

profit and to tap an inexhaustible source of energy, it could be carried out as a joint venture of several or many nations. The worldwide food shortages that have been forecast for the next decades could be alleviated substantially by the provision to developing nations of low-cost energy for the manufacture of agricultural chemicals (22). In the SMF approach, subsidies of that kind to the Third World could be given out of new, nonterrestrial wealth, not requiring sacrifice by donor nations.

The data in this article should be considered not as definitive, but as requiring substantiation or correction by additional research. So far, during a year of exposure of the SMF concept to technical review, no major changes in the basic concept have been necessary, but it is almost certain that further work will uncover both unsuspected problems and new technical possibilities. A modest amount of research on the key questions of productivity, life support needs, SMF and SSPS construction methods, and lunar materials transport could substantially improve our knowledge of the cost and time required for the achievement of the first beachhead in space, and of the speed with which the initial investment could be returned.

## Summary

The feasibility of establishing manufacturing facilities in a high orbit is under discussion. They could be used for the construction of satellite solar power stations from lunar materials. Estimates indicate that this may be considerably more economical than constructing power stations on the earth and lifting them into orbit.

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# Diversity and Adaptation in Rodent Copulatory Behavior

Species differences provide ideal material for a broadened comparative psychology.

Donald A. Dewsbury

A 9-year research program in my laboratory has revealed a remarkable diversity in the copulatory patterns of different species of rodents. My colleagues and I have studied more than 30 species in an attempt to determine the range of variability and the adaptive significance of such patterns. This research is part of a new look in comparative psychology which, like many new looks, really represents a return to an older approach—the broad-based study of

The author is professor of psychology at the University of Florida, Gainesville 32611.

naturally occurring behavioral patterns with a concern for the adaptedness of behavior (1).

Psychologists have placed primary emphasis on finding answers to questions that relate to the immediate causation and development of behavior. However, as Tinbergen (2) pointed out, answers to four classes of questions—immediate causation, development, evolutionary history, and adaptive significance—are essential to a comprehensive understanding of animal behavior. With the new look in com-

parative psychology, increased attention is being devoted to questions of evolutionary history and adaptive significance and to the relation between animal behavior as observed in the laboratory and adaptations that are relevant to the natural environment. This emphasis can be seen in the work of Bolles, Lott, Owings and Lockard, Seligman, Shettleworth, and Warren (3). Ties with other areas of whole-animal biology (4) are being rebuilt. My project is one attempt to tackle problems of evolution and adaptive significance head-on through a comparative approach to the study of naturally occurring behavioral patterns.

## Selection of Species and Behavior

Comparative behavioral studies are most useful when conducted on a group of closely related, but diverse, species (5). It is here that species differences can be most precisely attributed to particular factors. The rodent superfamily Muroidea represents an ideal group for such study (6). Rodents in this group are small, easy to obtain, and readily adaptable to the laboratory. Equally important, they are diverse. More than 200 genera are distributed throughout the world and are adapted to virtually every possible habitat. Many genera are large and diverse, too—the genus

Table 1. Taxonomy of species of muroid rodents studied. All Cricetinae are classified in the tribe Hesperomyini except golden hamsters, which are in the tribe Cricetini.

| Common name                | Genus and species                | Family     | Subfamily   | Hooper assemblage |
|----------------------------|----------------------------------|------------|-------------|-------------------|
| Norway rat                 | <i>Rattus norvegicus</i>         | Muridae    | Murinae     | I                 |
| Black rat                  | <i>Rattus rattus</i>             | Muridae    | Murinae     | I                 |
| House mouse                | <i>Mus musculus</i>              | Muridae    | Murinae     | I                 |
| Mongolian gerbil           | <i>Meriones unguiculatus</i>     | Cricetidae | Gerbillinae | II                |
| Israeli gerbil             | <i>Meriones tristrami</i>        | Cricetidae | Gerbillinae | II                |
| Montane vole               | <i>Microtus montanus</i>         | Cricetidae | Microtinae  | III               |
| Meadow vole                | <i>Microtus pennsylvanicus</i>   | Cricetidae | Microtinae  | III               |
| Prairie vole               | <i>Microtus ochrogaster</i>      | Cricetidae | Microtinae  | III               |
| California vole            | <i>Microtus californicus</i>     | Cricetidae | Microtinae  | III               |
| Pine vole                  | <i>Microtus pinetorum</i>        | Cricetidae | Microtinae  | III               |
| Golden hamster             | <i>Mesocricetus auratus</i>      | Cricetidae | Cricetinae  | IV                |
| Rice rat                   | <i>Oryzomys palustris</i>        | Cricetidae | Cricetinae  | V                 |
| Cotton rat                 | <i>Sigmodon hispidus</i>         | Cricetidae | Cricetinae  | V                 |
| Western harvest mouse      | <i>Reithrodontomys megalotis</i> | Cricetidae | Cricetinae  | VI                |
| Cactus mouse               | <i>Peromyscus eremicus</i>       | Cricetidae | Cricetinae  | VI                |
| California mouse           | <i>Peromyscus californicus</i>   | Cricetidae | Cricetinae  | VI                |
| Old-field mouse            | <i>Peromyscus polionotus</i>     | Cricetidae | Cricetinae  | VI                |
| Cotton mouse               | <i>Peromyscus gossypinus</i>     | Cricetidae | Cricetinae  | VI                |
| Plateau mouse              | <i>Peromyscus melanophrys</i>    | Cricetidae | Cricetinae  | VI                |
| Florida mouse              | <i>Peromyscus floridanus</i>     | Cricetidae | Cricetinae  | VI                |
| White-footed mouse         | <i>Peromyscus leucopus</i>       | Cricetidae | Cricetinae  | VI                |
| Canyon mouse               | <i>Peromyscus crinitus</i>       | Cricetidae | Cricetinae  | VI                |
| Golden mouse               | <i>Ochrotomys nuttalli</i>       | Cricetidae | Cricetinae  | VI                |
| Northern pygmy mouse       | <i>Baiomys taylori</i>           | Cricetidae | Cricetinae  | VI                |
| Southern grasshopper mouse | <i>Onychomys torridus</i>        | Cricetidae | Cricetinae  | VI                |
| Northern grasshopper mouse | <i>Onychomys leucogaster</i>     | Cricetidae | Cricetinae  | VI                |
| White-throated wood rat    | <i>Neotoma albigula</i>          | Cricetidae | Cricetinae  | VI                |
| Eastern wood rat           | <i>Neotoma floridana</i>         | Cricetidae | Cricetinae  | VI                |
| Desert wood rat            | <i>Neotoma lepida</i>            | Cricetidae | Cricetinae  | VI                |
| Peters' climbing rat       | <i>Tylomys nudicaudus</i>        | Cricetidae | Cricetinae  | VI                |
| Big-eared climbing rat     | <i>Otodylomys phyllotis</i>      | Cricetidae | Cricetinae  | VI                |

