AGGRESSION AND SELF-REGULATION OF POPULATION SIZE IN DEERMICE

by

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ABSTRACT

Sadleir (1965) proposes that the survival of juvenile deermice is determined by the aggressiveness of the adult population. During the summer, when adult aggression is high, juvenile survival is poor, but in the fall, when adult aggression is low, juveniles survive well. The purpose of this study is to examine some of the consequences of Sadleir's hypothesis experimentally.

Sadleir bases his hypothesis on the observation that the aggressiveness of males changes seasonally. This premise has been reexamined and confirmed. How adult aggression affects juveniles was studied first in the laboratory. Juveniles grow poorly when competing with adults in their home cage. Males appear to be more active aggressors than females, but only aggressive males are capable of inhibiting juvenile growth. Even though juveniles grew slowly when competing with aggressive adults, they seldom died from encounters with adults.

In order to avoid the crowded conditions and confinement implicit in the laboratory experiments, the relationship between adult aggressiveness and juvenile growth and survival was reexamined in field experiments. Two partly isolated plots of habitat were used, and on these plots artificial populations of aggressive or docile male deermice were established. Juveniles were then released onto the plots, and their growth and survival followed. In the field, as in the laboratory, juveniles grew poorly when competing with aggressive adults. Since emigration was not restricted in the field, however, juveniles disappeared in significantly greater numbers when the adult population was aggressive than when the adult population was docile. In addition to these experiments, the success of immigrants onto trapped out plots and plots with a resident population was examined. Immigrants were more successful in establishing themselves on trapped out plots.

All the data collected support Sadleir's hypothesis, and it seems reasonable to conclude that the correlation he drew between adult aggressiveness and juvenile survival is real. However, the data collected also provide some interesting clues as to the organization of deermouse populations. An organization is proposed in which the social unit is an animal and its immediate neighbours. Within the social unit mutual antagonism is reduced. But the members of the unit maintain a high level of aggressiveness, and are intolerant of any stranger that wanders into their home ranges. The system proposed would prevent immigrants from settling, while conserving energy by reducing antagonism between familiar animals. The system would also effectively regulate population size.

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INTRODUCTION

Animal populations fluctuate in numbers, but the fluctuations occur within certain definite limits. That is to say, whole populations do not go on increasing indefinitely, and they seldom become extinct. The way these fluctuations are regulated remains a mystery. It seems unlikely, in the light of present knowledge, that population size is governed entirely by factors operating from outside the population. Therefore the number of animals in a population must be determined partly by the animals themselves. This paper deals with such a self-regulatory mechanism in the deermouse (*Peromyscus maniculatus austerus*).

The working hypothesis used in this study was advanced by Sadleir (1965). The data which led to its development are reviewed by him. Briefly, during most of the breeding season (June through August) mice are scarce. In spite of the low population density few juveniles are recruited. In September and October, however, recruitment is very rapid, and the population density increases, so that in early winter there are two or three times as many mice as in summer. This fall rise in the survival rate of juveniles is correlated with a decline in the aggressiveness of the adult males. Sadleir hypothesized that juveniles survive poorly in the early part of the breeding season because they are competing with aggressive adults for habitat, and that survival is better in the fall because the adults are less aggressive.

I have attempted to test Sadleir's hypothesis experimentally both in the laboratory and in the field. For convenience the experiments are presented under the headings "Laboratory" and "Field", even though doing so partly disrupts the logical sequence in which the experiments were performed. The methods and results of each experiment are presented as a unit. The sort of social system these results indicate for Peromyscus maniculatus is taken up in the discussion.

Animals used in the experiments were either caught in the field or were first generation laboratory stock. No distinction will be made between adults of these two types since the process of selecting experimental animals counteracted any qualitative differences that may have resulted from rearing animals in the laboratory.

The term juvenile in this paper refers to animals three to four weeks old. These animals generally weighed between 11 and 13 grams. They had not moulted the grey juvenile pelage and were undeveloped sexually. All the juveniles were first generation laboratory stock.

Except where noted all the laboratory experiments were performed in an enclosed ventilated room kept constantly on 13L-11D reversed daylight. This lighting schedule was sufficient to keep the adults continuously in breeding condition. Plots used for field experiments will be described later.

LABORATORY EXPERIMENTS

The Cycle in Aggressiveness

Methods

Sadleir (1965) presents data which show a spring increase followed by a fall decrease in the aggressiveness of male deermice. Since these observations constitute an important premise in Sadleir's argument, I decided to retest them.

The fall decrease was retested in 1963 and 1964, and the spring increase in 1965. In the experimental situation six randomly chosen male deermice were housed on the Zoology building roof in 1963, and in an open shed in 1964 and 1965. These animals were thus subject to natural fluctuations in daylength and temperature. In the control situation six males were kept in the constant environment of the laboratory. The animals lived separately in 15 in. diameter steel washbasins provided with sawdust litter and excess food and water. The basins were stored on a "Dexion" steel rack and food and water were checked at least every two days.

The aggressiveness of experimental and control mice was measured in encounters with members of a graded series whose aggressiveness relative to one another was known. The organization of the graded series is discussed in Appendix I (see also Sadleir 1965). The procedure for these encounters was as follows: Three subjects from the experimental group and three from the control group were tested each week. In 1963 subjects were selected randomly each week except for two restrictions: No animal was fought more than two weeks in succession, and each animal met each member of the graded series only once during the experiment. In 1964 and 1965 experimental and control groups were each randomly divided into two sets of three animals, and the sets were alternated each week. Again encounters were organized so that each experimental or control male met a member of the graded series only once. Twenty-four hours prior to the encounters subjects were weighed and placed in 2 ft. by 1 ft. by 1 ft. glass sided arena cages and provided with food and water. Before an encounter the cage containing the subject to be tested was placed on an observation platform and the water dish removed. The observation platform was lighted from above by a single 40 watt red bulb. The subject was given 5 min. to settle down, then a member of the graded series was introduced and the ensuing activity observed from behind a screen for 5 min. The animals from the graded series had patches of fur clipped off so that they could be distinguished in the arena. Descriptions of what occurred were spoken into a tape recorder and transcribed later. In October 1963, three members of the experimental group were brought back into the laboratory. This was done to see if longer daylength and higher temperatures would cause an increase in the aggressiveness of animals which had naturally become docile in the fall.

All encounters were recorded except during the initial weeks of 1963 when control encounters were run every week but were recorded only every three weeks (Fig. 1). In 1963 the temporal pattern of events was examined by recording the data in 10 sec. time intervals. Every act which occurred within each 10 sec. interval was recorded, but if a particular act occurred more than once it was still scored only once (cf Sadleir 1965). In 1964 and 1965 simple frequency counts were made.

The following categories of behaviour were recorded in 1963 (from Eisenberg 1962 except where noted): Threat (see Sadleir 1965), chase, fight, aggressive grooming (Grant and Mackintosh 1963), grooming, washing, naso-nasal, naso-anal, exploring, and mutual upright. Exploring and washing were not recorded in 1964 and 1965. From these acts the total number of threats and chases in a 5 min. encounter was selected as the best index of aggressiveness. The reasons for this choice are given in Appendix II.

Results

The results of the two fall experiments are presented in Fig. 1 and the results of the spring experiment in Fig. 2. Occasionally animals escaped when they were being taken from the basins for testing. If this happened on the roof or out in the shed it usually meant the animal was lost. Sometimes animals escaped from the testing arenas. Consequently not all weeks show three encounters.

The total number of points on each graph was divided in half first by a vertical line, then by a horizontal line (dashed lines Figs. 1 and 2). If the mice are becoming less aggressive the points should be clustered in the upper left and lower right quadrats formed by the dashed lines. And this is what happened in the two fall experiments. If the mice are becoming more aggressive the points should cluster in the lower left and upper right quadrats. This was the case in the spring experiment.

