SPACE UTILIZATION OF PEROMYSCUS: SOCIAL AND SPATIAL FACTORS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
JAMES LESLIE HILL
1970

This is to certify that the

thesis entitled

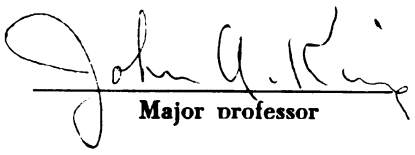
Space Utilization of Peromyscus:
Social and Spatial Factors

presented by

James Leslie Hill

has been accepted towards fulfillment of the requirements for

Ph.D. **degree in** Zoology



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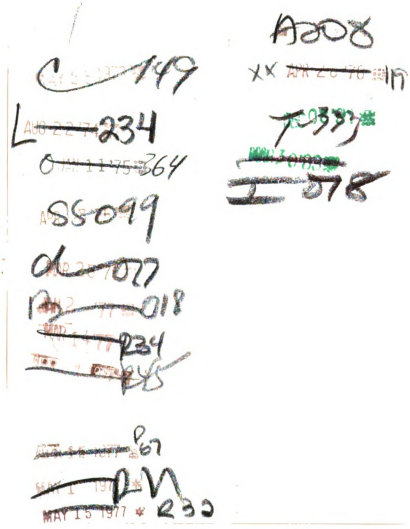

ABSTRACT

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By

James Leslie Hill

Space utilization of Peromyscus maniculatus bairdi and P. leucopus noveboracensis was studied in laboratory enclosures. The hypothesis tested was that both social interactions and the amount of space available would influence the utilization of space in these two species. Both space and social interactions were manipulated independently in order to determine the relative contribution of each factor, and interaction between factors. Two species were examined in order to gain insight into the generality of the results.

Individuals were permitted access to two adjacent compartments of a four-compartment enclosure for a period of one week. For an additional week the mice were given access to all four compartments. The two new compartments were either vacant or were occupied by a conspecific individual of similar experience. Within each species both sexes were tested as solitary individuals or they met another individual of the same or opposite sex. In each compartment daily indices of space utilization were amount of food and water consumed,

amount of wheel running activity, and choice of nest site. Site preferences and changes in location of preferences could be determined by comparing these data from each compartment. The number of movements between compartments was also measured daily. In addition, direct observations of social interactions were recorded.

The utilization of space was influenced by the amount of space available; the doubling of space from two to four compartments was accompanied by changes in all of the dependent variables. All individuals utilized the additional space. With access to an increased number of running wheels, food and water stations, and nest sites the mice shifted their preferences more frequently than before. These results suggest that Peromyscus readily exploits any new resource that becomes available.

The two species utilized space differently. It was suggested that the difference might be due to each species exhibiting a pattern of space utilization most suitable to the type of habitat in which it is found. A marked species difference in reproductive success was also found: nine of ten P. maniculatus pairs produced litters while P. leucopus females apparently did not become pregnant. Evidence indicates that P. leucopus females failed to recognize males, since the females behaved similarly regardless of the sex of the other mouse.

The two species responded similarly to the various social treatments. Despite species differences in patterns of space utilization, the presence of another individual had the same general effect upon space utilization in both species. Because social interactions influenced space utilization so consistently in these two species it was predicted that social factors might have the same general influence upon space utilization in other species. Therefore, it was recommended that future studies of the space utilization of other species concentrate upon social factors.

Suggestions that Peromyscus is territorial were not supported by the results of this study; there was no defense of mutually exclusive areas, but rather, the initial reaction of two individuals was one of avoidance. Therefore, both territorial behavior and avoidance are mechanisms for the spacing of individuals throughout a population area. The primary concern of this study was not to determine if a species was territorial, but rather, whether the species exhibited any form of social behavior which limited the utilization of space of individuals. The results of this study demonstrate that to study the social restriction of space utilization, it is advisable to determine first if social interactions influence space utilization at all.

SPACE UTILIZATION OF PEROMYSCUS:

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By

James Leslie Hill

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1970

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to Dr. John A. King for his counsel and guidance throughout this study, and for his careful editing of this manuscript which has added much to the clarity of the presentation. I also wish to thank Drs. M. Balaban and W. E. Cooper for their many helpful comments and suggestions, and to them and Dr. S. N. Stephenson I express gratitude for constructive criticisms of the manuscript. Much credit is due to my wife Joanna who proved to be a more-than-able assistant in all phases of this study. Finally I wish to thank my fellow graduate students in the Animal Behavior Training Program and those many others who have assisted either directly or indirectly in this project.

