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METHODS & DESIGNS

The use of muroid rodents in the psychology laboratory*

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The rodent superfamily Muroidea represents a group of animals with much potential for comparative behavioral study as they are readily acquired, easy to maintain, and exist with sufficient ecological and behavioral diversity to enhance the likelihood of significant results. The superfamily includes Old World rodents, gerbils, hamsters, and a considerable variety of New World rats, mice, and voles which inhabit all 48 adjacent United States. Potential uses of muroid rodents, their taxonomy, and their husbandry are described with particular reference to the 28 species that have been maintained in the author's laboratory. Although research on muroid behavior is just beginning, available data already support the proposed utility of these animals in behavioral research.

The Muroidea are a superfamily of rodents of diverse habits and distribution including many species of rats, mice, hamsters, gerbils, and lemmings. Many species are easy to handle and quite adaptable to the laboratory. The goals of the present paper are, (a) to suggest the use of native muroid rodents as a solution to many methodological problems of the animal psychology laboratory, (b) to describe the muroid rodents, their care and maintenance, and (c) to present some representative results obtained using muroid rodents as Ss. While various papers regarding the advantages, care, and maintenance of single species are available in the psychological literature (e.g., Thiessen, 1968; Boice, 1971), there has been no comparable comprehensive treatment of the muroid species—particularly those native to the 48 adjacent Unites States.

MUROID RODENTS IN THE PSYCHOLOGY LABORATORY

The author has argued that use or nonuse of the comparative method and the selection of species for research are a function of the problem under study and the generalizations which the investigator plans to make (Dewsbury, 1973a). Thus, studies utilizing just one species, such as laboratory rats, pigeons, or rhesus monkeys, are appropriate and fully adequate for many experimental purposes. However, there are other experimental purposes which require, or can be strengthened through the use of either an alternate species or a cluster of species. It is for these situations that the muroid rodents possess particular advantages. Three situations will be discussed: single species utilization, comparisons within muroids, and comparisons with other taxa.

Single Species Utilization

There are many reasons for the use of a species other than one of the standard laboratory species. One may simply wish to test the generality of a phenomenon characteristic of a laboratory species on another kind of organism. Alternatively, one may need to study a species that has not been subjected to the many generations of selective breeding that have characterized many laboratory species (see Lockard, 1968). This is particularly important when generalizations are to be made regarding behavior in the natural habitat or the adaptive significance of behavior. Finally, a species may have some particular advantage as an experimental animal because of some unique attribute of that species. The classical example is the utilization of the squid giant axon for studies of nerve physiology. Among muroids, the midventral sebaceous gland and associated behavior in gerbils has been well utilized as an experimental preparation (e.g., Thiessen, 1968).

While the above reasons suggest that alternate species may be appropriate for theoretical purposes, the practicing animal psychologist must deal with the realities of budgets and equipment. Thus, while suggestions regarding adoption of alternate species appear attractive, he may find it impossible to obtain and to maintain appropriate numbers of the exotic species the biologist is liable to suggest. Further, he may have a heavy investment in operant chambers, runways, running wheels, etc., which are appropriate for small rodents. In short, while the use of an alternate species sounds attractive, their use often appears impractical. Because of their availability, size, and ease of maintenance, the muroid rodents represent a group of animals which contain species that may be both appropriate for many purposes and highly practical.

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Comparisons Within Muroids

In addition to the use of single alternate species, comparisons among different species often can be invaluable in elucidating general principles (see Dewsbury & Rethlingshafer, 1973). King (1963, 1970a) has suggested that comparisons can be made at three levels: the genetic level, the phyletic level, and the species level. At the genetic level, comparisons are made among organisms of differing genotypes, but of the same species (siblings, strains, breeds, races, etc.). This level of comparison has been quite fruitful in behavior-genetic analyses. The most common comparisons in comparative psychology have been at the phyletic level–comparisons among genera, families, orders, classes, and phyla. King (1970a) believes that while this level of comparison can accasionally elucidate general principles, "It is the dead end which too often characterizes comparative psychology [p. 7]." King (1970a) suggests that the advantages of species level comparisons, those among closely related species, render such comparisons optimal for many purposes. At this level of comparison, species differences may be quite clear, but the species are not so diverse that it is impossible to relate these differences to particular factors.

While the practicing animal psychologist may wish to make species-level comparisons, he again is faced with the practical problems of acquisition, maintenance, and instrumentation. Muroid rodents, and various groups within the muroid rodents, are closely related and highly similar in many respects, but have diverged and adapted to many habitats and life styles. Thus, in addition to the advantages cited above, they have the advantage of the availability of a large number of diverse, yet closely related species. Many ecological data are available and more can be collected as the species are native to the United States and readily studied.