The significance of this clustering of points can be tested by means of a X^2 analysis in a 2 X 2 contingency table. These tables are presented in Table I. The clustering

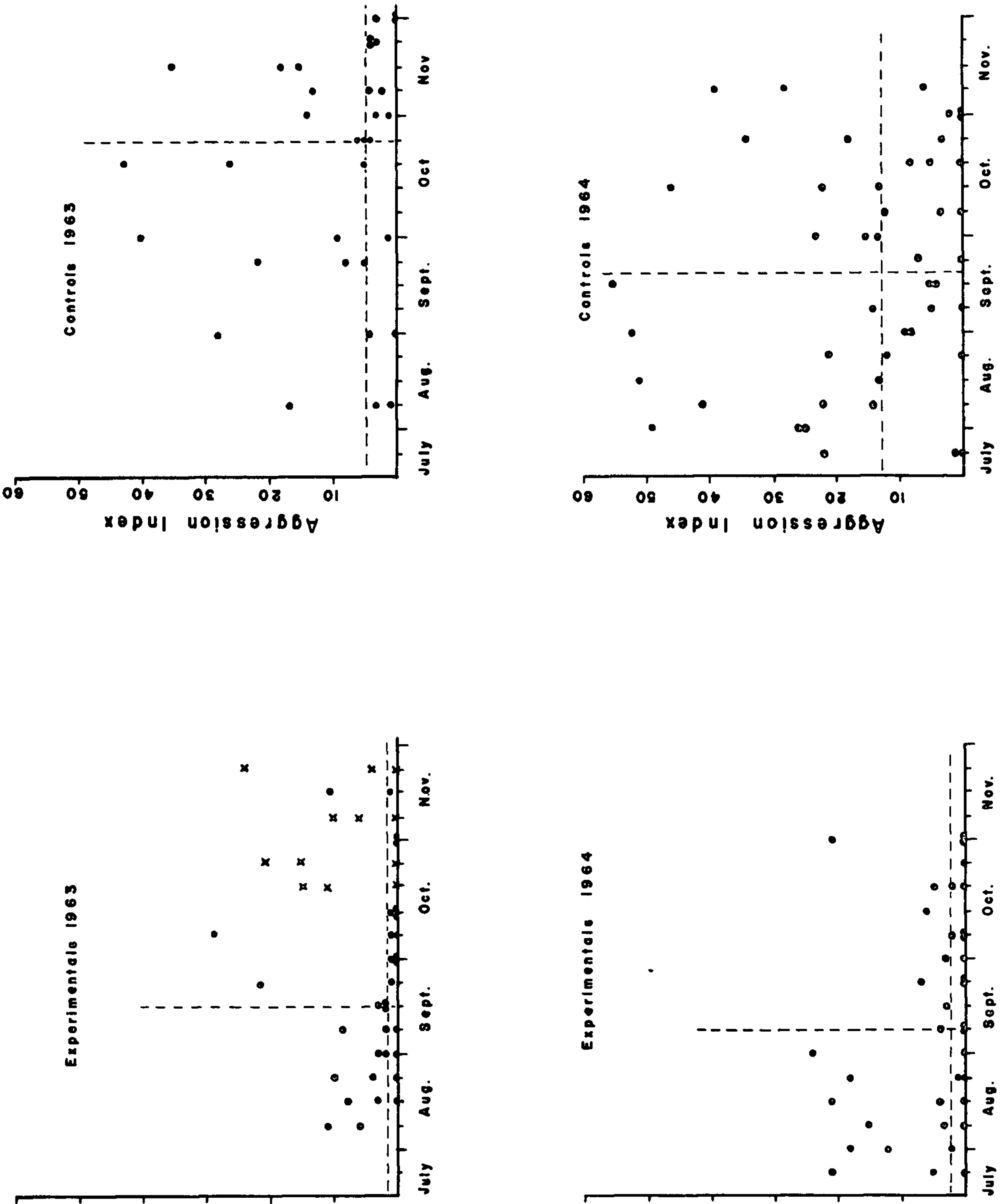
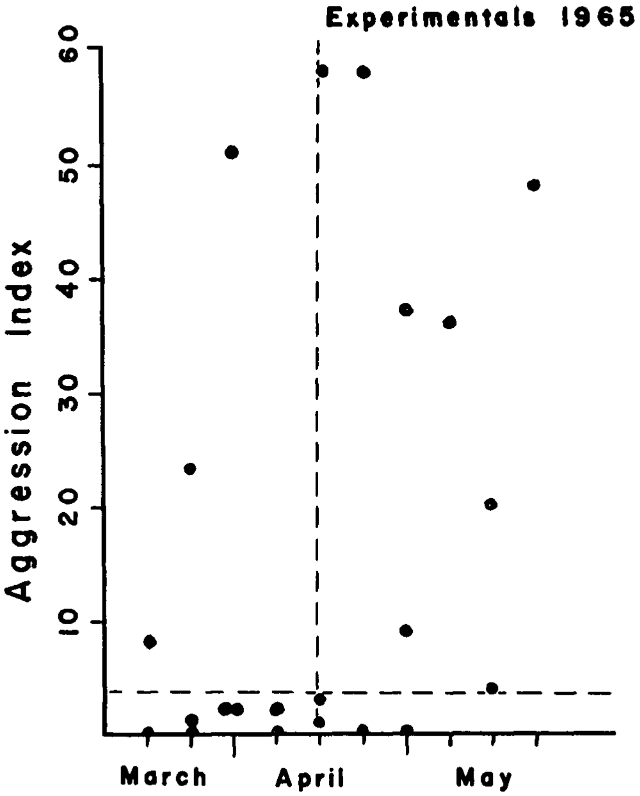


Figure 1. Changes in the aggressiveness of experimental and control males during the fall of 1963 and 1964.

● = Aggression score for one animal.

x = Aggression scores for experimental males moved back into the laboratory in October 1963.



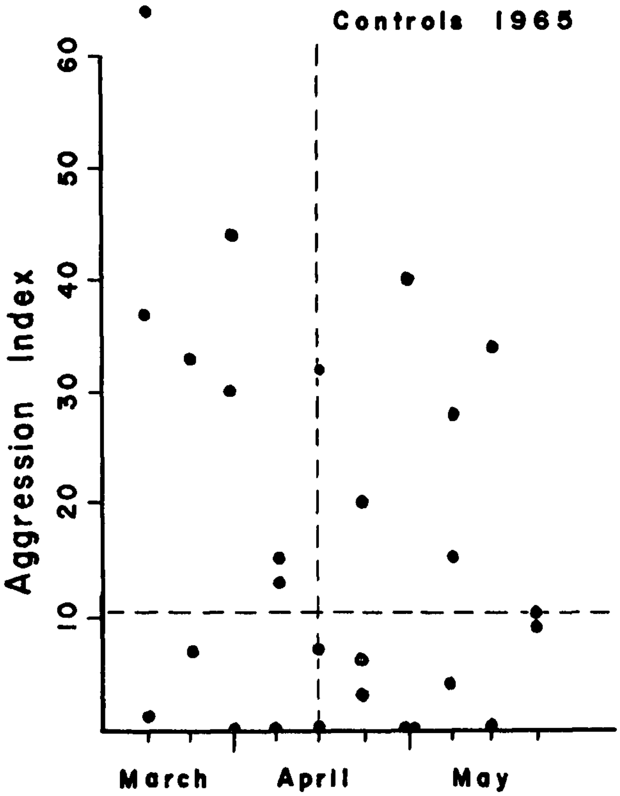


Figure 2. Changes in the aggressiveness of experimental and control males during the spring of 1965.

Table I Contingency tables for spring and fall changes in aggressiveness (from Figs. 1 and 2).

A. Fall Decline 1963

		EXPERIMENTALS			CONTROLS		
		First Half	Second Half				
Aggression	high	12.5	4	16.5	9	6	15
	low	4	12.5	16.5	6	9	15
		16.5	16.5	33	15	15	30

$X^2= 8.75$ $P<0.005$ $X^2= 1.20$ $P>0.25$

B. Fall Decline 1964

11	8	19	13	10	23
8	11	19	10	13	23
19	19	38	23	23	46

$X^2= 0.95$ $P>0.25$ $X^2= 0.72$ $P>0.25$

C. Spring Increase 1965

3.3	7.7	11	7.5	6	13.5
7.7	3.3	11	6	7.5	13.5
11	11	22	13.5	13.5	37

$X^2= 3.52$ $P< 0.10$ $X^2= 0.33$ $P>0.50$

of points for the experimental animals is significant only in the fall of 1963, however, the data from 1963 and 1964 may be lumped to give a X^2 of 9.7 with two degrees of freedom, which is significant ($P < 0.01$). None of the graphs for control animals show significant clustering. Lumping the data from control animals for the two fall experiments does not give a significant result ($X^2 = 1.92$, df 2, $P > 0.25$). The clustering of points for experimental animals in spring 1965 approaches significance and aggrees with what Sadleir observed. Similarly the animals which were moved back into the laboratory in October 1963 increased markedly in aggressiveness (Fig. 1).

