no longer retrieves. This is the age by which the eyes of all young have opened, and at which I observed the young to engage in independent movements outside the nest but within the burrow. Beginning with day 20 and extending to day 40 three marked transitions in behavior of the young take place. These are (1) initial explorations outside of but near the home burrow; (2) first extensive wanderings coupled with incomplete expression of food transport; and (3) termination of nursing. We may now pose a question: How can the mother-to-young relationship be manipulated in the light of some of Wiesner's and Sheard's findings?

They found that the maxium age of young retrieved declines exponentially from about 30 days old on the day of parturition to 1 day of age on day 40 of lactation. At least this trend held when small young were given first during a set of retrieving trials followed by successively larger ones. By removing a mother's own young or her foster young at 19 to 25 days of age and replacing them with foster new born ones lactation and retrieving can be continued for as much as a year. Furthermore, such "trained" mothers continue retrieving after lactation ceases. These results indicate the feasibility of intensifying and prolonging the retrieving behavior to the point where the mother prevents or interferes with any independent behavior of her young entailing moving away from the nest cavity. In terms of a rat's way of life, such procedures enable studying the phenomena of maternal overprotection and mother-child conflict.

For example: A female could be trained as a continuously lactating efficient retriever. When she had arrived at this stage 2 members of one of her consecutively "adopted" litters could be allowed to mature rather than removing them after 5 or 7 days of age as is done with members of the other adopted litters. During their maturation the mother could be kept in continuous lactation by the regular replacement of the other young she is nursing by several newborn ones. Now if the situation were designed to provide the possibility for independent movement by these two older young to a goal away from the nest compartment— one would anticipate that the mother would interfere with the attempts by her older adopted young to leave the nest and reach the goal. In contrast to young of normal mothers, there would be a delay in the expression of independent activity by these young. Furthermore, the young of such overattentive mothers should be weaned much later. Age of weaning could be delayed further by feeding the mother outside the nest cage and experimental situation, while at the same time preventing access to adequate solid food by the young. Perhaps weaning could be prolonged to the age of first expression of sexual behavior. Such rats should develop an ambivalent attitude toward their foster mother. They should be highly attracted toward her because of their long attraction toward her as a source of nourishment. On the other hand, they should have an aversion for her as a result of her interference with their attempts at independent behavior. When such rats in turn became adults one would anticipate significant deviations in behaviors involving interaction with other rats.

Continuation of closer maternal bonds between 23 to 40 days of age (the usual weaning period) must satisfy some need felt by the young but no longer supplied by their mother. This tentative deduction follows from the observations (pp. 147 and 151) of my free-ranging rats. Rats of this age range, and even older sexually immature young (i.e., under 80 days of age), are found in the nest cavity with females, other than their mother, who are still lactating.

G. *Aggressiveness during lactation.* Chitty and Southern (*31*) cite a record of a wild gray female who gave birth to a litter in a large cage containing 17 other adults. On the day of parturition the female and young occupied the usually occupied end of the cage while the remaining adults resided at the opposite, and usually unoccupied, end of the cage. This is the only record, other than my own observations, that I have been able to find indicating an increased aggressive state by a lactating female rat. Beach (*37*) states that aggressiveness is a general characteristic of vertebrate mothers with newborn young, although he makes

no specific mention of rats. There has no doubt been a loss of this behavior in the domestication of the Norway rat just as we have noted general aggressiveness to decline in the Wistar Institute breeding of wild Norway rats. Wiesner and Sheard (69) make no mention of aggressive actions by the females in their extensive study of retrieving of young. They used Wistar albino rats. I have also noted that parturient females of this strain fail to show any aggressive action. However, Fischer strain rats do exhibit considerable aggressiveness toward an observer who places his hand in with recently born young. Even so, I believe that we are justified in concluding a general reduction in aggressiveness, including that associated with lactation, as a result of domestication.

6. *Inhibition of Growth by Stressful Conditions*

Results from the study of the rats in the Towson colony showed that in a general way rate of growth and level of adult weight were inversely porportional to the degree of social disturbance and instability of interindividual relationships. This conclusion must stand as an unsubstantiated inference because I have no quantitative proof that caloric intake was not reduced among rats of low social status. However, qualitative observations indicated that all rats obtained sufficient food for optimum growth. If they did, there still remains the question: could the differential experiences of rats in a free-ranging social milieu be logically expected to produce physiological changes culminating in differential patterns of growth.

The theoretical basis for growth inhibition from the indirect effect of external events is that of Selye's (17, 18) "general-adaptation syndrome." Through undefined physiological routes, presumably of several kinds, signals reach the pituitary causing release of ACTH and other conditioning hormones. These stimulate the adrenal cortex to produce an array of corticoid hormones. It is not my intent to restate the manifold known or conjectured physiological effects of these corticoids. Suffice it to say that beyond certain specific effects, they produce a regular sequence of changes, regardless of a wide range of different kinds of deleterious external conditions, which act as stressors on the organism. In the continued presence of a stressor condition there is an initial "alarm reaction" in which among other changes there is a decrement in lipids in the adrenal cortex. There follows a "stage of resistance" in which adaptations to the threat posed by the stressor is at an optimum and lipids accumulate in the adrenal cortex. If the stressor continues to act, and at a level imposing greater demands on the organism than that to which it is able to adjust, there follows a terminal "stage of exhaustion," during which there is again a decrease of lipids in the adrenal cortex. Both the initial and terminal stages are catabolic and generally characterized by hypoglycemia, gastrointestinal erosion, hemoconcentration, and lowering of body temperature, metabolic rate, tissue proteins as well as calcium and phosphates, and of resistance to disease, and an increase in the urine of sulfates, phosphates, calcium, potassium, nonprotein nitrogen, and creatine. Just the reverse characterizes the anabolic stage of resistance. Retardation of growth might be anticipated whenever the individual is in a chronic sub-lethal stage of exhaustion characterized by a catabolic imbalance which counteracts the effects of simultaneous release of the growth promoting hormone (STH) from the pituitary.