Table 2. Summary of patterns of copulatory behavior.

| Species                          | Lock | Thrust | Multiple intromission | Multiple ejaculation | Pattern |
|----------------------------------|------|--------|-----------------------|----------------------|---------|
| <i>Tylomys nudicaudus</i>        | Yes  | Yes    | No                    | Yes                  | 3       |
| <i>Otodylomys phyllotis</i>      | Yes  | Yes    | No                    | Yes                  | 3       |
| <i>Onychomys torridus</i>        | Yes  | No     | No                    | Yes                  | 7       |
| <i>Ochrotomys nuttalli</i>       | Yes  | No     | No                    | Yes                  | 7       |
| <i>Neotoma albigula</i>          | Yes  | No     | No                    | Yes                  | 7       |
| <i>Neotoma floridana</i>         | Yes  | No     | No                    | Yes                  | 7       |
| <i>Onychomys leucogaster</i>     | Yes  | No     | No                    | Yes                  | 7       |
| <i>Baiomys taylori</i>           | Yes  | No     | No                    | No                   | 8       |
| <i>Mus musculus</i>              | No   | Yes    | Yes*                  | Yes                  | 9       |
| <i>Microtus montanus</i>         | No   | Yes    | Yes                   | Yes                  | 9       |
| <i>Microtus ochrogaster</i>      | No   | Yes    | Yes                   | Yes                  | 9       |
| <i>Peromyscus eremicus</i>       | No*  | Yes    | Yes                   | Yes                  | 9       |
| <i>Microtus pennsylvanicus</i>   | No   | Yes    | No                    | Yes                  | 11      |
| <i>Peromyscus californicus</i>   | No   | Yes    | No                    | Yes                  | 11      |
| <i>Microtus californicus</i>     | No   | Yes    | No                    | Yes                  | 11      |
| <i>Microtus pinetorum</i>        | No   | Yes    | No                    | Yes                  | 11      |
| <i>Rattus norvegicus</i>         | No   | No     | Yes                   | Yes                  | 13      |
| <i>Meriones unguiculatus</i>     | No   | No     | Yes                   | Yes                  | 13      |
| <i>Meriones tristrami</i>        | No   | No     | Yes                   | Yes                  | 13      |
| <i>Mesocricetus auratus</i>      | No   | No*    | Yes                   | Yes                  | 13      |
| <i>Sigmodon hispidus</i>         | No   | No     | Yes                   | Yes                  | 13      |
| <i>Oryzomys palustris</i>        | No   | No     | Yes                   | Yes                  | 13      |
| <i>Peromyscus polionotus</i>     | No   | No     | Yes                   | Yes                  | 13      |
| <i>Peromyscus leucopus</i>       | No   | No     | Yes                   | Yes                  | 13      |
| <i>Peromyscus crinitus</i>       | No   | No     | Yes                   | Yes                  | 13      |
| <i>Rattus rattus</i>             | No   | No     | Yes                   | Yes                  | 13      |
| <i>Reithrodontomys megalotis</i> | No   | No     | No                    | Yes                  | 15      |
| <i>Peromyscus gossypinus</i>     | No   | No     | No                    | Yes                  | 15      |
| <i>Peromyscus floridanus</i>     | No   | No     | No                    | Yes                  | 15      |
| <i>Neotoma lepida</i>            | No   | No     | No                    | Yes                  | 15      |
| <i>Peromyscus melanophrys</i>    | No   | No     | No                    | Yes                  | 15      |

\*Qualification due to complicated pattern.

*Oryzomys* (rice rats) has 68 species, while *Peromyscus* (white-footed mice) has 57.

The taxonomy of the 31 species that we have studied thus far is shown in Table 1. Traditionally, the muroids have been divided into two families, the Old World rats and mice, Muridae, and those of the New World, Cricetidae. However, on the basis of recent analyses, primarily those of penile morphology, Hooper and Musser (7) have suggested that these animals really represent six different assemblages, as shown in Table 1.

Ideally, a behavioral pattern selected for analysis should be highly stereotyped within species, but variable across species. It should be readily observable in the laboratory without prolonged training of animals, and it should be of considerable biological significance. Copulatory behavior fits these criteria well.

## Methods

Our basic strategy involves the attempt to bring into our laboratory as diverse a collection of muroids, especially Cricetidae, as possible. We begin with basic descriptive study, in which males and females are permitted to copulate in a standard test situation. The female is introduced into the male's home cage and the pair is allowed to copulate until satiated. Satiety is arbitrarily, but consistently, defined as a half hour with no copulations. Quantitative measures of both copulatory activity and the behaviors associated with copulation are recorded. Where possible, the basic descriptive work is followed by other research to study variability within species, the role of behavior in the initiation of pregnancy, and related behavioral patterns. Specific methods of maintenance, procedure, and testing have been described (6, 8, 9).

There is a certain paradox in conducting laboratory studies when asking questions of adaptive significance. The disadvantages of muroids for use in the study of adaptive significance are that they are small and generally nocturnal. Field observations of copulatory activity on the scale required for a program such as ours are impossible. We believe, however, that basic copulatory patterns are highly species-characteristic. While they may show quantitative variation as a function of situational variables including captivity, these patterns should show little, if any, qualitative alteration. The comparisons of field and laboratory observations on copulations in sand rats, *Psammomys obesus* (10), together with those in various primate studies (11), are all consistent with this view.