Aggressiveness, then, appears to be controlled by changing conditions of light and temperature. The main point to be made, however, is that Sadleir's observations are confirmed; seasonal changes do occur in the aggressiveness of male deermice.

All the animals were weighed each week, and no change in weight was associated with the change in aggressiveness. Nor was there any relationship between size and aggressiveness in control animals.

The size of each animal's testes was also estimated every week (except in 1963) by gently squeezing the testes into the scrotum between finger and thumb. Four categories of testis size were recognized: large, medium, small, and none discernable. As the experimental animals became less aggressive their testes got smaller, and as they became more aggressive their testes got larger (Table II).

Histological sections were made of the four categories of testes mentioned above. These showed that large and medium sized testes were actively producing sperm, while testes smaller than medium were not. Presumably testes which are actively producing sperm are also actively producing testosterone. Beeman (1947) showed that testosterone levels affect aggressiveness in white mice and Whitaker (1940) showed that day-length affected the breeding of *Peromyscus leucopus*. In deermice, therefore, the whole cycle in aggressiveness is probably related to sexual maturity and testosterone levels.

Defence of a Home Cage

Burt (1940) and Stickel (1960) have presented evidence that *Peromyscus* occupy individual home ranges during the breeding season. Unpublished data of my own support this view. Some authors (McCabe and Blanchard 1950, Howard 1949) have suggested that in the winter *Peromyscus* band together in small groups. Whether or not the summer home ranges are defended remains an open question. However, it is important to know whether adult aggression in summer is associated with

Table II Changes in testes sizes of males in the experiments on aggression cycle. Testes sizes range from: none palpable (1), small testes (2), medium testes (3), large testes (4). Bracketed figures in 1963 are males moved back into the laboratory in October (see text).

A. Fall Decline 1963

	Date	Aug.	Sep.	Oct.	Nov.
Experimentals	mean	3.7	1.7	1.3(2.2)	1.4(3.4)
	range	3-4	1-3	1-2(1-3)	1-3(3-4)
Controls	mean		3.2	3.2	2.9
	range		1-4	1-4	1-4

B. Fall Decline 1964

	Date	Jul.	Aug.	Sep.	Oct.	Nov.
Experimentals	mean	4.0	3.7	2.6	2.2	1.8
	range	4	1-4	1-4	1-4	1-3
Controls	mean	3.9	3.9	3.6	3.7	3.7
	range	3-4	3-4	1-4	1-4	2-4

C. Spring Rise 1965

	Date	Mar.	Apr.	May
Experimentals	mean	2.9	3.5	4.0
	range	1-4	1-4	4
Controls	mean	3.6	3.8	3.9
	range	2-4	3-4	3-4

territoriality (i.e. defence of an area) or whether adult aggression per se is all that is necessary to reduce juvenile survival.

Methods

The effects of territorial behaviour were tested by releasing juveniles into the home cage of a pair of adult deermice. Adult aggression divorced from territorial behaviour was examined by releasing juveniles and adults together into a similar, but unfamiliar cage.

The colony maze described by Sadleir (1965), divided into three regions (A, B, C Table III), was used for the cages. In region A an adult pair was released. At the same time two randomly chosen juveniles were isolated in small subregions of A, B, and C. A second adult pair was isolated in a separate subregion of C. After two days the isolated sections were connected to their respective maze regions. This produced the following situations: (1) In region A juveniles were dispersing into an area occupied by adults in breeding condition. (2) In region B juveniles were dispersing into an unoccupied area. (3) In region C juveniles and adults were dispersing together into an unoccupied area.

Regions A and C were made twice as large as B so that each mouse had the same amount of potential living space. Food and water were supplied in excess. Experiments were run for 14 days after the isolated sections had been connected to the main body of the maze. For the first hour after the isolated sections were connected to the maze a record was made of the antagonistic acts in regions A and C. For the remainder of the experiment spot checks were made of the positions of the adults and juveniles in the maze. This was done to see if the juveniles had free use of the maze and to see if they associated with the adults. At the end of each experiment the juveniles were removed and weighed.

Experiments were performed in blocks of two. For the second experiment in each block the same adults were used but their roles were reversed. That is, the pair that had been on home ground became the pair on neutral ground and *vice versa*.

Results

Juveniles grew much more slowly in region A than in either of the other two regions (Table III). The probability that the differences in growth are due to chance is low ($P < 0.10$). The result is not statistically significant but agrees well with the findings of other authors (cf Barnett 1958). Only three juveniles died, two in region A

Table III Growth and survival of juveniles after 14 days in the maze: A. competing with adults on home ground, B. alone, C. competing with adults on neutral ground.

Maze Region	A	B	C
No. Released	8	8	8
No. Surviving	6	8	7
$\bar{X}$ Wt. Increase	0.92 g.	2.81 g.	2.64 g.
S.E.	0.73	0.70	0.66

and one in region C.

On the average there was no difference in the amount of aggression between adults and juveniles in regions A and C, however, the way the aggression occurred was rather different. In region A the adults generally moved into the isolate section almost as soon as it was opened and attacked the juveniles it contained. In region C, on the other hand, altercations occurred when the adults and juveniles met while exploring the maze. The two juvenile deaths in region A were a result of direct adult attacks as described above. The juvenile that died in region C invaded the adult isolate section before the adults had left it. He was severely attacked, and never recovered from the beating. The adults ignored him after he left their home ground in their isolate section, however.

In spite of the aggressive interaction in region C the juveniles in this region grew as well as the juveniles in region B where no adults were present. There is some evidence that strange surroundings may produce fear in rats (Montgomery 1955) and it may be argued that the adults in region C were inhibited by the strangeness of the maze. It is unlikely that they would have explored the maze as quickly or shown as much aggression as they did if they were inhibited by the strangeness of the maze. All the evidence supports the conclusion that, in the laboratory at least, adults must have familiar surroundings before they can affect juvenile growth.

Sex of Aggressor

Methods

It is not possible to decide from the previous experiment which sex, if either, has the greater effect upon the juveniles. In order to answer this question juveniles were released into maze regions controlled by either males or females.

The colony maze used in the previous experiment was divided into eight vertical columns. Pairs of adult males were released into columns 1, 3, 6, and pairs of adult females into columns 2, 5, and 7. Columns 4 and 8 were used for control areas. Two days after the adults were released, pairs of juveniles were introduced into each column. Aggression between adults and juveniles was recorded for the first hour after the juveniles were introduced. The experiment was terminated after 14 days and the surviving juveniles were weighed. A small additional experiment was run using only one column of males and one of females, after the first experiment was completed.

Results

Survival was 100% in the columns containing female adults, but much less in the columns containing male adults ($X^2 = 7.27$ $P < 0.01$) (Table IV). Also males were much more aggressive toward juveniles than females were. Too few juveniles were used in this experiment to permit any meaningful analysis of growth rates. It should be pointed out, however, that females do not seem to have affected the growth rates of the juveniles.

<u>Aggressiveness of Males</u>

The results of the previous experiment suggested that it would be best to concentrate on the behaviour of the males, and how their behaviour affects juvenile survival. Consequently most of the remaining experiments are concerned with males only. The following experiment was designed to test a fundamental prediction of the hypothesis, namely that aggressive males have a greater effect than docile males upon juvenile survival.

Methods

The colony maze was used as in the preceeding experiment except that now columns 2, 5, and 7 each contained a docile male and columns 1, 3 and 6 each contained an

Table IV Survival and growth of juveniles in the maze with territorial adult males or adult females.

Territory	Male	Female	Control
No. Released	8	8	4
No. Surviving	3	8	4
X Wt. Increase	1.3 g.	2.1 g.	1.1 g.
S.E.	2.0	1.17	0.76

aggressive male. Aggressive and docile males were selected on the basis of their performance in encounters with members of the graded series. The method for conducting encounters with the graded series has been described in the experiment on the cycle in aggressiveness. The same index of aggression was used. Docile males rated <5 on the index and aggressive males rated >20 on the index.

Two days after the males were released into the maze, pairs of randomly chosen juveniles were introduced into the columns. Juvenile weights were recorded each day for seven days.