Willier [p. 602, (70)] succinctly summarizes this antagonistic relationship: ". . . both the growth and the adrenal cortical hormones alter metabolic processes but in the opposite directions. The growth hormone seems to have the property of promoting protein synthesis and retention, and as a consequence promotes bodily growth. The adrenal cortical hormones, on the other hand, owing to their capacity to accelerate the catabolic phases of protein metabolism, have a retarding effect upon rats." Willier is apparently referring only to the glucocorticoids (A-Cs) produced by the adrenal cortex. According to Selye (18) ACTH, under normal conditions, stimulates the adrenal much more effectively to secrete glucocoricoids than mineralocorticoids (P-Cs). The latter actually enhances the effect of the growth hormone, for as Gaunt et al (71) have shown, injections of desoxycorticosterone (DCA) actually promote more rapid growth. However, continued administration of ACTH or cortisone (71, 72) result in retarded growth.

Reference has already been made (pp. 260 to 261) to the work of Rosvold and his associates who showed that chronic electroconvulsive shocks to rats in a situation permissive of conditioning of this experience produced alterations of adrenal function consistent with those culminating in those physio-

logical changes which inhibit growth. Mother rats so treated exhibited retarded growth, as also did their young. Similarly, Holzbauer et al. (73) subjected rabbits to daily electroconvulsive shocks beginning at 11 and 18 days of age. Experimentals exhibited a marked retardation of increase in weight. Furthermore, after a time weight actually declined and terminated in death. Vogt (74) demonstrated that a strange, and presumably emotional experience, elicits adrenal cortical activity. She conditioned one group of rats to the procedure of having their rectal temperature taken. On the sixth day these, and a group of experimentals who experienced this procedure for the first time, were killed 1 hour following the taking of their rectal temperature. There was a more marked adrenal activity on the part of the experimentals as revealed by a 60 percent drop in the ascorbic acid content of the adrenals in the experimentals. The assumption here is that those rats chronically subjected to a mildly disturbing situation learned that the experience was not harmful and, therefore, found no need to go into the alarm stage of adrenal activity. Weininger (75) provides additional insight into this question. He gentled one group of Wistar albino rats by daily periods of handling and petting between 23 and 44 days of age. By 44 days of age the gentled rats had gained (161 vs. 141 g.) significantly more in weight than their nonhandled controls. This weight differential was maintained to time of autopsy at 79 days of age (319 vs. 265 g.).

To my knowledge no formulation has been forwarded as to the psychological basis for such weight differentials. Briefly stated, my hypothesis is as follows: For the nonhandled rat many of the events taking place in the laboratory external to its cage were of unknown meaning and were reacted to in an emotional way. However, the handled rat generalized its learning that a particular event was harmless to all other events of unknown meaning, and so existed at a low level of emotional reactivity.

At 79 days of age Weininger subjected these two groups of rats to 48 hours of a situation very strange to them. They were bound in an immobile state for 48 hours on their backs without food. At autopsy at the end of this time the nonhandled rats exhibited more bleeding points in the gut, more damage to the heart, and enlarged adrenals. These citations are adequate to indicate that events external to the organism and of a nonbiological character can generate release of adrenal corticoids with concommitant retardation of growth.

Social interactions can also produce alterations in the adrenal of a nature which the other studies cited above indicate may produce retardation of growth. Crowding in small cages has been the stressor producing such changes in house mice (76, 77, 78) voles (79) and Norway rats (51). Bullough's study (76) revealed a reduction of mitotic activity by such stressful conditions. Perhaps this finding is the key to the retardation of growth in animals subjected to chronic stressful events. According to Blumenthal (81) mitotic rate is inhibited by hypoglycemia. Thus, growth should be less during any chronic "stage of exhaustion" with its characteristic low blood-sugar level.

Similar lines of reasoning have been forwarded by Christian (82) and Clarke (80) to explain the rapid die-off of populations which have attained densities which may be designated as crowded. Disturbances in reproductive physiology, including malformation of young, and convulsive death of stressed hypoglycemic animals (83), were the avenues by which Clarke and Christian believe stressful conditions of life exert control over population density.

There is thus both a logical and a factual basis for anticipating retardation of growth whenever conditions or events external to the organism chronically overtax the adjustive ability of the adrenal cortex. Furthermore, social interactions form a category of events which may tax adrenal physiology. It is this line of reasoning which has led me to assume that the observed differences in growth from rat to rat in my Towson colony primarily resulted from social interactions. Thus, when one does not wish to sacrifice his subjects, growth rate may be taken as an index of social disturbance.

One must exercise considerable caution in utilizing growth rates as indices of social disturbances when the subjects include both domesticated and wild strains of rats. Domestication has produced marked alterations in adrenal and growth physiology (34) as judged by decrease in size of adrenal cortex and thyroid, and by an increase is size of the hypophysis. Richter shows that the wild Norway rat is highly resistant to direct insults on its physiology. The LD_{50} dose of ANTU is 400 times that for domesticated strains. In comparison to domesticated strains wild Norway rats are highly resistant to convulsive seizures of either audiogenic or magnesium deficient diet origin. However, the wild rats are more likely to show deleterious effects

from adrenalectomy, or from any situation involving chronic disturbing situations. No wild rats survived following adrenalectomy accompanied by salt therapy, whereas most domesticated rats survived. When placed in a situation demanding choice among a battery of new types of food stuffs, the wild rats refused the strange food, lost weight and died, whereas the domesticated rats made the proper selections and lived. Under conditions of temporary acute stress (low temperature, loud noise, or fighting) there appeared to have been little change in the adrenal, as judged by ascorbic acid content, in wild rats but marked change in domesticated strains (*84*). On the growth side administration of growth hormone to domesticated rats regularly produces giganticism, whereas in other animals such as the dog it results in diabetes (*85, 86, 87*). To my knowledge no one has subjected wild rats to chronic injections of growth hormone. A distinct possibility of diabetes is indicated.