## Patterns of Copulatory Behavior

The starting point for any comparative psychologist must be the laboratory rat *Rattus norvegicus*. Laboratory rats have a complex copulatory pattern involving three primary elements—mounts, intromissions, and ejaculations (12, 13). Mounts are scored when the male mounts the female but fails to gain vaginal penetration. Although penetration is achieved on both intromissions and ejaculations, sperm are transferred only on ejaculations. Copulatory activities are organized into ejaculatory series that consist of mounts, intromissions, and ejaculations, but always end with ejaculation. Typically, these rats require about ten intromissions before they attain their first ejaculation. These intromissions last only a quarter of a second (14) and are separated from each other by about a minute. There is a single intravaginal thrust per intromission. About seven ejaculatory series precede attainment of the satiety criterion.

In order to compare the pattern exhibited by laboratory rats to the patterns of other species, a classification system or taxonomy of behavior is necessary. Such a system is presented in Fig. 1 (15). We propose that species can usefully be regarded as varying in four respects. While some species, such as domestic dogs, display a lock, or mechanical tie between the penis and vagina, others, such as laboratory rats, display no such lock. Second, while some species, such as laboratory rats, have but a single thrust during each insertion, others, such as most primate species, show repetitive intravaginal thrusting during a single mount. Third, while some species, such as dogs, can ejaculate the first time the penis is inserted into the vagina, others, such as laboratory rats, require multiple intromissions preceding ejaculation. Finally, whereas laboratory rats attain more than one ejaculation in a single episode, other species, such as some ungulates, ejaculate only once. As each of these four attributes has two alternatives, there result  $2^4$  (or 16) possible patterns. With adequate data each species can be classified in this system.

### Muroid Copulatory Patterns

We have found that most muroid species, even nondomesticated forms, will copulate under observation in the laboratory. Thus far, we have succeeded in observing copulation in all 31 species that are shown in Table 1.

In all species, the male mounts the female from behind in a dorsal-ventral mount. Some variability in posture exists (16), but shallow, extravaginal thrusting

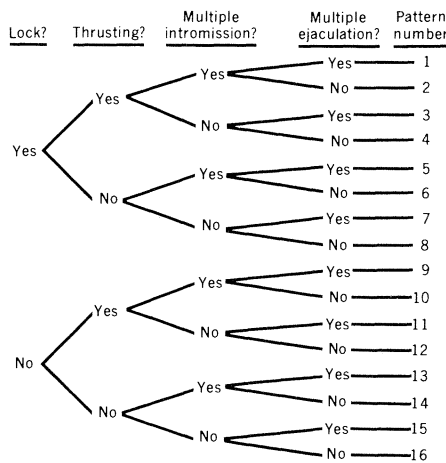


Fig. 1. Patterns of copulatory behavior in male mammals. [Dewsbury (15); courtesy of *Quarterly Review of Biology*]

generally precedes insertion. Females show a pattern of lordosis, the extent and form of which varies with the species (17).

The copulatory patterns of the 31 species with which we have worked are classified in Table 2. Muroid rodents show great variability between species in their copulatory patterns—each column in Table 2 has entries of “yes” for some species and “no” for others. As locking is generally thought to be a characteristic of the Carnivora, it was somewhat surprising to find that 8 of the 31 muroid species lock. A ninth, cactus mice, occasionally lock, but apparently not as a functional part of their copulatory pattern (18). Ten species show intravaginal thrusting; 14 species require multiple intromissions before ejaculating. Just one species, *Baiomys taylori*, ceases copulating after attaining one ejaculation (19). In all, 7 of the 16 possible patterns have appeared. Seven of the nine missing patterns are those in which multiple ejaculations would never occur; the other two missing patterns involve the combination of locking with prerequisite multiple intromissions. Laboratory rats are representative of the most common pattern in this sample, pattern 13, which is shown by 10 of the 31 species. However, as this is only one of a variety of muroid patterns, generalizations across species from laboratory rats or any other species can be made only with great caution.

The species with pattern 15 are of special interest. The most common laboratory muroids, laboratory rats (12), golden hamsters (20), and Mongolian gerbils (21), all display brief insertions, but require multiple intromissions before ejaculating. As far as we know, these species have never been observed to ejaculate without prior insertions, except perhaps after gross physiological manipulations. In species such as Western harvest mice (22), cotton mice (23), and Florida mice (24), however, ejac-

ulation on the first brief insertion has been repeatedly observed.

The ways in which the 30-minute satiety criterion is met varies greatly across species. In laboratory rats, the interval between the occurrence of ejaculation and the resumption of copulation, known as the postejaculatory interval (PEI), increases progressively with successive ejaculatory series. Typically the 30-minute criterion is met with a 30-minute PEI (that is, no new series is initiated) (12). Rice rats (25), prairie voles (26), and various other species show similar modes of attaining the satiety criterion. However, other species, such as montane voles (27), Mongolian and Israeli gerbils (28), and cactus mice (18) typically reach the criterion as a pause within an incomplete series. Usually there are more intromissions in these incomplete series than was sufficient to produce ejaculation earlier in the episode. These and other data we have gathered lead us to believe that ejaculations do not occur in these species because of an elevation in the male's ejaculatory threshold. Thus, sexual satiety in these species appears to reflect the operation of mechanisms quite different from those proposed for laboratory rats and mice (29).

Even more interesting is a group of species in which the basic copulatory pattern changes after a given number of organized series. For old-field mice (8), white-footed mice (30), and cotton rats (31), for example, there is often a shift after a given number of series, from the typical patterns of multiple intromissions organized in series to one in which intromissions are of longer duration and are spaced irregularly at average intervals longer than those that characterize series. As far as we have been able to determine, there are no sperm transferred during these longer copulations. Thus animals copulate according to a very stereotyped, apparently specialized pattern for a considerable time after the last sperm have been transferred. In Syrian golden hamsters, this phenomenon of postejaculatory copulations has been taken one step further so that males that display no intravaginal thrusting during their ten or so organized series do show intravaginal thrusting on their prolonged postejaculatory insertions (32). We believe that the presence of postejaculatory copulations constitutes an important new finding whose adaptive significance is worthy of detailed study.