This study was supported by Teaching Assistantships in the Department of Zoology and by Biomedical Sciences Support Grant 5 S05 FR07049-03 from the National Institutes of Health. Additional support was provided by the Animal Behavior Training Grant T01 GM01751 from the National Institue of General Medicine and by Research Grant No. 5 R01 EY00447 from the National Eye Institute to Dr. John A. King. Sufficient space to conduct the investigation was provided by the Chemistry Department at Michigan State University.

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INTRODUCTION

The maintenance of the spatial organization of animal populations has been attributed to behavioral interactions among population members (e.g., Wynne-Edwards, 1962). That is, the presence of one individual affects the utilization of space of another by limiting its movements. Further, this implies that individuals would use more space, or at least would utilize space differently if other individuals were not present. It was the object of the present study to determine quantitatively the influence of the amount of space available and of social interactions upon the utilization of space in two species of Peromyscus. It was hypothesized that both the amount of space available and social interactions would influence the utilization of space in the two species tested.

In the experimental design both the factors of space and of social interactions were manipulated independently so that the relative contribution of each factor, as well as any interaction between the factors, could be determined. By studying two species it could be determined if either factor influenced both species in a similar manner. It was assumed that the factor with the most consistent influence upon the

behavior of the two species is the one which may regulate the use of space by other species in the genus Peromyscus. It is suggested, therefore, that future studies with other species concentrate upon whichever of the factors has the most consistent influence upon the space utilization of the two species studied here, P. maniculatus and P. leucopus.

Many live-trapping, tracking, and nest box utilization studies of several different species of Peromyscus indicate that adults usually restrict their activities to only a part of the suitable habitat available (see Stickel, 1968; and Eisenberg, 1968). Because the areas occupied by neighboring individuals do not overlap, or overlap only slightly, Peromyscus has been considered as territorial (Burt, 1940; Metzgar, 1968). However, laboratory studies of the social behavior of several species of Peromyscus indicate that the typical pattern of interaction between males involves the establishment of dominant-subordinate relationships (Sheppe, 1966b), which has been referred to as territorial behavior (Eisenberg, 1962, 1963). In none of these studies has the simultaneous defense of two adjacent, mutually exclusive areas been shown as it has in house mice (Anderson and Hill, 1965).

This apparent contradiction between the results of studies of natural populations and those of laboratory studies may be a function of our incomplete knowledge of the social life of Peromyscus. No systematic observations of behavioral

interactions promoting dispersion in a natural population have yet been published. Therefore, the conclusion that Peromyscus is territorial is speculative at best, since it is based on data which indicate that adult members of the population tend to restrict their activities to only a part of the suitable habitat available. The results of laboratory studies, which indicate that male Peromyscus tend to establish dominance hierarchies without defending specific areas, may only suggest that we do not as yet know the basic parameters which influence the use of space by these animals. For example, in studies of house mice, territories or dominance hierarchies are formed depending on the density of the population, complexity of the environment, and immediate prior experience of the individuals concerned (Crowcroft, 1955; Davis, 1958; Anderson, 1961; Crowcroft and Rowe, 1963; Anderson and Hill, 1965; Reimer and Petras, 1968; Mackintosh, 1970). The influence of such parameters is largely unknown in Peromyscus, although some studies of the influence of the presence of others upon activity have been made (Orr, 1959; Kavanau, 1963).

Prior to labeling Peromyscus as territorial, detailed knowledge of both the utilization of space by individuals and the influence of the presence of others is essential. Such knowledge is unlikely to come from field studies because of the inherent difficulties in observing small, nocturnal rodents in the field, and because it is difficult to determine

how an individual utilizes space when the influence of the presence of other population members cannot be controlled. Therefore, the present study, conducted in the laboratory, was designed to control the amount of space available to an individual and the type of possible social interactions. Further, by conducting the study in the laboratory it was possible to observe social interactions.