Comparisons with Other Taxa

Some comparative psychologists maintain phyletic level comparisons as a major goal (e.g., Lester, 1973). While comparisons among single species can be valuable for some purposes (e.g., Bitterman, 1965), comparisons of groups of species may be more enlightening for other purposes: "Instead of comparing one ape to an Old World Monkey or one monkey to an insectivore, one should sample numerous species of each. As more species of a group are examined, it may be possible to understand its general pattern . . . Comparison between the two (or more) clusters of species will, in any case, facilitate separation of joint inheritance of inadaptive or generally adaptive features from those that reflect the functions under particular investigation [Gans, 1969, p. 509]."

Once more, the availability and ease of maintenance of a variety of muroid rodents makes the accumulation of at least one species cluster quite practical for the working animal psychologist.

Although the rodent line diverged from that leading to man a long time ago, rodents can be extremely useful in establishing general principles of behavior. Thus, whether one is searching for a single alternate species, for a group of species within which comparisons can be made, or for a cluster of species for phyletic comparisons, the muroid rodents have considerable potential for the psychology laboratory.

AN INTRODUCTION TO THE MUROID RODENTS

Taxonomy

The order Rodentia of the chordate class Mammalia is divided into three suborders, the Sciuromorpha (squirrels, kangaroo rats, beavers, etc.), Myomorpha (including muroid rodents), and Hystricomorpha (porcupines, guinea pigs, chinchillas, etc.) (Morris, 1965). The Muroidea are by far the largest of the three superfamilies of the Myomorpha. The muroid rodents have traditionally been divided into two families, the Cricetidae and the Muridae. The Cricetidae are predominantly New World rodents and include deer mice, wood rats, voles, and lemmings. The Muridae are predominantly Old World rodents and include the popular laboratory genera *Rattus* and *Mus*, in addition to a considerable variety of Old World rats and mice.

Of the 1,729 species of rodents listed by Morris (1965), 1,183 are Myomorpha. Morris lists 105 genera of cricetid rodents and 106 genera of murid rodents. The largest of the cricetid genera are *Oryzomys* or rice rats (68 species), *Peromyscus* or white-footed mice (57 species), *Microtus* or field voles (42 species), and *Gerbillus* or smaller gerbils (37 species). The largest murid genera are *Rattus* or rats (137 species), *Mus* or house mice (27 species), and *Melomys* or banana rats (25 species). Within a single species, such as *Mus musculus*, there may be many strains or subspecies. The taxonomic diversity of the muroid rodents is indeed considerable.

This paper will concentrate on the 28 species of muroid rodents that are being or have been maintained in the author's laboratory. The taxonomy of these species is summarized in Table 1.

It should be noted that whether a muroid rodent is called a "rat" or a "mouse" is more a function of size than of taxonomy. For example, rice rats and deer mice are both New World (cricetid) rodents, whereas Norway rats and house mice are both Old World (murid) rodents. Thus, the label "rat" or "mouse" provides little clue to the taxonomic status or distribution of a species.

As with many groups, the taxonomy of muroid rodents is in flux. For example, Hooper and Musser (1964), basing their conclusions primarily on a study of the morphology of the male phallus in a large number of species, suggested that the division of the muroids into two families is outdated. Rather, the two families "belong together morphologically and probably derive from one and the same ancestral stock [p. 50]." Hooper and Musser suggest that rather than two families, the muroids contain six "assemblages" of a taxonomic level