Results

Juveniles in the columns with docile adults grew almost twice as fast as juveniles in the columns with aggressive adults (Fig. 3); the slopes of the lines regressed on weight are significantly different ($t = 2.074$ $P < 0.05$). Clearly, aggressive adults are capable of exerting a greater effect on juveniles than docile adults are. In fact there was no difference between the growth of juveniles with docile adults and the growth of juveniles alone in columns 4 and 8.

Spontaneous Activity in Males

Even though aggressive males are capable of

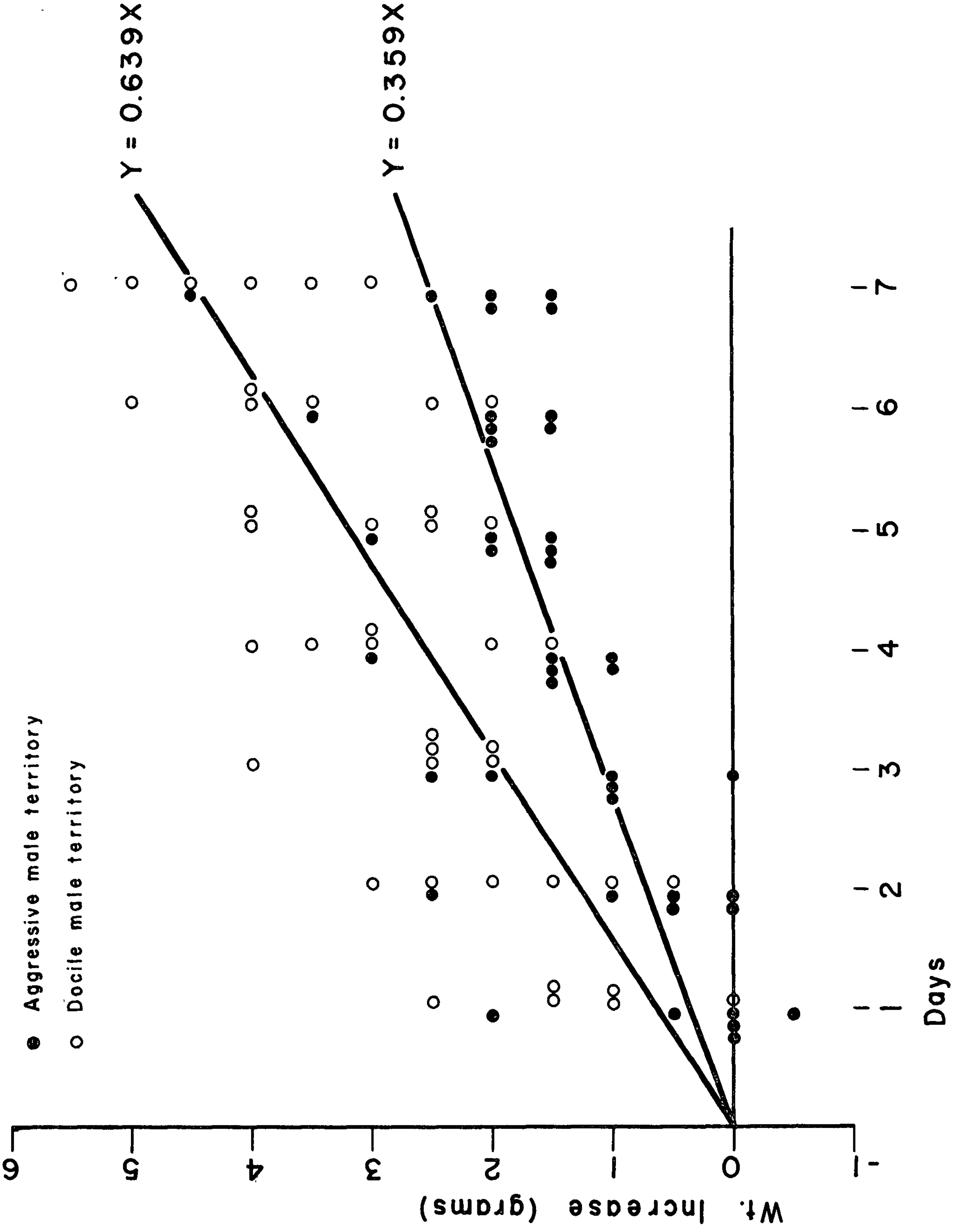


Figure 3. Weight changes of juveniles in the maze with aggressive males (solid circles) and juveniles in the maze with docile males (open circles).

influencing juvenile growth in the enclosed laboratory system, practically nothing is known about the way aggression occurs in the natural habitat. Data from the experiment on seasonal changes in aggression suggest that aggressive males might be more spontaneously active than docile males. If this is true then aggressive males should be capable of occupying larger home ranges or of patrolling their home range more efficiently. I decided to explore further the possibility that aggressive males are more active.

Methods

Experimental animals were first bouted against members of the graded series to assess their levels of aggressiveness. Highly aggressive or docile males were selected by the criterion previously noted. Before each test the animal to be tested was given 24 hours to become accustomed to a small (8 in. square) wire mesh cage. After 24 hours the cage was suspended by three elastic bands so that it bounced freely each time the animal moved. The cage was connected to a kymograph pen and the bounches were recorded as jiggles on a moving ink trace. After the cage was connected to the kymograph the mouse was left in the dark and activity was recorded for approximately 15 min.

Activity was scored by measuring the periods of activity to the nearest 1/10th of an inch along 12 in. of the ink trace. Measurement was begun one inch from the start of the trace in order to reduce any bias in the first part of the trace due to connecting the kymograph and shutting off the light. The length of the trace measured represents about 12 min. of time.

Results

Ten aggressive males averaged 6.29 in. of activity, while eleven docile males averaged 3.15 in. The data were transformed into logs and treated in a Student's t test. Aggressive mice were significantly more active than docile mice ($P < 0.05$). Lagerspetz (1964) found a similar relationship between aggressiveness and motor activity in a strain of white mice selected for aggressiveness and docility. In a complex environment like our coastal forests the number of social contacts a mouse makes must depend, at least in part, on how active it is. In this case the aggressive mice would be more likely to encounter and threaten a strange juvenile.

FIELD EXPERIMENTS

Isolated Plot Experiments

The laboratory tests showed that juveniles grew poorly when placed with aggressive adults. However, it may be argued that this result was a laboratory artifact resulting from crowded conditions and confinement. Therefore the prediction was retested in natural habitat at normal population densities.

Methods

Two isolated woodland plots were used to test the prediction that aggressive adults reduce juvenile survival. The first was a plot of about 3 1/2 acres (Sadleir's 1965 plot B). A grid of 19 traps (three lines of five traps each and one line of four traps) was set on this plot for five days and all captured animals were removed. Then four aggressive male adults were released onto the plot. One week later the plot was retrapped to census the surviving adults, and 13 juveniles were released. The plot was retrapped on days 4, 7, 11, and 14 after the juveniles were released, to census the surviving juveniles and measure their growth rates. After the 14th day the plot was intensively trapped to capture any juveniles that had been missed. Whatever adults had survived were retested at the end of the experiment to be sure they had retained their aggressiveness. After all the surviving mice had been removed a duplicate experiment was performed using docile adults. Six experiments (three of each type) were performed on this plot between May and October 1964, and five between these months in 1965. The second plot was much smaller, about 1 1/2 acres (Sadleir's 1965 plot A).

It was used only in 1965, and five experiments were performed on it concurrent with those on plot B. The experimental technique used on this plot was the same as that used on plot B except that three adults and ten juveniles were released initially.

On plot B adults were released at trap sites 1, 6, 11, 16, and on plot A (seven trap sites, two traps at each site) at sites 1, 4, and 7 (Fig. 4). On plot B juveniles were released at sites 2, 3, 5, 7, 8, 9, 10, 12, 13, 14, 15, 17, 19, and on plot A one juvenile was released at each of sites 1, 3, 5, 7, and two juveniles at each of sites 2, 4, 6. Nest boxes from Longworth live-traps, supplied with food and cotton bedding were used as release boxes.

Both plots A and B originally supported a resident population of deermice so the habitat was suitable. Four is an average summer complement of males for a plot the size of plot B; three was perhaps an overestimate for plot A (average for all plots in the summer of 1962 and 1963 was slightly more than one male per acre). Similarly 13 juveniles represent a reasonable juvenile production from four females on plot B (average litter size 4.5), and ten a reasonable number for three females on plot A.