This experiment was designed to record first the pattern of space utilization of individuals and then to determine the effect upon the pattern of doubling the amount of space available. With the increase in space individuals either had access to twice the area in the absence of any other mouse, or they encountered another individual, of equal experience, that had been inhabiting the new area available. Thus the relative influence of the amount of space available and of social interactions upon patterns of space utilization could be determined.

The two species used in this study were P. maniculatus bairdi and P. leucopus noveboracensis. Although these two species have been studied frequently, relatively little is known of their social life. Nicholson (1941, p. 233) suggested that the social life of the two species is "closely similar" although he reported that P. m. bairdi tended to be found in bisexual pairs in nest boxes more frequently than P. leucopus, which were found singly. A detailed comparison of the social aspects of space utilization of these two

species may not only clarify differences and similarities between these two species, but may also indicate some principles generally applicable to the entire genus.

These two species were chosen for comparison in this study because they inhabit distinct, although slightly overlapping habitats; P. leucopus occupies woodlands and P. maniculatus is found in neighboring grassland areas (Burt, 1940; Nicholson, 1941; Howard, 1949). It was expected that the pattern of space utilization of these two species would differ under the assumption that different types of environment require different patterns of utilization. Although the determination of species differences was not a major objective of this study, it was expected that the effect of the space and social manipulations might be emphasized by the differences between the two species.

LITERATURE REVIEW

Territorial behavior is a frequently discussed but often misunderstood phenomenon. The misunderstanding has resulted because of the indiscriminate application of the term territorial behavior to describe all social regulation of the dispersion of animal populations. Often species have been described as territorial even though they have never been shown to exhibit any form of territorial behavior. Also, confusion has resulted because many authors have assumed that territoriality is the only mechanism whereby population dispersion is maintained. However, territorial behavior may be only one possible mechanism promoting spacing in populations. Therefore, the primary concern of investigators should not be whether a species is territorial, but rather, whether the species exhibits any form of social behavior which limits the utilization of space of individuals. A review of the concepts of territoriality and of socially restricted space utilization is presented below. As an example of the confusion that can result when species are described as territorial without corroborative behavioral evidence, the problem of territoriality in Peromyscus will be discussed. Finally, an experimental approach designed to determine the influence

of social interactions upon space utilization in Peromyscus will be outlined.

The concept of territoriality was first delineated for birds. Although observations of the phenomenon date from the writings of Aristotle (Lack, 1944; Nice, 1953), much of the ground work for recent studies of territoriality was laid by Howard (1920). The extension of the concept from birds to the movements in space of other animals probably was done first by Heape (1931). The relationship between territoriality and movements within the home range in mammals, and in rodents in particular, was discussed by Burt (1940, 1943, 1949). Many recent authors note that territoriality occurs throughout the vertebrate phyla as well as in some invertebrate groups. Of these authors Wynne-Edwards (1962, 1964), has made the most noteworthy contribution. His views of territoriality as a population regulatory mechanism and associated theories of group selection have promoted a controversy which, in turn, has lead to a large number of scientific investigations which may not have been conducted otherwise.

A territory is most frequently defined as "any defended area" (Noble, 1939). This definition of the territory has been criticized as too limited and leading to conventionalized thinking (Emlen, 1957), since behaviors such as the advertisement of possession of the area as well as overt attack and threat are used to "defend" the area (e.g., Wynne-Edwards,

1962). A useful definition of territoriality would be one similar to that suggested by Anderson and Hill (1965): Territoriality is a behavioral phenomenon which effects the exclusion of some category of conspecific organisms from space inhabited by an individual or group. Such a definition emphasizes the spatial and social aspects of territoriality, but does not implicate any particular social behavior as the mechanism. Also, there is no specification as to particular attributes of the space such as what the space is used for or whether it is stationary or "moves" as the resident moves. Any such specification would limit the generality of the definition since only a few species may use the space in a similar way. Attempts to categorize territorial behavior among social organization systems (Fisler, 1969) may require as many categories of territories as there are species to be categorized. Categorization of the different types of social systems does reveal that a variety of approaches are used by different species in regulating the use of space. However, the cataloging of species differences is of little value unless it leads to a better understanding of some biological principle. The principle in this case is the social restriction of space use, not territorial behavior.