Table 1
Taxonomy of Muroid Rodent Species Studied in the Author's Laboratory

Common Name	Genus and Species	Family	Hooper Assemblage
Norway rat	*Rattus norvegicus*	Muridae	I
House mouse	*Mus musculus*	Muridae	I
Mongolian gerbil	*Meriones unguiculatus*	Cricetidae	II
Montane vole	*Microtus montanus*	Cricetidae	III
Meadow vole	*Microtus pennsylvanicus*	Cricetidae	III
Prairie vole	*Microtus ochrogaster*	Cricetidae	III
Golden hamster	*Mesocricetus auratus*	Cricetidae	IV
Cotton rat	*Sigmodon hispidus*	Cricetidae	V
Rice rat	*Oryzomys palustris*	Cricetidae	V
Western harvest mouse	*Reithrodontomys megalotis*	Cricetidae	VI
Cactus mouse	*Peromyscus eremicus*	Cricetidae	VI
California mouse	*Peromyscus californicus*	Cricetidae	VI
Canyon mouse	*Peromyscus crinitus*	Cricetidae	VI
Oldfield mouse	*Peromyscus polionotus*	Cricetidae	VI
White-footed mouse	*Peromyscus leucopus*	Cricetidae	VI
Cotton mouse	*Peromyscus gossypinus*	Cricetidae	VI
Guatemalan deer mouse	*Peromyscus guatemalensis*	Cricetidae	VI
Florida mouse	*Peromyscus floridanus*	Cricetidae	VI
Golden mouse	*Ochrotomys nuttalli*	Cricetidae	VI
Northerm pygmy mouse	*Baiomys taylori*	Cricetidae	VI
Southern grasshopper mouse	*Onychomys torridus*	Cricetidae	VI
Northern grasshopper mouse	*Onychomys leucogaster*	Cricetidae	VI
White-throated wood rat	*Neotoma albigula*	Cricetidae	VI
Desert wood rat	*Neotoma lepida*	Cricetidae	VI
Eastern wood rat	*Neotoma floridana*	Cricetidae	VI
Climbing rat	*Tylomys nudicaudus*	Cricetidae	VI
Climbing rat	*Ototylomys phyllotis*	Cricetidae	VI
Alston's brown mouse	*Scotinomys teguina*	Cricetidae	VI

yet to be assigned. These include the cricetines (hamsters), microtines (voles and lemmings), South American cricetines (e.g., cotton rats and rice rats), gerbillines (gerbils), murines (Muridae), and neotomynes-peromyscines (e.g., wood rats and white-footed mice). The appropriate assemblage for each species is indicated in Table 1. While the present paper is concentrated on New World "cricetid" species, the broader term, muroid, is used in view of these developments in taxonomy.

Information Sources

There are many excellent sources of information regarding native muroid rodents. Walker's (1964) *Mammals of the World* provides an overview of each genus. The "bible" for North American mammals in Hall and Kelson (1959). Hall and Kelson provide keys for the identification of species, range maps showing the locations in which each species is to be found, and brief summaries of the characteristics of the various North American rodents. A field guide, such as that of Burt and Grossenheider (1964) can be quite useful. For most areas, there exist books describing the local mammalian fauna, usually under the title of "Mammals of . . . " (e.g., Bailey, 1931; Hoffmeister & Mohr, 1957; Hoffmeister, 1971; Doutt, Heppenstall, & Guilday, 1967). More detailed information can be found in the usual assortment of specialized books and journal articles. The *Zoological Record* provides a particularly complete source for a literature survey of any particular species.

Background Information

Evaluation of New World muroids for psychological research requires some understanding of their characteristics and habits. Perhaps the genus with most research potential is the genus *Peromyscus*. An excellent review of the genus is provided in King (1968). One or more of the 57 species and 235 subspecies of *Peromyscus* occurs in each of the 48 adjacent states. The Southwest is particularly rich in *Peromyscus*. There are seven subgenera. Within these groups, different species often are interfertile in the laboratory. The potential for research on behavioral development in such cross-species hybrids has not been appreciably tapped. *Peromyscus* impress the O as bright, alert, clean animals with big eyes and big ears. They are generally nocturnal and quite active. Some species breed well in captivity (Drickamer & Vestal, 1973). Their ease of acquisition and maintenance, general alertness, and range of ecological diversification render *Peromyscus* ideal Ss for research (e.g., Southwick, 1964).

Microtus impress the O as less clean and less alert than *Peromyscus*. They generally appear slower and less active. Whereas *Peromyscus* often are found in woods, forests, and trees, *Microtus* are primarily creatures of grasslands. Some of the disadvantages of *Microtus* are offset by their reproductive potential. As in rabbits, cats, and short-tailed shrews, ovulation in *Microtus* is copulation induced. In the natural habitat, voles are noted for marked cycles in breeding and population size, including virtual population explosions. In the laboratory, they are easily and routinely bred and maintained. Maser and Storm (1970) provide an excellent summary of Northwestern microtines.

Wood rats, pack rats, or trade rats of the genus *Neotoma* are of rat size, but otherwise resemble *Peromyscus*. In the natural habitat, they generally build elaborate houses, to which they carry a wide array of objects. They are hard to handle, but may provide an excellent contrast to animals of other genera.