7. *Mortality in Rat Populations*

If we begin with a group of rats at weaning and follow them as they grow older we note that death gradually exerts an attrition on its members. Surprisingly enough few populations of rats have so been followed.

In addition to the data of the present study of the Towson population, there are available in the literature three other studies of survival among populations of rats. These will be examined to determine some of the major factors affecting survival. The four populations in order of decreasing severity of environmental conditions are:

1. Davis (*88*). Wild Norway rats on a farm where food and shelter was apparently in abundance but where heavy predation from owls, cats, and dogs existed in addition to the bacterial disease, Salmonella. Free play of social interaction also presumably occurred.
2. Calhoun—present study. Wild Norway rats maintained in an enclosure with excess food, absence of predators, but presence of certain diseases such as bronchiectasis and helminth parasites, and with opportunity for full expression of social interaction.
3. King (*64, 63*). A wild type of Norway rat maintained in the laboratory for 25 generations after capture from the wild state. The survival data refers to this entire period.

Rats were maintained in large cages (see further comment on pp. 262 to 264) in groups of 5–7 related individuals. This permitted a certain amount of social conflict but predation was absent and disease was presumed to be at a low level. Only rats belonging to litters all of whose members survived to 60 days of age were included in this study.

4. Wiesner and Sheard (*65*). Wistar albino strain of Norway rats. These were maintained in small cages with one male and one female and their unweaned young. All factors contributing to mortality including complex social interaction were at a minimum.

The data for each of these populations were recalculated in terms of proportion of survivors dying each 50 days. These proportions represent age specific mortality rates. Lines approximating the calculated points were fitted by eye (figs. 153 and 154). Inspection of the trends of change of mortality rate indicate that they are of two types: those in which mortality rate decreases with age and those in which it increases with age.

A. *Decreasing mortality rate with age.* Three (Davis' males, Calhoun's males and females) of the eight sets of data exhibit decreasing mortality rates with increasing age over an initial portion of the life span. From the statistics alone we cannot gain further insight into the origin of these trends. But interestingly enough they only characterize populations inhabiting environments, complex with regard to both their social and physical aspects. My own observations indicate that rats just weaned in the complex environment of the free ranging state have much to learn. Each unlearned aspect of the environment places the rat at a disadvantage with reference to his older associates. We can, therefore, suspect that it is such a learning to cope with the conditions and exigencies of the environment, which for a time following weaning, continually reduces the proportion of survivors which die. And yet in each of these three cases there arrives an age when the advantages accruing to the learning process were no longer adequate to compensate for the debilities of the ongoing aging process which increase the probability of death at each successive age.

A close parallel to the above phenomenon characterizes the changing death rate due to motor vehicle accidents for humans. As may be seen in figure 8.1 of the vital statistics for the United States
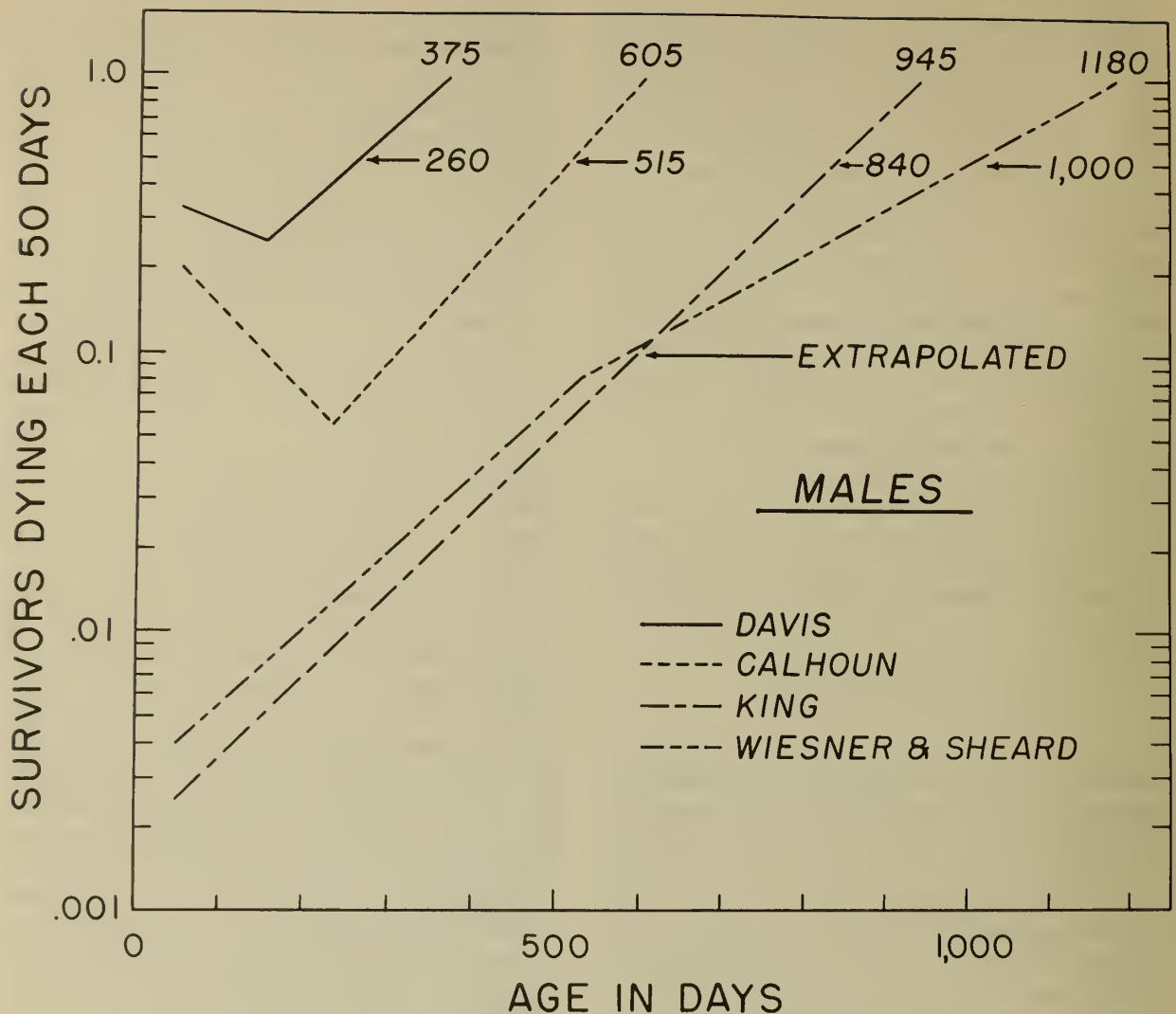
Figure 153.—Males.