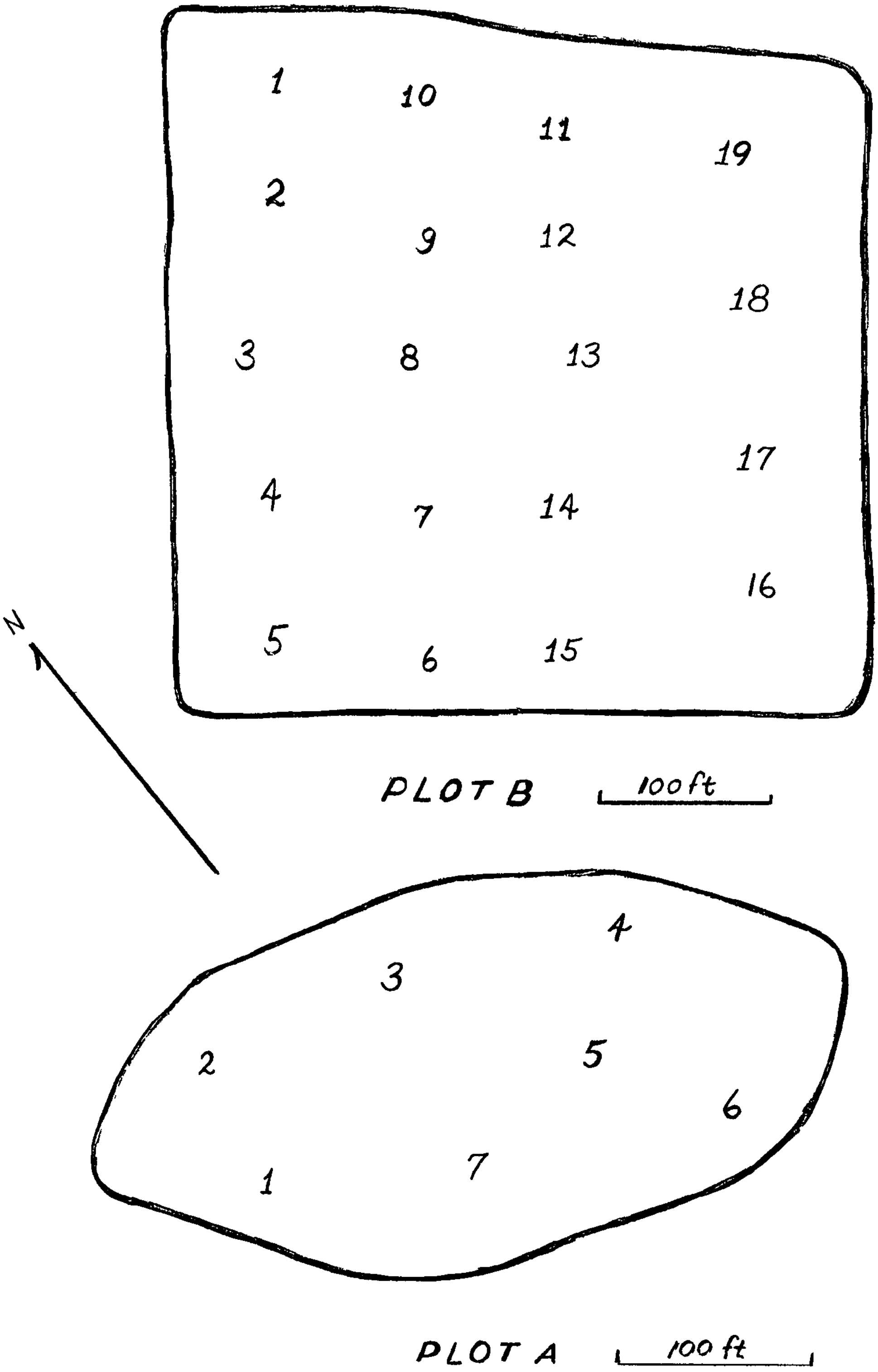


Figure 4. Diagram of plots A and B showing approximate locations of trap sites.

Table V Survival of juveniles on plots A and B when adult aggression was constant.

Plot B: Aggressive Adults

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13			
		day 4	7	11	14
May '64	1	-	6	-	5
Jun.-Jul. '64	2	7	4	4	2
Aug. '65	2	6	4	4	4
$\bar{X}$	1.75	6.5	4.7	4	3.7

Plot B: Docile Adults

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13			
		day 4	7	11	14
Jun. '64	2	10	7	3	3
Jul. '64	3	12	11	10	9
Sep. '64	3	12	12	12	12
Sep. '65	3	13	10	10	8
$\bar{X}$	2.8	11.8	10	8.8	8

Plot A: Aggressive Adults

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13			
		day 4	7	11	14
Jul. '65	3	7	4	3	1

Plot A: Docile Adults

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13			
		day 4	7	11	14
Jun. '65	1	8	4	2	1
Aug. '65	3	6	5	4	4
Oct. '65	3	8	7	7	6
$\bar{X}$	2.3	7.3	5.3	4.3	3.7

Table VI Growth rates of juveniles on plots A and B when adult aggression was constant.

Plot B: Aggressive Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
May '64		-0.7		0.0
Jun. - Jul. '64	-0.9	-0.5	1.1	3.0
Aug. '65	-0.8	1.0	1.8	2.2
$\bar{X}$	-0.85	-0.1	1.5	1.7

Plot B: Docile Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Jun. '64	-0.2	0.9	2.1	3.7
Jul. '64	-0.1	0.1	1.1	2.6
Sep. '64	0.3	0.3	2.5	2.8
Sep. '65	-0.1	0.7	0.6	1.1
$\bar{X}$	-0.02	0.5	1.6	2.6

Plot A: Aggressive Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Jul. '65	-0.6	0.0	0.7	2.6

Plot A: Docile Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Jun. '65	0.1	0.4	0.0	1.0
Aug. '65	-0.1	-0.5?		2.2
Oct. '65	0.3	0.25	0.5	2.0
$\bar{X}$	0.1	0.05	0.25	1.7

Table VII Survival of juveniles on plots A and B when adult aggression changed.

<u>Plot</u> <u>B</u>: <u>Aggressive</u>--<u>Docile</u> <u>Adults</u>

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13 day 4	7	11	14
Aug. '64	3	11	11	11	11
May '65	2	11	7	3	3
Jun. - Jul. '65	4	11	8	6	3
$\bar{X}$	3	11	8.7	6.7	6

<u>Plot</u> <u>B</u>: <u>Docile</u>--<u>Aggressive</u> <u>Adults</u>

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13 day 4	7	11	14
Jul. '65	1	7	4	3	1

<u>Plot</u> <u>A</u>: <u>Aggressive</u>--<u>Docile</u> <u>Adults</u>

Date	No. of Adults Surviving to day 14	No. of Juveniles Surviving out of 13 day 4	7	11	14
Sep. '65	3	8	7	7	7

Table VIII Growth rates of juveniles on plots A and B when adult aggression changed.

Plot B: Aggressive--Docile Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Aug. '64	-0.4	0.3	1.4	2.5
May '65	0.3	0.7	1.7	2.8
Jun. - Jul. '65	0.5	1.7	2.2	2.7
$\bar{X}$	0.1	0.9	1.8	2.7

Plot B: Docile--Aggressive Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Jul. '65	-0.9	0.1	-0.2	2.5

Plot A: Aggressive--Docile Adults

Juvenile Growth ($\bar{X}$ g.)

Date	day 4	7	11	14
Sep. '65	-0.6	-0.8	1.0	1.6

Results

The survival and growth of juveniles released onto the plots when docile adults were present was considerably better than the survival and growth of juveniles released onto the plots when aggressive adults were present (Tables V and VI). In four experiments adults which were aggressive when released were docile when retested at the end of the experiment. In one experiment adults which were docile when released were aggressive when retested. These experiments were not included in the statistical analysis. Survival and growth in these experiments were intermediate (Tables VII and VIII).

Differences in juvenile survival rates on plot B were compared in an analysis of variance; treatments were significant ($F = 140.6$ $P < 0.001$). Because few experiments were done on plot A and the results varied widely I felt that separate statistical treatment of the data from plot A would be meaningless. However, survival rates from plots A and B may be lumped and tested together in an analysis of variance. The lumped data still show that aggressive males reduce juvenile survival significantly more than docile adults do ($F = 18.5$ $P < 0.001$).