A considerable array of simple baculum muroids (Hooper assemblage VI) is native to the United States. Golden mice are a semiarboreal species native to southeastern United States. Climbing rats and brown mice are of Central American origin and difficult to obtain. Pygmy mice are probably the smallest muroids and are native to Mexico and the Southwest. The two southwestern species of the grasshopper mice (*Onychomys*) are of particular interest. The bulk of their diet is provided by animal material. They are known to stalk mice and to kill them by gnawing through the brainstem at the base of the skull (see Clark, 1962). They emit a high-pitched call which poetic writers liken to the cry of wolves. The carnivorous habits of grasshopper mice provide an excellent source for study of characteristics in convergent evolution of carnivory.

Cotton rats and rice rats are generally field dwellers which use runways and are found through much of the South. We have trapped the two species in the same trapline in and around Gainesville.

Gerbils and hamsters are not native to the United States but are excellent Ss for much research. Information on their maintenance is widely distributed. Both Norway rats and house mice exist as laboratory strains and in the wild. There are many advantages to comparing the behavior of wild-trapped animals to that of animals that have been in the laboratory for many generations (e.g., Price, 1972). Techniques for work with wild rats were described by Boice (1971). Techniques described below are appropriate for wild *Mus musculus*, with which we have worked.

HUSBANDRY

Acquisition, care, and experimentation with native muroids require little more effort than work with laboratory forms. Most are inexpensive, hardy, and easy to maintain.

Acquisition

Animals can be obtained by trapping, through purchase, or as gifts. Trapping is feasible and less difficult than imagined by the laboratory scientist. For example, with no prior background, we have trapped eight species within the State of Florida. One should check with the State Board of Conservation to determine whether a collector's permit is required. Many kinds of traps are available and will work for different species. Sherman traps (H. B. Sherman Co., DeLand Fla.) work particularly well for all native species except wood rats. These traps are inexpensive and easy to use. Folding models of aluminum are ideal where traps are to be transported over rough terrain. More sturdy traps of 40 lb tin or galvanized iron may be better if strength is important, as in trapping in fields where livestock may step on traps. Results appear best when the size of trap is varied to fit the size of the target species. Traps appropriate for larger muroids, such as wood rats and Norway rats are described by Boice (1971).

Familiarity with the natural history of the species can be of great help in trapping. The published literature and local mammalogists are of great help. As most species show population cycles, one is best trapping during a season when aniamals are plentiful. Ideally, food should be scarce. In hot weather, it may be necessary to set traps in the evening and pick them up in the morning. Rodents can easily die in hot traps during a day. Care should be exercised in the placement of traps. For field dwelling species, such as cotton rats and voles, they may be most effective when placed near burrows, old logs, dead stumps, etc. The combination of peanut butter and rolled oats is an effective bait for muroid rodents (see Patric, 1970).

Few firms have nondomesticated rodents for sale. We have purchased animals from the following two firms: The Pet Corral, 4146 Oracle Road, Tucson, Arizona 85705, and Ecodynamics, Inc., 82 West Louise Avenue, Salt Lake City, Utah 84115. The booklet *Animals for Research,* published by the National Academy of Sciences and revised periodically, provides a list of suppliers of all species.

Many zoologists either maintain a colony of a particular species or routinely trap in regions they inhabit. We have found them most cooperative in providing animals once they were convinced of our seriousness of purpose and preparation. The program of the author's laboratory would be impossible without the generous cooperation of individuals throughout the country who have been helpful in providing animals.

Maintenance

Small native muroids, those referred to as "mice" or voles, are easily housed in solid bottom cages. Many investigators use one of various styles of plastic cages. Maryland Plastics Inc. (9 East 37th St., New York, N.Y. 10016). Series 20 cages (11½ x 7¼ x 5 in.) are inexpensive and excellent for housing these animals. Wire mesh lids (E-0280) are necessary for *Baiomys* and other very small species which can escape through the straight wire lids. Series 30 cages (19 x 10½ x 5-1/8 in.) are excellent for breeding these animals. Both sizes of cage are available in a variety of materials, varying in strength, transparency, and price.

Larger species (cotton rats, rice rats, wood rats, etc.) can be maintained in the Series 30 cages. However, we prefer larger cages and have had success with Maryland Plastics Series 70 cages (20 x 16 x 8½ in.) and with Wahmann LC-66 metal cages (20 x 22 x 14 in.). The latter have the advantage of removable partitions between cages so that social encounters can be staged without handling the animals. We have maintained small native muroids in standard hanging cages (Wahmann LC-75/A), but prefer the solid-bottom cages.