Trends in death rate. The Davis data refer to wild gray rats living on a farm where both predation and disease were prevalent. The Calhoun data are that of the present study where predation was absent but disease and internal strife were present. The King data are that for wild gray rats bred for 25 generations in cages in groups of 4 to 7 rats. The Wiesner and Sheard data refer to domesticated Wistar albinas caged in pairs. There were approximately 100 rats of each sex in the Davis and Calhoun data, and approximately 1,000 rats of each sex in the King and in the Wiesner and Sheard data. The curves for King's data are extrapolated beyond 600 days of age on the basis of the trend exhibited prior to that time.

for 1950 (89), there is a declining death rate between 22 and 35 years of age. After 35 years of age the mortality rate increases rapidly. It certainly looks as though increased experience with driving automobiles enhances our chances of avoiding involvement in a fatal accident. Beyond 35 years of age some process of aging begins to counteract the advantage gained through these prior years of experience.

B. *Increasing mortality rates with age.* Beyond some age in each of the eight sets of data each increase in age has a higher mortality than the preceding one. In environments reduced to the barest minimum, that is the caged state of King's rats and of Wiesner's and Sheard's rats, the aging phenomenon of increasing probability of death is evident from the time of weaning.

Comfort (90) terms this phenomenon the "force of mortality". When this force is predominating, the log of mortality rate plotted against age forms
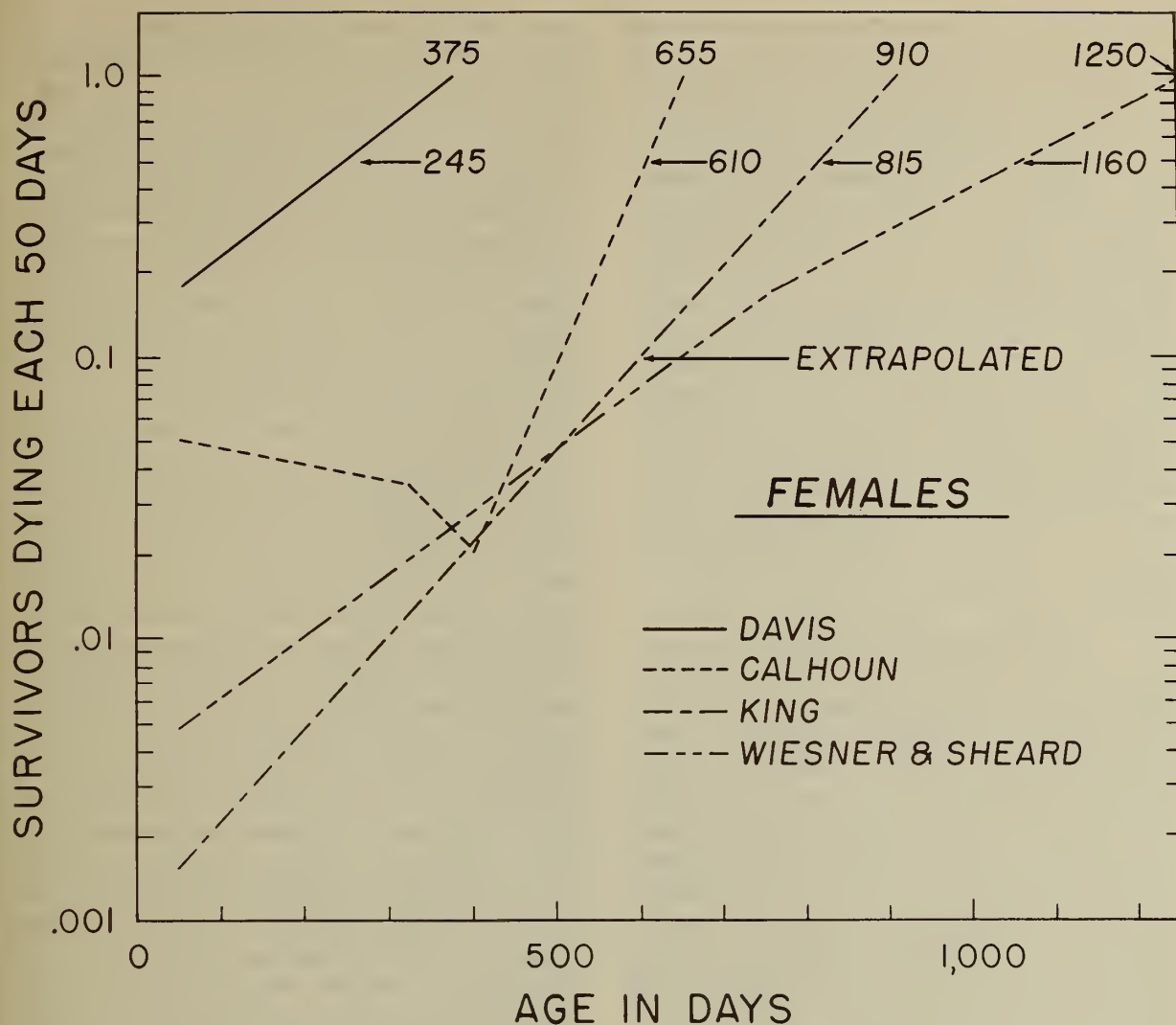
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Figure 154.—Females. (See explanation for Fig. 153.)