The magnitude of these species differences requires comment. In many species comparisons in comparative psychology, one deals with statistically significant quantitative differences, but there may be considerable overlap among the scores of individual animals of the different species

(33). By contrast to such quantitative differences, the species differences described are often of a qualitative nature. When classifying copulatory patterns by dichotomous characteristics one should expect some ambiguous cases. Thus far, however, these have been surprisingly few (Table 2). My colleagues and I have never observed an animal from a nonlocking species to lock, or vice versa. Multiple intromission species always require multiple intromissions, although single intromission species can display the multiple intromission pattern. There is a sharp dichotomy between thrusting and nonthrusting species. If a vole of unknown species escaped its cage, I would be more confident of

correct identification on the basis of copulatory pattern than of morphology.

In addition to the qualitative differences among species with different patterns, there also exist quantitative differences that can be meaningfully compared. Greater caution is needed in interpreting these differences because they are more susceptible to effects of situational variables, such as captivity itself. Nevertheless, quantitative variation should be studied because apparently small variations in copulatory pattern can be of the utmost importance for successful reproduction (34).

The period of latency from introduction of the female until the first intromission is highly variable. In our studies, laboratory

rats, golden hamsters, and three species of voles all had mean intromission latencies (IL's) of less than 3 minutes (26, 27, 32, 35, 36). By contrast, cactus mice (18), old-field mice (8), and California mice (37) required 38, 41, and 49 minutes, respectively. Pygmy mice had a mean IL of more than 1½ hours (19).

Similar variability, although less extreme, is seen in other measures. The number of intromissions that precede ejaculation, intromission frequency (IF), is highly variable across species as well as across series. The reduction from the first to the second series in the number of intromissions that is required to attain ejaculation is highly reliable in laboratory rats and has been regarded by some (38) to be a general rodent characteristic. However, as shown in Fig. 2, patterns of change in IF across series vary greatly across species. Whereas some species do show simple decreases in IF from the first to later series, others show increases, or even more complex patterns. There is no general rodent pattern.

If there is one characteristic of virtually all species that we have studied, it is the progressive increase in the PEI's that follow successive ejaculations.

Among the locking species with pattern 7, there is a perfect inverse correlation across species between the mean number and mean duration of locks (39).

The standard measures of copulatory behavior are defined in terms of male patterns, mounts, intromissions, and ejaculations. This may produce the mistaken impression that the male completely controls the copulatory episode. However, the occurrence, timing, and topography of all copulations represent the result of continuing patterns of interaction between male and female. Recently Diakow and I have used motion picture analysis to develop a classification system for detailed treatment of characteristics of the movements and postures that are associated with copulation in muroid females (17).

### Behavior That Accompanies Copulation

In addition to determining various frequency and latency measures of actual copulatory activity, my colleagues and I have developed a system that enables us to present profiles, for both males and females, of the behavioral patterns that accompany copulation. In many tests of copulatory behavior, actual copulation occupies only 1 percent of the total testing time (35); some accounting for the remaining 99 percent of time is in order. Such data permit much finer comparisons of species. A sample categorization for male cactus mice is shown in Fig. 3. The chang-