The low mortality rate among eastern woodrats in our laboratory contrasts with that of Powell (1973) and may be attributable to the larger cages in which ours are housed. Animals originated from the same wild population in Vero Beach, Florida.

Standard litter materials are appropriate for solid-bottom cages. We use San-i-Cel (Paxton Processing Co., Paxton, Ill.) routinely and with good success. Wood shavings are better for *Scotinomys* and appear acceptable for other species.

Nesting material is provided for all species. "Nestlets" (Ancare Corp., 47 Manhasset Avenue, Manhasset, N.Y. 11030) are small pads of nesting material that are easy to store and handle; also, they are readily shredded by most species. For those species that do not shred Nestlets, unbleached blended cotton felt batting material can be obtained from an upholsterer or upholstery supply house. Stringy bedding material, such as medical grade absorbent cotton, should generally be avoided. The fibers can get wrapped around the hindleg above the ankle of adults or around the necks of pups, thus eliminating circulation from distal areas and causing unnecessary suffering. Nest jars, cans, or boxes may be helpful in work with some species.

We provide water for all species, although at least gerbils are reported to do well without a source of water. All species drink from standard water bottles. Purina Lab Chow is our standard food. Montane voles and prairie voles are fed Purina Rabbit Chow. Lettuce, fresh fruit, or rolled oats sometimes are used to supplement the diet. Such food supplementation may not be necessary for most species, but does appear to improve health and reproduction in others, particularly voles. *Scotinomys* require a special diet of Purina Cat Chow and mealworms (Hooper, personal communication).

Handling

Techniques for handling the larger species were described by Boice (1971) and Powell (1973). The metal mesh safety gloves described by Boice are useful with woodrats and others of the larger rat species. Thick gloves are essential and a net may prove useful.

An advantage of the smaller species is their ease of handling. Although we prefer a thin cotton glove for work with these animals, they can be handled with bare hands. Most of the native "mice" are fairly docile and easy to handle. The only problem comes with their speed of movement. Virtually all of the movements of native muroids appear faster than those of laboratory species. After working with these species, laboratory animals appear terribly sluggish. In order to minimize escapes, we transfer the entire cage to a larger container before opening it. Then, if the animal escapes, it cannot get beyond the container. A large aquarium or wooden box serves well. A few Sherman traps are kept set in the colony room for the occasional escapee.

Breeding

For breeding, we generally house animals as pairs in relatively large cages. As most muroid species display an estrous period soon after giving birth, permanent pairing can greatly increase productivity as one litter will be developing *in utero* while another is being nursed. Extra space appears to increase the likelihood of successful breeding. Solid-bottom cages are helpful for the rearing of young. A harem arrangement, in which one male is housed with several females, has proven useful with *Microtus.*

Photoperiod is a critical variable with long daylengths most effective for most species. Thus, a 14:10 or a 16:8 regime of white light may promote breeding. Attempts should be made to minimize inbreeding. Good record keeping is essential. Ages of first breeding vary greatly across species. This and other information regarding reproductive physiology in these species is provided by Asdell (1964).

Good nutrition and freedom from disturbance are critical determinants of good breeding.

The best age for weaning should be determined for each species. Weaning too late can result in the presence of two litters simultaneously. Species such as *Scotinomys teguina* and *Baiomys taylori* may destroy the first litter. Development of the second litter may be retarded in species such as *Microtus.*

Overall, we have had good success breeding *Microtus,* cactus mice, white-footed mice, cotton mice, and grasshopper mice. Our California mice breed well but tend to lose litters. Deer mice (*Peromyscus maniculatus*) breed well and probably are the native muroid most frequently used in laboratory research.

Experimental Methods

Most of the experimental methods appropriate for laboratory animals appear applicable to work with native muroids. They will run in wheels, learn mazes, learn operant tasks, etc. While some kinds of apparatus may have to be scaled to suit the size of the animal, smaller muroids will perform in many experimental situations designed for work with laboratory rats.

Sequential injections of estradiol benzoate and progesterone, developed for work with laboratory rats, generally are effective in bringing females of these species into behavioral estrus. It should be noted that these hormones also provide effective contraception, and thus cannot be used as a short-cut for breeding. In our laboratory in thousands of successful mating tests using these exogenous hormones, no female has ever produced a litter.

REPRESENTATIVE RESULTS OF WORK WITH NATIVE MUROIDS

The proof of the utility of a species or species group lies not in theory or in potential, but in the nature of the data that can be generated. While comparatively little behavioral research has been conducted on native muroids, some interesting results already are available. A few will be presented. Such results often produce evidence for a similarity or difference between laboratory species and native muroids. Results are particularly interesting when these results bear on general principles and when conclusions are testable.