an upward sloping straight line. The relative strength of this force of mortality may be visualized in terms of the length of time required for a doubling of the mortality rate.

Despite differences in heredity and environment this doubling of the mortality rate takes about 130 to 135 days for male rats in each of the four populations. Likewise the mortality rate doubles each 130 to 135 days for the females in the population Davis studied as well as in Wiesner's colony. This strongly suggests that physiological aging is a phenomenon independent of both heredity and environment. If physiological aging really is independent of both heredity and environment we must perforce inquire as to the origin of the shorter interval of time required for the mortality rate to

double for females in two of the populations. This interval was 90 days for the females in King's colony during the entire life span, and only 47 days for the females in Calhoun's colony after 400 days of age.

Now, considering only the portions of the trends of mortality rates which consistently increase with age we find that mortality rate doubles as follows: Calhoun's females, 47 days; King's females, 90 days; and all the remaining six sets of rats between 130 and 135 days.

Why females should be more variable in this characteristic than males can not be determined from these data. However, a phenomenon encountered by Calhoun (91) suggests a probable reason. He studied four populations of Osborne-

Mendel strain rats, each consisting of approximately 75 adults confined in rooms within which each individual had the opportunity of ranging among four subareas. Food, water, nesting material, and nestboxes were located in each subarea of each room. Females born into such already socially structured groups frequently exhibited difficulty in carrying embryos to term. Following death of near term embryos some females died from toxemia associated with the large mass of dissolving embryonic tissue. For those females who survived this phase, one site of resorbtion of a full-term embryo often became the site of an abscess developing from the decaying fetus. Death usually ensued by the time the abscess reached a diameter of 50mm. Several weeks might elapse between death of the near-term embryos and the mother's death. Some females were able to resorb near-term fetuses, although transient abscesses could be detected by palpation.

Although no such overt symptoms were recognized among the females of the present study of the rats in the Towson enclosure, it nevertheless remains a distinct possibility that female physiology was impaired as a consequence of resorbing embryos. A similar line of reasoning may also account for the increased force of mortality characterizing King's females. Caged with other adults of both sexes they were unable to avoid disturbances attendant to this crowded association. Thus from the very start of reproductive life they would be exposed to alterations of physiology accompanying resorbtion of embryos. This leads to a tentative hypothesis: Toxic reactions resulting from resorbing embryos leads to an acceleration of the hereditary aging process.

However, most of the mortality curves shown in figures 153 and 154 exhibit a force of mortality in which the proportion dying doubles each 130–135 days. When the life table of a species results in this form of mortality curve, one must conclude that mortality rate is proportional to a physiological process of senescence, which begins early in life and continues to death. The nature of this process is unknown. Physiologically the implication is that the older an animal becomes the longer it takes to accomplish a unit of function, and furthermore the more the function is slowed down by some physiological antagonism, the greater is the likelihood of the antagonizing agent accumulating in the cells. Accumulation within the cell of enzyme inhibitors (92, 93), whether acquired through foodstuffs or resulting from enzymatic activity within the cell itself, suggests a mode of origin of such senescence [(90), pp. 310–311].

However, our concern here is not so much with the origin of the physiological basis of senescence, but rather with the manner in which environmental factors interact with the phenomenon of senescence to produce altered mortality rates. The mortality curves for male rats fall into three discrete groups Each of the out-of-doors populations (Davis' and Calhoun's) form a separate group, while the two laboratory populations (King's and Wiesner's) are similar enough to form a single group.

For a given age the mortality rate of Davis' rats was approximately seven times that of Calhoun's, while Calhoun's was approximately seven times that of King's or Wiesner's and Sheard's. Thus Davis' rats exhibited mortality rates about 49 times that of King's and Wiesner's. When these differences are considered along with the similarity of rate of senescence (i.e. rate of change of mortality with age), the following hypothesis is suggested: Mortality rate is proportional to the product of (a) degree of senescence characteristic of the age in question and (b) the frequency of intensity of deleterious events in the environment. Measurement of intensity or frequency of all events which favor mortality is difficult. However, provided rate of senescence is constant, the ratio of age specific mortality rates between populations should provide an index of the relative severity of the environments. For the comparison Wiesner and Sheard:Calhoun:Davis the ratio is 1:7:49. These ratios parallel the observed apparent severity of environmental conditions contributing to mortality. Thus one may conclude that the actual probability of death within a given age span is the product of the probability of death from inherent aging factors and the probability of encountering environmental debilitating factors. It follows that even though the force of mortality remains constant, the greater the severity of the environment, the shorter will be the life span of any cohort.