Differences in juvenile growth rates between treatments on plot B are also significant ($F = 18.3$ $P < 0.025$).

Growth rate data from plots A and B may again be lumped. When this is done the differences are still significant ($F = 4.50$ $P < 0.05$). The most striking thing about these growth rates is the great loss of weight shown during the first four days by juveniles released onto plots with an aggressive male population. This weight loss is in marked contrast to the mild loss or gain shown by juveniles released onto the plots when docile adults were present.

In experiments with docile adults, juveniles survived better in the latter part of the summer. The probability that this improvement in survival was due to chance is low ($F = 9.95$ $P < 0.01$). However, as will be pointed out later, the biological significance of such a result may be questioned.

As far as juvenile survival and growth are concerned, experiments in which aggressive adults became docile are more like experiments with docile males (Tables VII and VIII). Similarly the one experiment in which docile males became aggressive resembles an experiment with aggressive adults. Probably the changes in aggressiveness occurred very quickly. Loss of data from these experiments might have been avoided, therefore, if the adults had been retested just before the juveniles were released, as well as at the end of the experiment.

Despite the fact that densities on the isolated plots were lower than normal, owing to the loss of some of the adults, the results of the laboratory experiments were confirmed. It seems justifiable to conclude from these experiments that the aggressiveness of adults in summer reduces the survival of early litters, and that declining aggressiveness in the fall permits the rapid recruitment of juveniles at this time.

Artificial Immigration onto Trapped Out and Natural Plots

Methods

The hypothesis also predicts that, besides reducing juvenile survival, aggressive resident animals should hinder the settling of adult immigrants. The following experiments were designed to test this prediction.

The experiments were performed on two trapping grids located in the Endowment forest around the University campus. Each grid consisted of four lines of five traps with about 15 paces between each trap. Eight experiments were performed on these grids, three in 1964 and five in 1965. Early in 1965 one of the grids used in 1964 was bulldozed and a new grid had to be set up in a different part of the forest. In addition to these eight experiments three more were done in 1964 on grids half the size.

At the beginning of each experimental series the grids were trapped for five days. On one grid the trapped animals were marked and released, and on the other they were removed. At the end of the five days, six adult deermice (three males and three females) were released at the centre of each grid. The grids were retrapped four and seven days later and the survival rates of these artificial immigrants recorded. After the seventh day trapping ceased for one week, then a new experiment was begun. With each new experiment, the grid that had been trapped out in the previous experiment became the grid with the resident population and *vice versa*.

Three adults were released instead of six in the experiments using half size grids. Instead of using the same grids each time and alternating the grid which was trapped out, new grids were set out for each experiment. Otherwise the procedure on the smaller grids was the same as that outlined above.

Results

The released mice were more successful in establishing themselves on trapped out plots than on plots with resident animals (Table IX). For both trapping days the differences in the ability of mice to establish themselves on the two plots were significant (day 4, $t = 1.935$ $P < 0.05$;

Table IX Survival of animals released onto trapped out plots and onto plots with resident populations.

			No. Surviving to Day 4				No. Surviving to Day 7			
	Original No. of Residents	No. of Immigrants Released	Residents	Immigrants to Unoccupied Area	Immigrants to Occupied Area	Difference	Residents	Immigrants to Unoccupied Area	Immigrants to Occupied Area	Difference
1964										
June	6	6	5	5	1	4	5	3	1	2
July	4	6	2	1	2	-1	2	1	2	-1
Aug.	6	6	5	3	2	1	5	3	2	1
July	7	3	3	1	0	1	3	1	0	1
July	8	3	5	2	1	1	5	2	0	2
Aug.	6	3	4	2	2	0	3	2	2	0
1965										
May	4	6	3	6	5	1	3	6	3	3
June	13	6	11	3	3	0	7	2	3	-1
June	4	6	2	5	3	2	2	4	3	1
July	5	6	3	4	5	-1	3	4	1	3
Aug.	5	6	4	3	2	1	4	3	2	1
					Σ	9			Σ	12
					$\bar{X}$	0.82			$\bar{X}$	1.1
					S.E.	0.42			S.E.	0.37

day 7, $t = 2.972$ $P < 0.01$, paired sample t test).

Despite the fact that the mice were more successful in establishing themselves on the trapped out plots, a considerable number did settle down on the plots with resident populations. Not only that but some of the normal resident animals moved away after the artificial immigrants were introduced (Table IX). Flooding the grids with artificial immigrants may have caused a breakdown in the social relationships of the residents, allowing the population to reassort itself. Andrzejewski *et al* (1963) observed that introducing a large number of strangers into an established colony of white mice caused disruption of the existing population structure. Residents fought with each other as well as with the newcomers. When the colony finally settled down some of the new animals had been accepted and some of the original colony members were dead.

Homing in Peromyscus

In the 1964 tests of immigrant success, animals were sometimes moved from one plot to another. When this was done several instances of homing were observed. In fact two experiments had to be terminated because of homing. In 1965 this problem was avoided by releasing only animals which had been kept in the laboratory over the winter. The nine instances of homing observed in 1964 are reported in Table X. The most interesting part of these observations is that six of the nine mice homed after being released onto trapped out plots. The stimulus that makes a mouse home when there are no residents to hinder settling in the release area presents a perplexing problem. This sort of homing may shed some light on the social organization of natural populations and will be discussed later.

Neighbour and Stranger Responses

One of the more recent discoveries in ornithology is that a territorial bird is more tolerant of his immediate neighbours than he is of complete strangers (Stenger and Falls 1959, Falls and Brooks 1965). It seemed worthwhile to test the possibility that there is reduced antagonism between male *Peromyscus* on adjacent home ranges. Any reduction in antagonism would indicate that deermice are able to recognize at least their immediate neighbours.

Methods

Grids of live-traps were set in the forest around the campus. Males captured at the same site or adjacent sites were placed together in a neutral arena, and their behaviour recorded for 10 min. Subsequently the individual

Table X Nine instances of homing in P. m. austerus.

Sex	Days Between Initial Capture And Release	Distance Homed	Plot Type Homed From	To	Time Days (Max)
m	12	300 yd	-	-	14
m	12	300 yd	-	-	14
m	1	600 yd	+	-	4
m	3	600 yd	-	-	6
m	3	600 yd	+	-	4
m	3	600 yd	-	-	4
f	2	600 yd	-	-	4
f	2	600 yd	+	-	4
m	3	1 mile	-	-	4

- Unoccupied plot

+ Occupied plot

Table XI Mean number of aggressive responses of neighbours and strangers during 10 min bouts in a neutral arena.

Neighbours					Strangers				
N	Threat	Chase	Agg/Groom	Fight	N	Threat	Chase	Agg/Groom	Fight
11	1.73	0.45	0.00	0.27	12	6.7	0.75	1.1	0.67
Range	0-5	0-3		0-3		0-15	0-7	0-5	0-4

males were placed in the arena with a strange member of the laboratory stocks, and behaviour again recorded for 10 min. Encounters between neighbours and strangers were randomly ordered to eliminate any effects of experience in the arena. Acts recorded were: threat, chasing, fighting, aggressive grooming, grooming (friendly), naso-nasal, naso-anal, washing, exploring, and mutual upright.

Results

When encounters between neighbours were compared with encounters between strangers, it was found that only the aggressive acts showed large and consistent differences. Means and ranges for each of these acts are presented in Table XI. The aggressive acts were summed for each animal and the differences between the two groups were tested by means of a Mann-Whitney U test for ranked scores. The differences were significant ($U = 27$ $P < 0.01$).

DISCUSSION

On the basis of Sadleir's (1965) descriptive study, and the experimental work described in this paper it seems reasonable to conclude that social interaction determines population densities in <u>Peromyscus</u> <u>maniculatus</u> <u>austerus</u>. There can be little doubt that males show seasonal changes in aggressiveness, and that these changes are regulated by changing environmental conditions. Increasing aggressiveness in the spring affects population densities through intolerance for strange animals and the establishment of individual home ranges. As Sadleir (1965) suggests, early litters survive poorly because they must compete with aggressive adults for a place to live.