Karczmar, Scudder, and their colleagues are conducting a program of drug research utilizing a sample of muroid species including *Mus musculus, Peromyscus maniculatus, Reithrodontomys raviventris, Onychomys leucogaster,* and *Microtus ochrogaster* (e.g., Scudder, Karczmar, Everett, Gibson, & Rifkin, 1966; Richardson, Karczmar, & Scudder, 1972). They are attempting to relate differential responsiveness to drugs to the differing brain levels of biogenic amines which characterize these different species.

In a series of studies, Layne (1969, 1970, 1971; Layne & Ehrhart, 1970) has shown that behavioral characteristics of various species of *Peromyscus* in the laboratory can be related to their natural habitat. For example, *P. floridanus* is nocturnal, a poorer digger, a poorer climber, and a poorer nest builder than *P. gossypinus.* These characteristics appear related to the adoption by *P. floridanus* of burrow nesting habits in warm, xeric climatic conditions. They tend to adopt the burrows of other species. King (1970a, b) has conducted an extensive program on vision and light reinforcement in different taxa of *Peromyscus,* and has related light reinforcement to experiential and ecological factors.

Kavanau (1967) reported results of behavioral research using relatively complex tasks and instrumentation on *Peromyscus.* Several interesting phenomena were revealed that had not been apparent with other species. For example, captive animals appear to "counteract or avoid unexpected and nonvolitional deviations from the status quo [p. 1624]." The fact that an animal can act to counter a change imposed externally may be more important than the nature of the stimulus or the direction of the change produced by the animal's response. Kavanau found that mice prefer running in complex wheels, wheels that were square or contained barriers, to the standard running wheels. *Peromyscus* were able to master very complex operant regimes and mazes with relative ease. Logan and Boice (1969) studied the aggressive behaviors of a variety of paired rodents in the avoidance context. Inclusion of a variety of muroids assured generality of proposed phenomena. The hoarding behavior of 11 species of muroids has been studied in the author's laboratory (Lanier, Estep, & Dewsbury, submitted for publication). Hoarding of different foodstuffs and under both deprivation and nondeprivation conditions appeared related to field behavior.

The primary function of the author's laboratory is the study of copulatory behavior. Dewsbury (1972a, b) has proposed that mammalian copulatory patterns can be characterized according to whether or not (a) they have a lock or mechanical tie, (b) there is intravaginal thrusting, (c) multiple ejaculations occur, and (d) multiple intromissions are prerequisite for ejaculation. While most laboratory rodent research has been done on rats, guinea pigs, and house mice, copulatory behavior in 22 muroid species has been observed in this laboratory. A vast diversity of behavioral patterns has been found. Six species in four genera have been found to lock during copulation. Some species ejaculate on a single insertion while most do not, and others have intravaginal thrusting while many do not. Several species continue to copulate, sometimes with a different stereotyped pattern, long after the last sperm of an episode have been transferred. The range of patterns within such a restricted taxon is indeed great.

A real test for the student of behavioral evolution is to attempt to relate behavioral differences to ecological and morphological factors in order to elucidate general principles of evolution and adaptation. The tendency of simple-baculum muroids to lock or thrust appears related to the morphology of the male penis (Dewsbury, submitted for publication). Species which lock or thrust have relatively thicker penes than those which do neither. This is a post hoc correlation. However, with a group of animals like the muroids, it is a testable hypothesis. New species can be tested and the proposed correlation evaluated. With such a wealth of available species, the dead end of post hoc correlational interpretations of species differences can be avoided. This is an important methodological advantage in this area of research. Species which lock all tend to have relatively safe nesting places. Again, the generality of this proposal is testable with the addition of new muroid species.