8. *The Significance of Social Class to Survival of a Population*

In his review of the relationship between home range and regulation of population density Kalela (94) points out that there are three main consequences of home range development: (1) Emigration (2) Death through hypoglycemic shock; (3) Reduc

tion in reproductive performance. According to him these consequences operate to insure an adequate food supply for members remaining in their original home ranges. For these phenomena to develop the number of individuals mutually tolerated within a given home range, as well as the proximity of groups inhabiting adjoining home ranges, must have definite limits. In the present study there was no evidence of death of Norway rats by shock disease. Although extensive emigration was precluded by the fence surrounding the pen, limited movements from the place of birth regularly occurred. These movements were accompanied by formation of new groups, usually not exceeding 10–15 rats, such that the minimal distance between centers of adjoining colonies was approximately 25 feet (see fig. 128). Intolerance to further crowding gave rise to stressful interactions that indirectly curtailed reproduction. From these conditions, two elaborations to Kalela's general concept are suggested. 1. For the Norway rat under the experimental circumstances home range primarily applies to that region about a burrow which is used nearly exclusively by the group inhabiting that burrow. The point being made here is that there appears to be a minimal distance tolerated between home range centers which is independent of insurance of an adequate food supply. This, however, does not obviate the possibility that within the evolutionary history of commensal association with man, this tolerance distance between colonies was of survival value for the species in relation to adequacy of the food supply. 2. Kalela at least implies that density control by emigration, shock disease, or decreased reproduction, equally protects all members inhabiting favorable habitats. That is, within each home range the members enjoy equal opportunity for access to food and performance in reproduction. In the present experimental situation groups possessing comparable home ranges met quite different fates. For example, compare the rats inhabiting Area I versus those in Area IV, or those in the South Alley versus those in the North Alley. Despite the physical comparability of these locations the inhabitants of Area I and the South Alley were leaving many descendants, while the inhabitants of the other two localities were leaving practically none. The important difference between the two regions is that of cultural history which produces differential segments of the population. These we may

logically designate as belonging to different social classes.

These social classes are not to be construed as synonymous with social hierarchies, although both social hierarchies and the phenomenon of home range and its defense contribute to its origin. The defense of home ranges, that is the development of territory, is an outgrowth of both home range and social hierarchies (6, 94) and it also contributes to population control and survival of the species. Formation of social classes is then a third and higher order phenomenon. Its contribution to survival of the species is that it provides assurance of the maintenance of a few favored groups. These not only enjoy an adequate food supply but also relative freedom during maturation and reproduction from the marked stresses of social interaction encountered by most of their associates.

9. *Strange Object Reaction and its Relationship to Periodicity of Activity*

In the study of the rats in my Towson colony a number of examples were cited of avoidance of strange objects, reluctance to reenter traps, caution in initiating an excursion, slowness in exploring a new portion of the habitat, and retreat into the burrows upon detection of any sudden strange stimulus. Chitty and Southern (31) cite many similar experiences with the wild Norway rat. They measured food consumption of a group of rats during 17 nights. On six of these nights some strange object, such as a tin can, was placed near the food hopper between 6 p.m. and midnight. During these 6 nights only 45 percent of the food consumed was eaten before midnight in contrast to the 60 percent before midnight during the 11 control days. Where access to a food pen was by a single entrance, the placing of any new object at the entrance for a few minutes completely inhibited passage during such time. Even replacement of one food hopper with an apparently identical one caused delay in initiating feeding. Prebait stations in the form of small wooden sheds or clay drain tiles produced a typical avoidance reaction in which the amount of food eaten per night normally did not reach a maximum until 2 weeks had elapsed. Once the habit of feeding at such a station was established its removal to a new location only a few feet away again produced an avoidance, but of shorter duration. The frequent approach and withdrawal from the hopper

at the new location revealed that the rats were able to detect it immediately. It seems as though the perception of a stimulus such as this is not specific, but embodies other objects in the environment. If the food hopper had been repeatedly moved from one location to another one could determine if rats can develop the behavior of immediately responding to this stimulus irrespective of the other stimuli in the surroundings. Even though this might prove to be the case, the initial observation of the importance of location remains relevant, since occasional changes rather than repeated changes are the more customary sequence of events in the life of a rat.

In a study of the effect of DDT dusting on the prevalence of typhus antibodies in rats (67) DDT dust was placed across rat runways and at access openings in buildings. Reuse of runways can be determined by presence of tracks through this insecticide dust. "Whenever possible, rats abandoned old well-established runways in favor of new undusted runways." There was also evidence of rats moving out of dusted areas into surrounding undusted areas, with return to the home sites only after the surrounding area was also dusted.

These behaviors of the wild Norway rat suggest the following generalization: Rats develop an habituation to particular stimuli and to pattern relationships among them, and thus those responses may be expressed which immediately lead to satisfaction of some drive. Any change in the normal stimuli impinging upon the rat interferes with elicitation of the appropriate response by engendering some of the physiological changes associated with Selye's (18) General Adaptation Syndrome. Alleviation of these physiological changes and resumption of a situation where responses are appropriate to existing stimuli can only be made by avoiding the place where the new stimuli occur and by returning to the burrow or to other places in the environment where such changes have not taken place.

Psychologists [e.g. (95); (59)] have dealt with essentially the same phenomenon with domestic breeds of the Norway rat, but in situations which preclude complete avoidance of the new stimuli. The most widely used test situation is that of the "open field." In this test rats which have previously lived in the confines of a small cage are placed in the center of a much larger cage. Avoidance is permitted only in the sense that retreat to the peripheral wall allows a contact response similar to that previously experienced in their home cage. Urination, defecation, and excessive grooming are the outward manifestations of the stress experienced by such rats. Any new situation that cannot be avoided elicits similar responses. In the absence of definitive experiments one is led to infer that the ability of free-ranging rats to avoid strange stimuli reduces the frequency of such marked physiological changes.