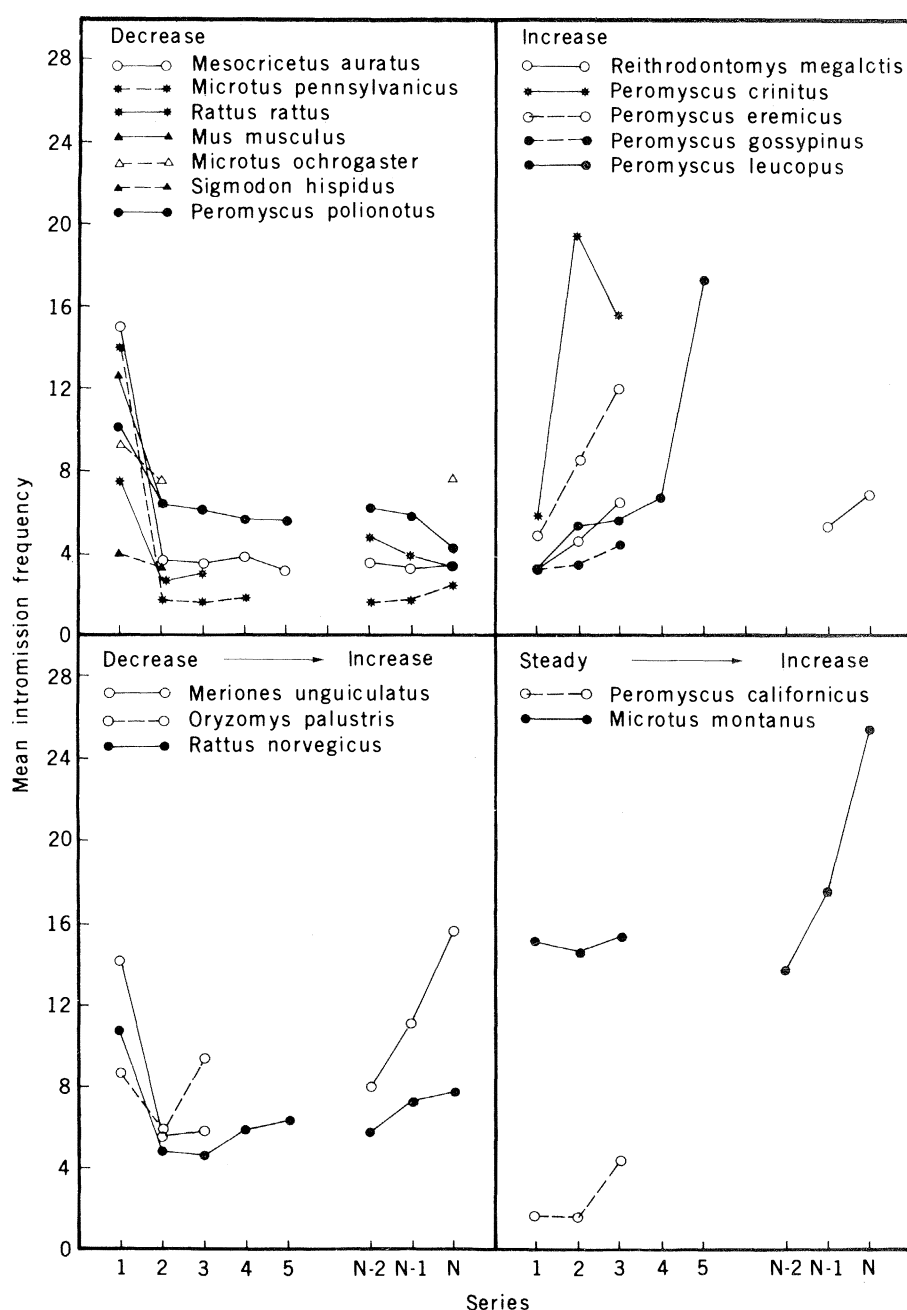


Fig. 2. Intromission frequency as a function of ordinal number of ejaculatory series for 17 species of muroid rodents that have differing patterns of change.

ing behavior of the male as the episode progresses is readily apparent. Comparisons between species are just as revealing. Data for allo-grooming by males and females of 12 species in the interval before the first intromission are shown in Fig. 4. While some species show considerable mutual grooming, others show very little. Where allo-grooming is shown, however, males always groom females more than females groom males.

Similar variability is present with respect to the extent that females of different species run from males in the interval prior to the first intromission. Beach (40) proposed that the tendency of females to run from males was a soliciting pattern and may reflect "a fundamental motivational pattern common to females of every mammalian species." While we have found that many species display appreciable amounts of running during the IL period, others show little at all. For example, southern grasshopper mice, golden mice, and white-throated wood rats do virtually no running (6). All three are locking species with protected nest sites. Once more, a generalization that was proposed on the basis of early data appears to have limited generality as more data are collected. Our data indicate that several such generalizations be discarded. We hope that our hypotheses will be similarly tested and recognize that some will be similarly discarded.

### Variation Within Species and Effects of Domestication

It has long been known that there are genetically based differences in the quantitative measures of copulatory behavior among different strains of the same species (41). We have extended these observations in both laboratory rats and house mice (42).  
A more important question for present purposes deals with the magnitude of variation within species among natural populations. Like most biologists, we typically study animals from one population each of several different species and attribute such differences as are observed to species differences per se. It seems that some of these differences might really be a function of the population rather than of the species. In order to consider this possibility, animals from different natural populations of several species—cactus mice, old-field mice, and cotton mice—were studied (18, 23, 43). While some significant quantitative differences across populations were found, no qualitative variability in the basic copulatory pattern was observed.

Similar conclusions can be drawn with respect to the influences of domestication

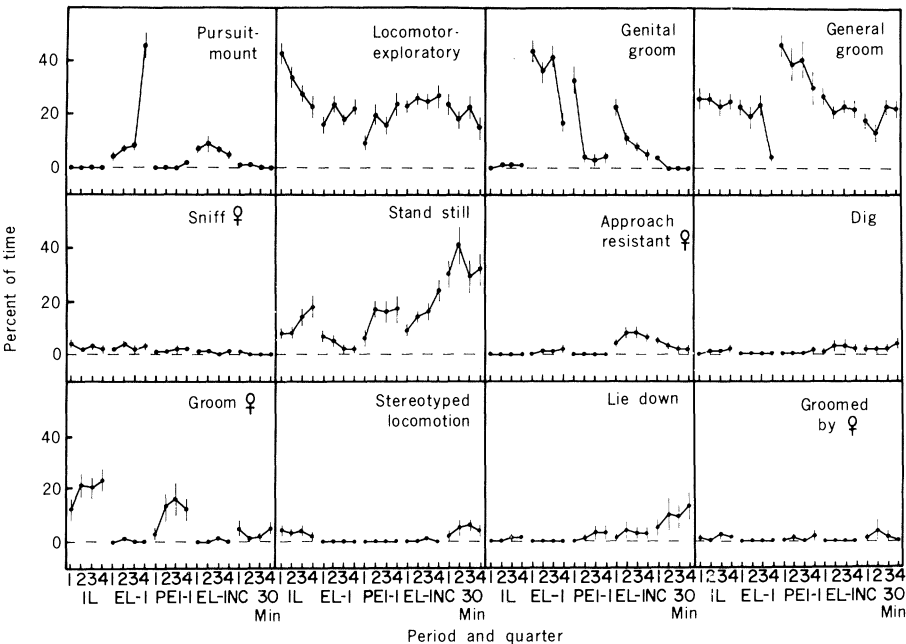


Fig. 3. Categorization of behavior of male cactus mice, *Peromyscus eremicus*, during tests of copulatory behavior [from Dewsbury (18)]. Abbreviations for intervals: IL, intromission latency period; EL-I, time from the first intromission of the first ejaculatory series to the ejaculation; PEI-I, interval from ejaculation to the next intromission; EL-INC, interval of the incomplete series; 30-minute period during which the 30-minute satiety criterion was attained. Each interval was divided into quarters. [Courtesy of Academic Press and *Behavioral Biology*]