While the goal of the present program is the elaboration of principles related to behavioral evolution and adaptation, the existence of a body of descriptive data on a variety of species permits a test of earlier proposals regarding reproductive behavior. For example, Beach (1969) proposed that the tendency of females to run from males may reflect "a fundamental motivational pattern common to females of every mammalian species [p. 983]." While this proposal was reasonable when made, it is not supported by more recent data. Presented in Fig. 1 are data relating to the percent of the intromission latency period (time from the initiation of a test to the first vaginal penetration) that the females of 12 muroid species run from the male. It can be seen that whereas the females of some species, such as laboratory

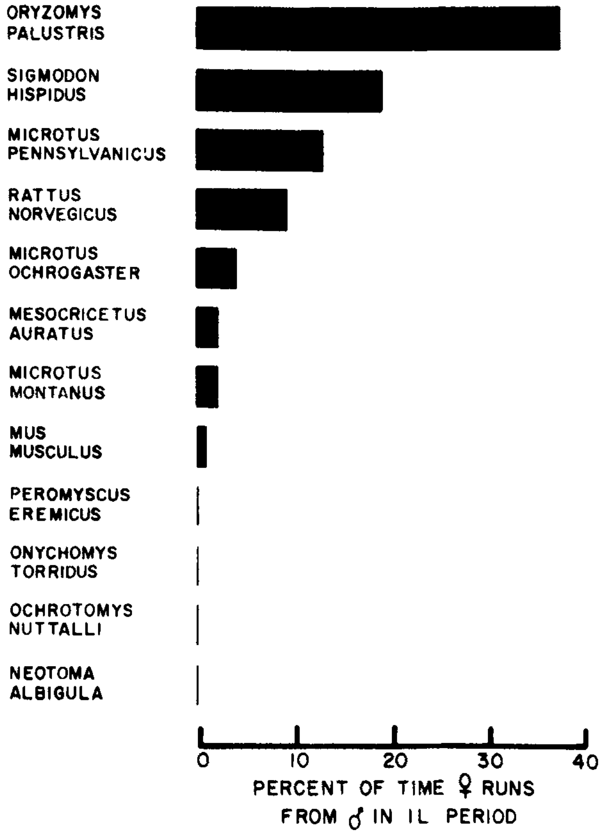

Fig. 1. Percent of time the females of different muroid rodent species run from the male during the intromission latency period (time from the beginning of a test until the first vaginal penetration). Data are from Dewsbury (1967; 1970; 1973b), Dewsbury and Jansen (1972), and unpublished data from this laboratory.

rats, run from males quite a bit, the females of four species hardly run at all. Interestingly, the nonrunning species all attain some sort of lock during copulation. It is possible that the failure of females to run may be related to existence of a safe site for copulation and pressure against exposure to predation.

While research on native muroids really is just beginning, it should be apparent that their potential is great. This diverse group of easily maintained animals may present solutions to a variety of methodological problems in comparative behavioral research.

REFERENCES

Asdell, S. A. *Patterns of mammalian reproduction.* (2nd ed.) Ithaca, New York: Comstock, 1964.

Bailey, V. *Mammals of the Southwestern United States.* New York: Dover, 1931.

Beach, F. A. Locks and beagles. American Psychologist, 1969, 24, 971-989.

Bitterman, M. E. Phyletic differences in learning. American Psychologist, 1965, 20, 396-410.

Boice, R. Laboratizing the wild rat (*Rattus norvegicus*). Behavior Research Methods & Instrumentation, 1971, 3, 177-182.

Burt, W. H., & Grossenheider, R. P. *A field guide to the mammals.* Boston: Houghton-Mifflin, 1964.

Clark, L. D. Experimental studies of the behavior of an aggressive predatory mouse, *Onychomys leucogaster.* In E. L. Bliss (Ed.), *Roots of behavior.* New York: Harper, 1962. Pp. 179-186.

Dewsbury, D. A. A quantitative description of the behavior of rats during copulation. Behaviour, 1967, 29, 154-178.

Dewsbury, D. A. Copulatory behavior of rice rats (*Oryzomys palustris*). Animal Behaviour, 1970, 18, 266-275.

Dewsbury, D. A. Patterns of copulatory behavior in male mammals. Quarterly Review of Biology, 1972a, 47, 1-33.

Dewsbury, D. A. Copulatory behavior of cotton rats (*Sigmodon hispidus*). Zeitschrift für Tierpsychologie, 1972b, 30, 477-487.

Dewsbury, D. A. Comparative psychologists and their quest for uniformity. Annals of the New York Academy of Sciences, 1973a, 223, 147-167.

Dewsbury, D. A. Copulatory behavior in montane voles (*Microtus montanus*). Behaviour, 1973b, 44, 186-202.

Dewsbury, D. A., & Jansen, P. E. Copulatory behavior of southern grasshopper mice (*Onychomys torridus*). Journal of Mammalogy, 1973b, 53, 267-278.

Dewsbury, D. A., & Rethlingshafer, D. A. *Comparative psychology: A modern survey.* New York: McGraw-Hill, 1973.