It might be argued that juveniles seldome die from encounters with aggressive adults in the laboratory experiments, and that this result refutes the hypothesis that aggressive adults affect juvenile survival in the field. It is easy to reconcile low mortality in laboratory experiments with high losses in field experiments when one remembers that laboratory experiments do not permit dispersal. In the field competition between adults and juveniles for space would probably result in the emigration of a lot of juveniles. Those juveniles that persisted in the field experiments grew poorly for the first few days, but later appeared to have been accepted into the population, and thereafter grew well. Only the effect of adult aggression on growth was measured in the laboratory experiments, and in this respect they agree well with the field experiments.

Intraspecific aggression in the field between small nocturnal rodents like deermice is difficult to demonstrate unequivocally. The high level of possessiveness shown by some males for a home cage, and the poor success of immigrants into natural populations are good indirect evidence for territorial defence in the field, at least between strangers. Terman (1961) made a few direct observations of the response of a resident animal to a strange animal in field enclosures. His general conclusion was that intraspecific aggression was rare. However, he was using laboratory bred stocks, and I have some indications that my own laboratory bred mice behave differently from wild mice. Whatever the method of communication between animals in the field, an animal's chance of settling in an area is affected by the aggressiveness of the resident animals. The way that aggression and the other bits of data presented above fit into the complex problem of animal interrelations in the field will be considered next.

The Social System in *Peromyscus*

The relationships between individuals in a *Peromyscus* population appear different in winter and summer. Some authors have suggested that in winter the mice live together in small family or social groups (Howard 1949, McCabe and Blanchard 1950). The evidence for such clumping is slight. However, home ranges are about the same size in winter and summer (Healey unpub.), higher numbers are present in winter, and intraspecific aggression is practically nonexistent, so clumping is not unlikely. In spring the situation changes. Generally more mice survive the winter than can live together compatibly in the breeding season, so that in spring there is a dispersal period (Sadleir 1965, McCabe and Blanchard 1950, Howard 1949). Some animals take up home ranges or territories where they overwintered, and the excess moves away. Probably the animals which settle down at once are either the adults resident there in the fall of the preceding year, or their progeny. Success in settling no doubt depends on an animal's ability to achieve social dominance over its winter mates. The dispersal period produces a settled breeding population and a wandering group. Wanderers probably do not take part in breeding and are more vulnerable to predators.

The maintenance of the balance between residents and wanderers presents an interesting problem. We know from laboratory studies that several factors impart a social advantage to an animal. These are: (1) past successes in intraspecific encounters (Scott and Frederickson 1951), (2) sexual maturity (Beeman 1947), (3) familiarity with the area where the encounter takes place (Petrusewicz 1959, Barnett 1964, this study), (4) presence of familiar animals (Petrusewicz 1959). The settled animal possesses all four of these. By winning the right to settle he has presumably been successful more often than not in intraspecific combat.

He has the advantage of familiar surroundings, sexual maturity, and familiar neighbours. Wanderers have only sexual maturity in their favour, and so are at a disadvantage in competition with residents. Weanlings are at the bottom of the list, possessing no social advantage at all. If a territory becomes vacant, therefore, a wanderer would have a better chance of taking over than a weanling. On the other hand, in the absence of a wanderer it should be possible for a weanling to set up permanent residence in a vacant territory. In this scheme wanderers represent genes dispersing through the population which can contribute to the gene pool only if they find a place to settle.

Because an animal in a resident population possesses a psychological and reproductive advantage over wandering members of the population, gaining resident status must be very desirable to the wanderer. Also the resident animal displaced from his normal population niche should suffer anxiety and show appetitive behaviour directed toward regaining familiar surroundings. Such appetitive behaviour would explain the homing from trapped out plots observed in 1964.

There is some additional evidence in support of the social system outlined above for Peromyscus maniculatus. Dr. Paul Anderson (pers. com.) has suggested that in the population of house mice he studied on Great Gull Island (Anderson *et al* 1964) juveniles were more likely to be reproductively successful if they settled near their birth place. Rasmussen (1964) has evidence that gene flow through a continuous population of *P. maniculatus* is restricted, and that the actual panmictic unit is small (10-75 animals). This unit is tiny compared with the dispersal capabilities of deermice, and indicates that an animal's chances of breeding are severely limited when it moves any distance from its birth place.

It is important for an animal to gain resident status, but established animals resist the settling of strangers, so that some sort of competitive interaction must occur between residents and animals which are looking for a place to settle. However, a high level of interaction among established animals would waste energy. The measurement of interaction between neighbour animals and strangers indicated that interaction between neighbouring animals is inhibited. The social unit then comprises an animal and its neighbours, among whom mutual aggression is reduced, and whose range boundaries are maintained by habit and mutual avoidance.

The social system described does not exclude the possibility of a wanderer supplanting a resident; it merely makes it extremely unlikely. In experiments where immigrants were released onto a grid with a resident population, the sudden influx of a lot of strange animals caused a population reshuffle with some of the established residents moving out and some of the released animals settling in. These experiments probably represent extreme cases of interaction between residents and wanderers, since wanderers seldom arrive in large groups. The reshuffles did show that there is a degree of variability in the optimum summer population, making it even more likely that summer populations are controlled by behaviour rather than some quality of the environment.

Although adult aggression is important in regulating population density, other factors may be operating as well. When juveniles are released onto plots with docile residents one would expect that chance mortality factors would cause wide variability in survival. The survival of juveniles released onto plots with aggressive residents should be uniformly low. This is what happened. However, on both plots A and B in experiments with docile residents the survival of juveniles improved progressively from spring to fall. Poor juvenile survival in the spring even with docile residents suggests that other factors associated with season may be operating to enhance the effects of aggressive behaviour; factors which may or may not be associated with behaviour.

Up to this point females have been ignored. No careful quantitative study was made of the effects of females on juveniles. However, there is some evidence that their responses to strange animals are similar to the responses of the males. Females occupy individual home ranges in the summer, as do the males. If male and female home ranges are plotted separately, male home ranges are mutually exclusive, and so are female home ranges. However, a male and a female home range may overlap completely (Burt 1940, Stickel 1960). There is probably competition within sexes for space, then, but no, or very little competition between sexes. Like males, female *P. m. austerus* will defend a home cage against a stranger of the same sex. This contradicts Eisenberg's (1962) observation that during induced territorial conflict between pairs of *Peromyscus* the females play a passive role while the males fight. Nevertheless I have observed that when females are alone many show a high level of cage possessiveness. Female aggressive postures are quite similar to those of the male. The resident social group probably behaves as a unit then, with males repulsing strange males and females repulsing strange females, but with intragroup aggression inhibited in the interest of economy.

The Selective Advantage of the Self-Regulatory System

The fact that self-regulatory systems have evolved suggests that they must give some advantage to the species. However, what advantage there is in a system that regularly destroys most of the yearly production of new animals presents a problem. Weather, predators, parasites, in fact the whole milieu of a population affects numbers and survival. But are these alone sufficient to regulate population density within permissible limits? I doubt it. To be successful a species must be able to survive the bad years as well as the good years. In order to do this the reproductive potential of the animals must be geared to the infrequent catastrophic event. The population cannot predict in advance a harsh winter, or a sudden influx of predators, or an outbreak of disease. Consequently the populations must provide a buffer of excess animals on the off chance that a random catastrophe will occur. However, the population must not over exploit its habitat during the good years either.

I shall consider only the situation in *Peromyscus*, although the example probably holds for small mammals in general (Chitty 1964, King 1955), and with modification for all populations (Chapman 1962, Wynne-Edwards 1962). During most of the breeding season numbers are low, and the buffer to any local catastrophe is the continuous production of new animals. But towards the end of the breeding season a rapid recruitment of juveniles takes place. This recruitment provides the buffer for any random catastrophe over the long non-breeding season. Depending on the winter and chance there are three possible situations which may exist in local populations in the spring.

(1) In most years winter mortality is low so that many more animals are present in spring than can be socially compatible in the breeding season.

(2) Mortality may reduce the population to some number which can form a socially compatible breeding population.

(3) Mortality may reduce the population to the point that too few animals are present to exploit the habitat efficiently.

If situation (1) obtains dispersal must occur, presumably with the most socially dominant animals settling down and their less fortunate winter mates moving away. It is this spring dispersal period which ensures that animals never become abundant enough to over-exploit the environment.