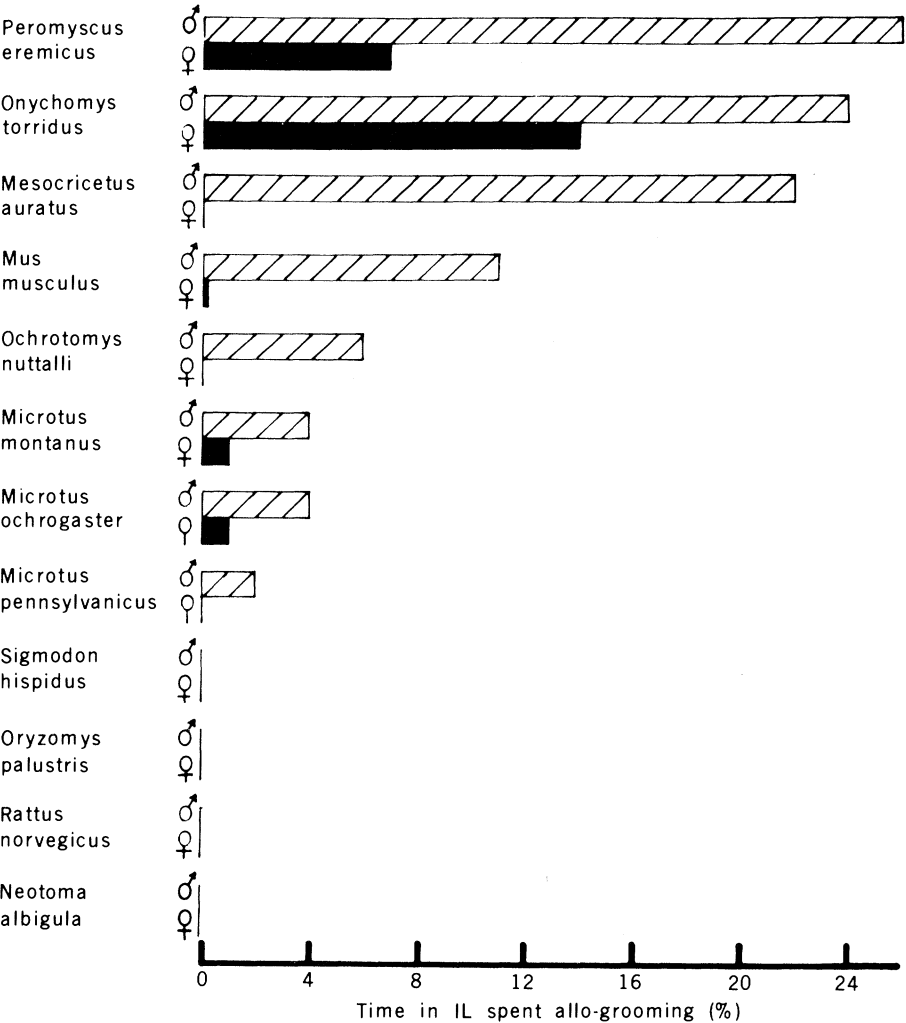


Fig. 4. Percent of time in the intromission latency period (IL) that was spent in allo-grooming by males and females of 12 species of murid rodents.

Table 3. Ratio of the glans diameter to glans length times 100 for simple baculum muroid rodents with differing copulatory patterns. [Table based on (49, 51) and research in our laboratory]

| Lock and/or thrust             |       | No lock or thrust                |       |
|--------------------------------|-------|----------------------------------|-------|
| Species                        | Ratio | Species                          | Ratio |
| Original species               |       |                                  |       |
| <i>Neotoma albigula</i>        | 47    | <i>Peromyscus truei</i>          | 23    |
| <i>Onychomys torridus</i>      | 47    | <i>Peromyscus gossypinus</i>     | 22    |
| <i>Ochrotomys nuttalli</i>     | 45    | <i>Reithrodontomys megalotis</i> | 22    |
| <i>Peromyscus californicus</i> | 32    | <i>Peromyscus polionotus</i>     | 18    |
| <i>Peromyscus eremicus</i>     | 29    | <i>Peromyscus maniculatus</i>    | 16    |
| Additional species             |       |                                  |       |
| <i>Neotoma floridana</i>       | 53    | <i>Peromyscus crinitus</i>       | 28    |
| <i>Baiomys taylori</i>         | 51    | <i>Peromyscus leucopus</i>       | 24    |
| <i>Ototylomys phyllotis</i>    | 40    | <i>Peromyscus melanophrys</i>    | 23    |
| <i>Tylomys nudicaudus</i>      | 37*   | <i>Peromyscus floridanus</i>     | 14    |
| <i>Onychomys leucogaster</i>   | 31    | <i>Neotoma lepida</i>            | 11    |

\*Value based on *Tylomys fulviventris*.

on behavior. The copulatory patterns of wild house mice are virtually identical to those of inbred strains (44). Similarly, McClintock (45) has found interesting quantitative, but no qualitative, differences in the basic copulatory patterns of domesticated and wild *Rattus norvegicus*. Wild-trapped and laboratory-reared cactus mice do not differ substantially in their basic patterns (18).

Evolutionary History

My colleagues and I have found a number of new phenomena that we believe to be important. Our goal is to use these descriptions to study the evolutionary history and adaptive significance of behavior. While we have not yet approached our goal of a full understanding of such considerations, we do have a number of working hypotheses. Some of these are quite conservative and others are highly speculative. Although they are our first attempts at synthesis, we hope they represent an approach that will play an increasing role in comparative psychology.

In general, data from all available species enter into the formulation and evaluation of these proposals. However, few measures can be evaluated for all the species studied because (i) some measures are not applicable to species with particular patterns (for example, locking species have no IF); (ii) we have been unable to collect some kinds of data for some species due to limitations in the numbers of animals available, time, and so forth; and (iii) some data collection is still incomplete. These same considerations prevent the use of factor analytic techniques.

There appears to be no simple progressive pattern of evolution with respect to copulatory behavior. In broad perspective, rodent copulatory patterns have some commonalities with those of primates, carnivores, insectivores, and others. Within

the muroids studied there is appreciable variation within genus. Some species of wood rats, *Neotoma*, show locking patterns, whereas others do not (16, 19, 39). Among *Peromyscus* there are species that thrust and those that do not, and in both *Peromyscus* and *Microtus* there are single and multiple intromission species. If our behavioral data are considered in relation to the probable course of muroid evolution (7), no convincing, simple patterns in evolutionary history appear. Rather, it seems that copulatory patterns may be evolutionarily rather labile, changing as different, closely related species adapt to different habitats and respond to different selective pressures. Thus, while the development of copulatory patterns appears well buffered from environmental alterations (that is, environmental factors appear to affect only the presence or absence of a pattern and its quantitative features), these behaviors are highly plastic evolutionarily and are sensitive to the actions of natural selection.