In the section, "Social Stress and Proneness to Enter Traps", (pp. 95 to 99) it was pointed out that socially low-ranking rats tended to enter traps more frequently than did their higher ranking associates. Chitty and Southern [(31), p. 317] cite an observation which confirms my observations that low-ranking rats exhibit a reduced avoidance of strange or disturbing situations: "Other populations have contained a proportion of rats that would come out for token baits in the afternoon, while their fellows refused to move out from cover. These 'bolder' rats were frequently attacked upon their return from the wheat, the younger ones sometimes being thrown over on their backs, and the wheat removed into the jaws of the assailants." Presuming that these observations are typical and represent examples of a general principle, three hypotheses may be forwarded to explain the origin of reduced avoidance of emotionally disturbing situations by rats which have experienced marked social stress from their associates:

1. The situation is actually less emotionally disturbing to them.
2. Perception is impaired; that is they are less able to discriminate between noxious and favorable stimuli.
3. They actually seek out situations which produce emotional disturbance; that is emotional disturbance has embodied in it the characteristic of a reward.

Hypothesis 2 is merely a special case of why hypothesis 1 might be true. The only evidence that I am aware of negates these two explanations. Seitz (59) has reared domestic rats in litters of sizes 6 and 12, and isolated the members at weaning. There was more competition among larger litters for nursing opportunity. When placed in an open field the members of larger litters defecated more and also walked much less about the field. These data suggest that rats who have experienced unfavorable social interactions are actually more emotional in a strange situation.

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Furthermore, Seitz found that these members of larger litters more frequently avoided entering a strange situation in the form of a differently structured cage placed temporarily at the open door of the home cage. This observation is in apposition to that of free-ranging rats. However, the conditions surrounding the experience of the free ranging rats were quite different. They were frequently exposed to emotionally disturbing conditions up to the time at which the observations of reduced avoidance were made. That is emotional disturbance and stimuli leading to its origin was the normal rather than the unusual situation. One might then anticipate that these disturbed rats would actually seek out situations which fostered reestablishment of their normal state of physiology. It is for this reason that I believe that the third hypothesis is the best tentative one for explaining the origin of this masochistic type behavior by socially low-ranking free-ranging rats.

The strange object reaction, social stratification, and periodicity of activity are interrelated phenomena; even though the basis of this interrelationship is by no means clear. In addition to the "bold" rats who come out early in the evening, and their stronger associates who appropriate their transported food, Chitty and Southern cite another type, one which never goes to the original food source but resorts to gleaning morsels dropped by other rats after transport to the vicinity of the harborage. These observations support my contention that social behavior is a major determinant of periodicity of activity.

Thompson (96) provides some detailed data on the activity of 10 marked rats at a pig farm over a period of 5 nights. The number of visits to a hopper of wheat during each 5-minute interval was recorded for each marked rat. From his data I attempted to verify further the belief that there is a time stratification of activities of different members of a population. There was considerable overlap of periods of activity, and yet a cursory examination of Thompson's histograms for these 10 rats indicated differences in periodicity. Two indices of periodicity were taken: (a) The first 5-minute interval during which the rat visited the bait; (b) The midpoint time of activity. For each rat the latter index was the particular 5-minute interval, before and after which equal number of visits were made to the wheat. Each day the 10 rats were rank ordered according to these indices of times of activity. The fifth day was omitted since by that time a nearly 6-hour forward shift in activity had occurred so that differentiation of individuals on a time basis was difficult and for some reason the two rats which usually showed up last at the bait failed to make their appearance.

These data were amenable for determining if the order of visiting the food was consistant from day to day (97). When r=rows (rats) and c=columns (days); T_i=totals across rows (i.e. sum of ranks for days 1 to 4).

$$X^2 = \left[\frac{(r-1)+(c-1)}{cr(r+1)} \right] \left[\sum_{i=1}^{r} T_i^2 - 3c(r+1) \right]$$

$X^2 = 23.54$; p less than .01 for 1st visit.
$X^2 = 23.71$; p less than .01 for midpoint time at bait.

This argues for the reality of the stratification of colony members over time with reference to these specific portions of their overall activity at the bait. A contingency test of Chi Square for the similarity of mean rank between the two indices (table 70) gave a X^2 of 3.44; p $\approx$ .95. We are therefore on fairly sure ground for believing that the entire condensed period of time of activity of each rat has the same rank ordering as reflected by the indices. Schematically the stratification of these rats through time is shown in figure 155. Two of the rats, N and U did not appear until the food was nearly exhausted. In contrast to the other eight rats the number of visits by these two rats exhibited a marked decline on successive days until by the fifth day neither appeared. Thus, time stratification can result in complete exclusion from a limited source of reward.

TABLE 70.—*Mean rank-order of the visitation of rats at a pan of bait during the first four days of its availability (based on data from Thompson, circa 1953)*

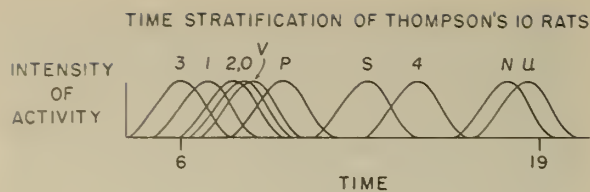| Rat	Rank of first visit to bait	Rank of mid-point time of visits to bait
1	3. 63	3. 38
2	4. 00	3. 88
3	3. 00	3. 00
4	7. 75	6. 83
N	9. 63	8. 25
O	3. 38	4. 88
P	4. 63	5. 13
S	6. 25	6. 50
U	8. 88	9. 75
X	3. 88	4. 63

TIME STRATIFICATION OF THOMPSON'S 10 RATS

Figure 155.—Time stratification of Thompson's 10 rats. Relative time was taken as the sum of the two mean rank orders in table 70.