In situation (2) no dispersal would occur, and the residents would allow no immigrants to settle.

If situation (3) occurs then either immigrants will come in from adjacent areas or early litters will survive to bring the number of animals back up to a level which can efficiently exploit all the habitat.

The point is, that in order to prevent extinction during years of high mortality the reproductive potential of the animals must be high, and some sort of mechanism must be evolved to get rid of the excess during years of low mortality. This mechanism must be intrinsic to the population. In deermice it is dispersal and presumably the death of most of the excess. The mechanism could well be exclusion of the excess from breeding sites (Carrick 1963), or some physiological mechanism to prevent breeding and so allow natural mortality to reduce numbers (Crowcroft and Rowe 1958). Whatever the mechanism it must operate through social interaction.

SUMMARY

1. In a recent paper Sadleir (1965) proposes that the survival rate of juvenile Peromyscus maniculatus is determined by adult aggressiveness.

2. Sadleir's data on the seasonal changes in male aggressiveness were retested and confirmed. In addition, laboratory experiments showed that adults on home ground

inhibit juvenile growth while adults on neutral ground do not; that males have a greater effect in this regard than females; and that aggressive males inhibit juvenile growth but docile males do not.

3. Aggressive males were shown to be spontaneously more active than docile males. This trait may serve to increase the number of contacts between aggressive males and weanling juveniles in the field.

4. The survival of juveniles in competition with aggressive or docile males was studied experimentally in the field. Aggressive males had a significantly greater effect on juvenile growth and survival than did docile males.

5. The survival of artificial immigrants onto trapped out plots was compared with the survival of artificial immigrants onto plots with resident populations. Survival was significantly better on trapped out plots, indicating that resident animals resist the establishment of newcomers.

6. Nine instances of homing were noted; in six of the nine instances animals homed from trapped out plots.

7. The amount of aggression between animals from adjacent home ranges was much less than the aggression between animals which had never encountered each other. Animals from adjacent home ranges are probably familiar with

one another, and maintain home range boundaries through mutual avoidance rather than overt aggression.

8. It is proposed that during the breeding season an animal and his immediate neighbours act as an organized social unit. Aggression between members of the unit is reduced to conserve energy, but each animal shows aggression toward any strange animal attempting to settle within his home range. The function of such aggression would be to keep numbers of mice within certain limits. The selective advantage of such a self-regulatory mechanism is discussed.

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Appendix I

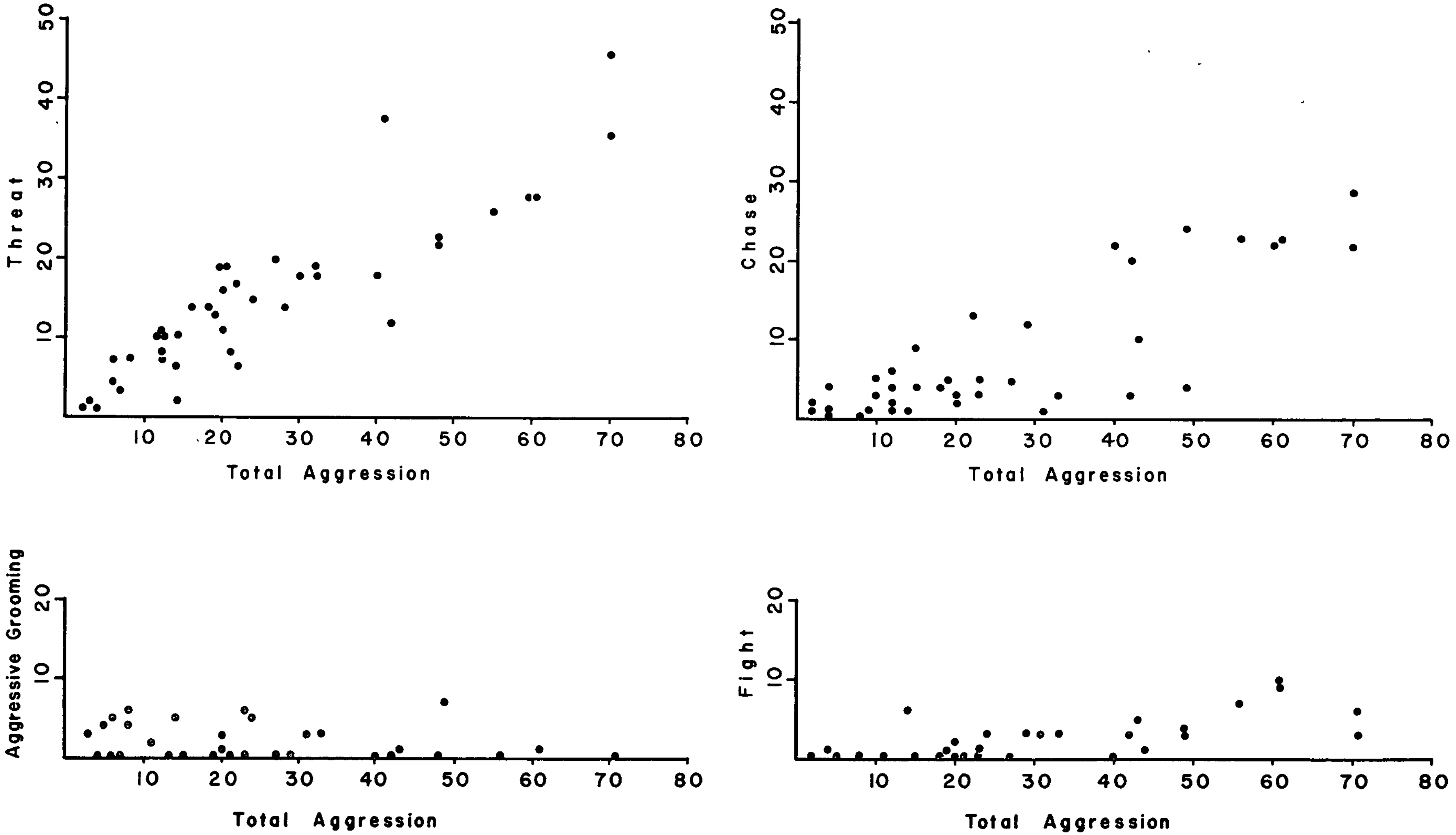
The graded series is a group of males originally established by Dr. Sadleir to be used as a standard in measuring the aggressiveness of his field-caught animals. Every member of the series was matched against every other member in a neutral arena, and the number of aggressive acts performed in 10 min. was recorded. These data were used to rank the males in order of aggressiveness.

Tests of aggressiveness in this study generally involved an experimental male on home ground with a member of the graded series used as an intruder. For such a test to be reliable the members of the graded series must maintain a constant level of aggressiveness and the responses of the experimental male must not be influenced by the behaviour of the introduced animal. It is improbable that either of these two conditions is fulfilled by the graded series. The aggressiveness of the graded series no doubt changes as the animals age and suffer more and more social defeats in the experimental encounters, to say nothing of possible endogenous seasonal and diurnal changes in behaviour. Any bias of this sort was partly offset by periodically retesting the members of the graded series against one another. They maintained their relative positions of dominance, although the amount of aggression each male showed fluctuated considerably. As the original members of the series aged they were replaced by laboratory-reared males. The range of aggressiveness within the series of laboratory-reared males was less than within the series of wild-caught males. I feel the laboratory-reared animals maintained their individual levels of aggressiveness better too. It is impossible to eliminate the effects of the introduced animal on the behaviour of the experimental animal. After one became familiar with the graded series, though, it was possible to recognize such effects and compensate for them with additional encounters. Multiple encounters added little to the precision with which aggressive or docile animals were selected, however. In more than 90% of the tests performed the results of the first encounter were confirmed in subsequent encounters.

Appendix II

In the behavioural repertoire of the male, threat behaviour, chasing, fighting, and aggressive grooming may be regarded as good indicators of aggressive interaction. The question is, which of these acts, or what combination of them, is the most sensitive indicator of aggressiveness in males? This question was partly answered by plotting each act against the sum of all four acts for each bout. Data from the control series in the experiments on seasonal

Figure 5. Relationship between four aggressive acts and total aggression.



changes in aggressiveness were used. The four resulting scatter diagrams are shown in Fig. 5. Only threats and chases show a consistent relation to total aggression, hence the sum of threats and chases was chosen as an index of aggressiveness.