A hypothesis has been proposed (46) that there has been a differential evolution of copulatory behavior among the myomorph rodents, including the muroids, and the hystricomorphs, including guinea pigs and chinchillas. The hystricomorphs, in contrast to the myomorphs, are said to display ejaculation on a single insertion, inconsistent receptivity among females, spontaneous development of a luteal phase of the female cycle, and short estrous cycles. This hypothesis now appears to be incorrect. California mice, for example, are myomorphs with short estrous cycles; they display a copulatory pattern that is nearly identical in many respects to the guinea pig-chinchilla pattern. All thrust, do not lock, can ejaculate on a single insertion, and can attain multiple ejaculations (37). Copulatory patterns vary among the hystricomorphs just as among the muroids (47). Thus, there is much overlap among the two suborders.

Adaptive Correlation: Anatomy

If copulatory patterns do not follow orderly progressive patterns in evolutionary history, they must be considered as specific adaptations to find order in their evolution. There are at least three methods for the study of adaptive significance, the behavior-genetic method, the method of adaptive correlation, and the experimental method (48). While I have used all three with muroids, I shall concentrate here on adaptive correlation. With this method, several species are compared with respect to a target characteristic (such as copulatory behavior) and several other variables (such as behavior, ecology, social organization, and anatomy). An attempt is made to infer the function of the target characteristic by determining the other characteristics with which it is usually associated. For example, certain adaptations can be seen repeatedly in different taxa as appropriate for flight, aquatic environments, bipedalism, and the like.

The method can be illustrated with two of the anatomy-behavior correlations that I have proposed. The revision of muroid taxonomy that is proposed by Hooper and mentioned above is based primarily on penile morphology and is the result of a series of studies by Hooper *et al.* (7, 49). Thus, while there exist exquisitely detailed studies of penile morphology in muroids, there is little understanding of the functions of these structures. It seemed reasonable that they might be related to copulation. Two kinds of glandes have been described in muroids, simple and complex. Our emphasis has been on species with the simple form. The simple glans contains a single bone with or without a cartilaginous tip, and spongy, vascularized layers (7). In 1972, I proposed that in species which lock the glans penis is thicker and the penile spines are larger than those in species which neither lock nor thrust (16, 50). Species that thrust appeared to be intermediate. Examples of relatively thick and thin glandes are shown in Fig. 5. This correlation was based on the anatomical data of Hooper and his associates (7, 49) and behavioral data from my laboratory and those of Tamsitt and Clemens (51). The primary anatomical datum is the ratio of the glans diameter to the length times 100.

The relevant data to the original proposed correlation are shown in the upper portion of Table 3. Since the time of my original proposal, my colleagues and I have studied 12 additional species whose copulatory patterns were hitherto not well described. With the original proposed correlation we were able to predict correctly whether a species would display a pattern

with locking or thrusting (or both), or with neither in 12 of 12 instances. One of the major problems with studies of adaptive significance is that they often produce post hoc hypotheses that are not amenable to experimental testing. By contrast, correlations of the sort discussed in this article are highly testable as previously unstudied species are added.

A second anatomical correlate of copulatory pattern can be found in male accessory glands. Anatomical characteristics of male accessory glands for 24 genera of muroids were described by Arata (52). He summarized his findings by writing that "*Peromyscus* and *Reithrodontomys* have retained relatively complete sets of accessory glands, but others (*Neotoma*, *Onychomys*, *Ochrotomys*, *Baiomys*, and *Tylomys*) have highly modified accessory gland compliments." Since *Peromyscus* and *Reithrodontomys* are nonlocking, while *Neotoma*, *Onychomys*, and *Ochrotomys* lock, I proposed that a reduction in accessory gland component, with the exception of the preputials, is associated with the locking pattern (16, 50). More recently, my colleagues and I have partially validated the proposal by finding that, consistent with our expectations, both *Baiomys* and *Tylomys* lock. Not all glands are reduced in all genera, and the specific glands that are lost or reduced in size vary from genus to genus. Nevertheless, the reduction appears to be correlated with the locking pattern.

#### Adaptive Correlation: Ecology and Behavior

Use of the method of adaptive correlation with ecological and behavioral variables in order to understand the adaptive significance of copulatory patterns has thus far been less successful than its use with anatomy. For example, we hoped to find a simple ecological correlate of the variability that is observed in copulatory patterns. We had hoped for a correlation with feeding habits, habitat, or pattern of social organization. Thus far, we have found no such simple relationships. However, we do have some tentative correlations to propose.

It seems reasonable that a safe nest site might be a necessary, but not sufficient, condition for the evolution of a locking pattern of copulation. While locked together, a pair would seem highly susceptible to predation. The nature of the nest sites of locking species studied appears to be consistent with this proposal. Wood rats (pack rats, trade rats) are famous for their elaborate houses; grasshopper mice dig a variety of burrows; golden mice nest in

trees; *Tylomys* and *Ototylomys* are highly arboreal (53). Because the actual site of copulation is known for only a few rodent species, it is not yet clear whether or not these nest sites actually are used for copulation. However, it is interesting to remember that these locking species are the ones in which females show little running from the males. This would be consistent with courtship patterns that are adapted to narrow confines.

It seems likely that patterns characterized by ejaculation on a single brief insertion represent adaptations to life with sparse cover. Western harvest mice, Florida mice, and cotton mice all display this copulatory pattern (22-24). Western harvest mice do not burrow and have very poor cover during some seasons (54). Florida mice live in relatively xeric, open habitats (55). Cotton mice typically nest in holes in logs, stumps, or trees, underneath objects on the ground, or in human dwellings (56).