Doutt, J. K., Heppenstall, C. A., & Guilday, J. E. *Mammals of Pennsylvania.* Harrisburg: Pennsylvania Game Commission, 1967.

Drickamer, L., & Vestal, B. M. Patterns of reproduction in a laboratory colony of *Peromyscus.* Journal of Mammalogy, 1973, 54, 523-528.

Gans, C. Some questions and problems in morphological comparison. Annals of the New York Academy of Sciences, 1969, 167, 506-513.

Hall, E. R., & Kelson, K. R. *The mammals of North America.* New York: Ronald Press, 1959 (2 Vols.).

Hoffmeister, D. F. *Mammals of Grand Canyon.* Urbana: University of Illinois Press, 1971.

Hoffmeister, D. F., & Mohr, C. O. *Fieldbook of Illinois mammals.* Urbana: University of Illinois Press, 1957 (reprinted by Dover Publications, 1972).

Hooper, E. T. Classification. In J. A. King (Ed.), *Biology of Peromyscus (Rodentia).* Lawrence, Kansas: American Society of Mammalogists, 1968. Pp. 27-74.

Hooper, E. T., & Musser, G. G. The glans penis in neotropical cricetines (family Muridae) with comments on classification of muroid rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 1964. No. 123, 57 pages.

Kavanau, J. L. Behavior of captive white-footed mice. Science, 1967, 155, 1623-1639.

King, J. A. Maternal behavior in *Peromyscus.* In H. L. Rheingold (Ed.), *Maternal behavior in mammals.* New York: Wiley, 1963. Pp. 58-93.

King, J. A. *Biology of* Peromyscus *(Rodentia).* Lawrence, Kansas: American Society of Mammalogists, 1968.

King, J. A. Ecological psychology: An approach to motivation. Nebraska Symposium on Motivation, 1970a, 18, 1-33.

King, J. A. Light reinforcement in four taxa of deermice (*Peromyscus*). Journal of Comparative & Physiological Psychology, 1970b, 71, 22-28.

Layne, J. N. Nest-building behavior in three species of deer mice, *Peromyscus.* Behaviour, 1969, 35, 288-303.

Layne, J. N. Climbing behavior of *Peromyscus floridanus* and *Peromyscus gossypinus.* Journal of Mammalogy, 1970, 51, 580-591.

Layne, J. N. Activity responses of two species of *Peromyscus* (Rodentia Muridae) to varying light cycles. Oecologia, 1971, 7, 223-241.

Layne, J. N., & Ehrhart, L. M. Digging behavior of four species of deer mice (*Peromyscus*). American Museum Novitates, 1970, No. 2429, 16 pages.

Lester, D. *Comparative psychology—phyletic differences in behavior.* New York: Alfred, 1973.

Lockard, R. B. The albino rat: A defensible choice or bad habit? American Psychologist, 1968, 23, 734-742.

Logan, F. A., & Boice, R. Aggressive behavior of paired rodents in an avoidance context. Behaviour, 1969, 34, 161-183.

Maser, C., & Storm, R. M. *A key to the Microtinae of the Pacific Northwest.* Corvallis, Oregon: Oregon State University Book Stores, 1970.

Morris, D. *The mammals—A guide to the living species.* New York: Harper & Row, 1965.

Patric, E. F. Bait preference of small mammals. Journal of Mammalogy, 1970, 51, 179-182.

Powell, R. E. Laboratory study of wild rats. Bulletin of the Psychonomic Society, 1973, 1, 119-120.

Price, E. O. Domestication and early experience effects on escape conditioning in the Norway rat. Journal of Comparative & Physiological Psychology, 1972, 79, 51-55.

Richardson, D., Karczmar, A. G., & Scudder, C. L. Intergeneric

behavioral differences among methamphetamine treated mice. Psychopharmacologia, 1972, 25, 347-375.
Scudder, C. L., Karczmar, A. G., Everett, G. M., Gibson, J. E., & Rifkin, M. Brain catecholamines and serotonin levels in various strains and genera of mice and a possible interpretation for the correlations of amine levels with electroshock latency and behavior. International Journal of Neuropharmacology, 1966, 5, 343-351.
Southwick, C. H. Peromyscus leucopus: An interesting subject for studies of socially induced stress responses. Science, 1964, 143, 55-56.
Thiessen, D. D. The roots of territorial marking in the Mongolian gerbil: A problem of species-common topography. Behavior Research Methods & Instrumentation, 1968, 1, 70-76.
Walker, E. P. *Mammals of the world.* Baltimore: Johns Hopkins Press, 1964 (2 Vols.).

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