10. *The Role of the Physical Structure of the Environment*

McCabe and Blanchard (*98*) and Harris (*11*) have shown that within the genus of mice, *Peromyscus*, each species and even each subspecies may respond to and be attracted by remarkably restricted physical characteristics or configurations of the microhabitat. Since such characteristics typically exhibit a mosaic rather than a uniform distribution, their absence in portions of the environment imposes restrictions on the potential population density of each species. Specificity for attraction to particular configurations of the environment has also been shown for the Norway rat. Attraction to isolated or continuous vertical objects, to flat surfaces when digging is initiated, or to various low overhanging surfaces, etc. are observed for the Norway rat. Within the Towson colony pen, locations of tree trunks, fences, passages through fences, preplaced harborage boxes, etc., certainly did control development of trails, and burrows, and thus the association patterns among rats. These lines of evidence suggest that we should diligently seek those configurations or conditions of the physical environment, which, by heredity or culture, attract or repel the species we are interested in. Once these are ascertained, our general course of action is dictated. This is to systematically vary the distribution of these configurations or conditions through space and time. Within each set of conditions a population may be allowed to develop and its members permitted to interact. Observations may then be made with the objective of delineating the dependent variables under two categories: (a) the population and its subgroups or (b) the characteristics of the individual. Under the former fall: (1) population growth and limitation; (2) the formation size, composition and stability of subgroups; and (3) the interrelations between subgroups. Under the latter fall: (1)

growth, maturation and aging; (2) physiology, such as adrenal or cardiac function, and many others; (3) the kinds, frequencies and durations of interactions with other individuals; and (4) reproductive performance and survival. All of these dependent variables may be quantified and related in some causal sequence to the manner in which we have structured the environment with independent variables.

I view the importance of the present paper on the life history of the Norway rat, not from the specific findings and interpretations, interesting though some of them may be, but rather from the insight it provides to the opportunity and feasibility of developing an experimental approach to problems of social biology and population dynamics on the vertebrate level. The naturalist and ecologist can gain insight, and even formulate principles about those conditions which govern the life of the individual and the population of which it is a member. Anyone who has studied animals (including man) in their native habitat is cognizant of the fact that the characteristics of the environment are so irregularly distributed as to make evaluation of their effect difficult. Not until we begin systematic experimental manipulation of the environment can we hope to develop principles of precise predictive value. On the vertebrate level such systematic manipulations have been extremely rare, possibly because of technical and financial difficulties. However, the need for such studies imposed by a "shrinking" world, as human populations expand at the expense of most of the rest of the vertebrate fauna, is paramount. One question stands out: What are the configurations and spatial limitations requisite for an optimum state of existence of each species? Space requirements may be restricted with appropriate structural configurations, but restrictions beyond certain limits is certain to be accompanied by deleterious effects. For many years we have been concerned with the role of availability of food for static or expanding populations. Just as McCabe and Blanchard found for mice of the genus *Peromyscus* and I for Norway rats, that needs for space and particular configurements impose limitations on population growth in the presence of adequate food supplies, so it is likely to be found for other animals including man. Experimentation on animals as to these needs and how they may best be fulfilled in relation to spatial limitations would provide valuable insight into their application to

man. There is a great effort being made to increase the amount of foodstuffs available to man. A derivative, if not its motivation, of this effort is the widely held opinion that we should produce more foodstuffs in order that more people can be born and survive. This demands that we maintain so long as possible an expanding population. There is no doubt that agriculturists and biochemists have made, and may continue to make, marked strides in accomplishing this objective. The question remains: What will be the impact on the lives of individuals and the structure of groups as we progress toward this goal of maximum amount of human protoplasm? It is apparent that an effort to maximize this goal will simultaneously restrict realization of other needs and goals.

Experimentation on infrahuman sociology and population dynamics will assist us in arriving at conditions which foster a compromise in various goals possible of achievement. The sort of compromise I think we should look for is one which imposes some limatations to population expansion, yet allows members and complexity of groups sufficient to insure benefits derived from cooperative action, while permitting the individual some freedom of action, and freedom of inaction, repose, or even retreat from the activities of others.

Persons from two long separated disciplines have the opportunity of contributing to an understanding of what such a compromise might be. They are ecologists and psychologists. In either case they must deal experimentally with groups which at the upper level approach a population. By a population I mean a group which has reproductive continuity through several generations, and where there is the opportunity for learned behaviors or culture from one generation to affect the succeeding one. The ecologist must become familiar with the concepts and techniques of the psychologist. The psychologist must learn from the ecologist that the experimental animal is not just a machine to manipulate without regard to the fact that its heredity governs the expression of many behavior patterns, preference for particular characteristics of the habitat, and ability or probability of participating in specific social relations.

Thus, if an experimental approach to population dynamics and social organization on the vertebrate level is to develop, it requires a coalescent discipline, ecopsychology. To the extent that my study of the life history of the Norway rat may stimulate further and more experimentally oriented studies of vertebrate population dynamics will I feel satisfaction in accomplishment.

I have not been alone in my concern with the characteristics of space, its utilization through time, and the need for more experimentally oriented comparative investigations which include function of the individual in the context of others of its species. Hediger (99) has ably marshaled much circumstantial evidence of such bonds between the organism and its environment. He particularly emphasizes the principle of psychic inertia which binds the individual to learned or hereditarily determined tropistic relations to its physical and social environment. This empathy with the environment he designates as the archetope or psychic characterization of the environment by the individual. Disruptions in the archetope resulting from displacement or changes in the environment lead to nostalgia, homesickness, and malfunction of physiology and behavior. Donald O. Hebb of McGill University in a seminar at the National Institute of Mental Health similarly stressed the importance of this area, which he designated as "homesickness" and the lack of experimental studies relating to it.

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