For several years we have considered the

possibility that certain aspects of copulatory patterns that are observed in the laboratory may reflect a tendency toward pair-bonding in the natural habitat. A primary difficulty in evaluating this possibility lies in the lack of adequate field data on pair-bonding. It appears that old-field mice (57) and grasshopper mice (58) may form bonds that may persist for an entire breeding season. It seems reasonable that long IL's may characterize pair-bonding species. The behaviors that occupy the prolonged IL, including much mutual grooming, may represent a compressed and somewhat distorted version of the process of bond formation that may occur in the natural habitat. One would expect more care in mate selection among monogamous than polygamous species (59). Some putative pair-bonding species (such as old-field mice and southern grasshopper mice) have very long IL's (8, 9), while most species with short IL's (for example, laboratory rats, golden hamsters, and voles) seem unlikely to form such bonds. However, complete evaluation of this proposed correlation must await better field data.

A similar fate awaits the proposal that the lack of a Coolidge effect may characterize pair-bonding species. The Coolidge effect is a phenomenon that refers to the resumption of copulation in satiated males as a result of introduction of a new partner (60). It has been proposed (61) that there might be no Coolidge effect among species with stable pair-bonds. That old-field mice failed to show a Coolidge effect seemed consistent with this proposal (8). More recently we have found that northern grasshopper mice, putative pair-bonders, show some evidence of a Coolidge effect (62), while prairie voles, putative nonbonders, show none (26). Although these data appear inconsistent with the proposed relation, final evaluation again must await better field data.

Among native muroids, the greatest diversity in copulatory patterns appears among species that live in warm climates, particularly in southwestern United States. Whether this variability is attributable to climate, habitat diversity, the presence of many closely related species and associated isolating mechanisms, or is just a chance result of the presence of so many species in these regions is as yet uncertain.

Five species of voles differ from the other species in our laboratory in that they are induced ovulators (that is, females ovulate only in response to stimulation derived from copulation) (63). The question arises as to whether the copulatory patterns of induced ovulators differ sharply from those of spontaneous ovulators. No dramatic differences have been observed, probably because all other species studied probably

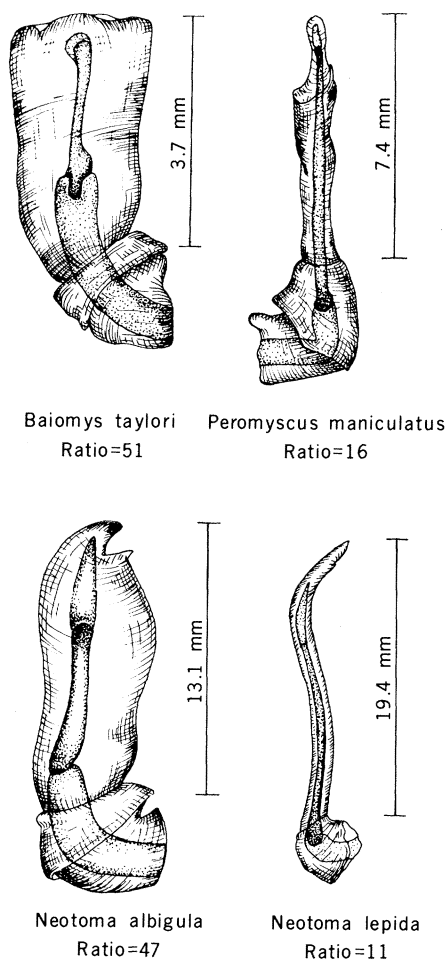


Fig. 5. The glans penis of two species of muroid rodents that have locking copulatory patterns (*Neotoma albigula* and *Baiomys taylori*) and two species that do not lock (*Peromyscus maniculatus* and *Neotoma lepida*). [Adapted from (49); courtesy of University of Michigan Museum of Zoology, Ann Arbor]



have a female cycle in which the initiation of a functional luteal phase and consequent preparation of the uterus for implantation are contingent on copulation (64). There is no obvious reason why the induction of ovulation in females of some species should require a different amount or quality of copulatory stimulation from the initiation of a luteal phase in other species.

## Pregnancy Initiation

A more experimentally oriented analysis of adaptive significance in rodent copulatory patterns is under way. The role of specific behavioral patterns in triggering those neuroendocrine responses of the females that are critical to successful pregnancy (that is, ovulation or a functional luteal phase) is being examined. From research in my laboratory as well as others (34, 65), data on 13 muroid species have been collected. The conclusion that seems to be emerging is that, in species with relatively little copulation after the first ejaculation, females are maximally stimulated by engaging in a single complete ejaculatory series. In species with large numbers of ejaculations or much postejaculatory copulation (or both), prolonged copulation facilitates the initiation of pregnancy (66, 67). The probability of ovulation, probability of a luteal phase, and even litter size can vary as a function of the number of ejaculatory series received. The functions of postejaculatory copulations may come to be understood through studies such as these that link specific behavioral patterns to successful pregnancy (67).

Another potential function of specific copulatory patterns that may emerge from such studies concerns reproductive isolation. If female responsiveness is contingent on a specific patterning of stimulation (68) in addition to specific quantities, it is possible that heterospecific matings would fail to elicit critical neuroendocrine responses. Such a mechanism would minimize wastage of precious ova or time in short-lived species (26, 36).

## Summary

Copulatory patterns of muroid rodents provide an ideal locus for comparative behavioral research. Such patterns are highly stereotyped within and between the individuals of a given species, variable across species, readily elicited in the laboratory, and of great biological significance. Detailed behavioral comparisons of a broad range of muroid species have revealed ex-

tensive behavioral diversity that was not anticipated from research confined to laboratory rats. Various muroid species display postejaculatory copulations without sperm transfer, locking, thrusting, and other behavioral patterns. This behavioral diversity appears not to be the result of a simple linear pattern of evolutionary history. Rather, patterns appear to have evolved repeatedly in response to particular selective pressures acting on particular species. While understanding of the adaptive significance of these behavioral patterns remains rudimentary, important beginnings have been made.

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