Territoriality is a phenomenon of populations. Although the behavior may be exhibited by individuals, it is relevant only as a population parameter which promotes the exclusion of conspecifics. By excluding each other, population members

move apart until the whole population becomes evenly dispersed (Calhoun, 1963). Such a regulation of the dispersion pattern of a population has been postulated as a mechanism to control or limit the size of the local population (Wynne-Edwards, 1962). However, it should be noted that the evidence used to support this theory of population regulation has been brought under serious question recently (Brown, 1969). Although territorial behavior may promote an even or equal spacing of population members, it is not valid to assume that an even pattern of dispersion results from territorial behavior. An even pattern may occur in species in which individuals avoid contact with each other but do not defend any areas. In those species for which no direct observations of any form of territorial behavior have been published the assumption of territoriality is speculation.

The characterization of a species as territorial seems to have depended upon the visibility of that species to human observers. Because of their songs and diurnal activity birds are relatively easy to locate and observe. This is undoubtedly why territoriality was first described in birds. The domestic dog (Tinbergen, 1951; Krushinskii, 1960) is another familiar, visible example. Among rodents many species with diurnal habits are easily observed, which may, in part, be why squirrels (Blair, 1953) and black-tailed prairie dogs (King, 1955) have been described as territorial. Those nocturnal species which display territorial behavior include the

intensely studied Norway rat (Calhoun, 1962 a and b; Barnett, 1963), and house mouse (Eibel-Ebesfeldt, 1950; Crowcroft, 1955; Davis, 1958; Anderson, 1961, 1964; Anderson and Hill, 1965; Reimer and Petras, 1967; Mackintosh, 1970, and Vessey, 1967). As an indication of the confusion that exists concerning the phenomenon of territoriality, the occurrence of territorial behavior in house mice is still questioned despite the increasing supportive evidence (Scott, 1966). Although some other nocturnal rodents have been described as territorial, such as Apodemus (Brown, 1966), some heteromyid rodents (Eisenberg, 1963a), and some species of Peromyscus (Burt, 1940; McCabe and Blanchard, 1950; Eisenberg, 1962, 1963b), the evidence of territoriality is not convincing and may be circumstantial. In Peromyscus, for example, conclusions of territoriality are based only upon dispersion patterns observed in natural populations (Burt, 1940; Metsgar, 1968). Further, evidence from laboratory studies indicates that Peromyscus males establish dominant-subordinate relationships without maintaining mutually exclusive areas (Eisenberg, 1963b; Sheppe, 1966b).

The problem of determining if territorial behavior occurs in Peromyscus leads to a more basic issue. Are we concerned with whether a species exhibits territorial behavior per se, or are we concerned with whether the species exhibits some sort of behavior that would promote spacing of population members? I suggest that the latter should be of primary

concern since territorial behavior is only one mechanism whereby spacing within a population can be maintained. A behavioral mechanism that has been suggested to promote spacing in Peromyscus populations is mutual avoidance (Terman, 1961; see Stickel, 1968 for review). Such avoidance behavior, though active need not be overt or directed towards intruders.

An even more fundamental question than whether a species exhibits socially restricted space utilization is whether social interactions influence space utilization at all. If social interactions do not influence use of space then questions concerning restricted use of space mediated by any social mechanism are irrelevant. Therefore, for any species we should determine first, if social interactions influence space utilization, second, if this influence results in restricted space use, and third, what behaviors promote this restriction of space use. Only after these determinations have been made can a classification of territory types according to factors such as, the function, season, duration etc. become useful (Nice, 1943; Fisler, 1969). Because these factors are species specific and individually variable within a species, it is difficult to draw general conclusions concerning territorial behavior. However, if we consider the spacing of population members as the general phenomenon, then variability in territorial behavior is not too surprising or confusing. Since species differ with respect to many different behaviors, different social behaviors are to be

expected even when these different behaviors achieve the same end.

As has been pointed out above, the evidence concerning territoriality in Peromyscus is contradictory. Our understanding of territoriality in this genus may have become confused by attempting to study factors related to territorial behavior before determining if social interactions influence space utilization. Little is actually known concerning space utilization itself. For example, investigations of space utilization in relation to resources have shown that individuals in an artificial population relocated their areas of activity in response to the experimental moving of a food hopper (Sheppe, 1966a). Also, by examining trails used by individuals Blair (1951) determined that much of a mouse's movement was near or associated with food sources. However, systematic, replicated observations of an individual's movements and use of the food and water resources in its environment are lacking.

Studies have been made to determine if social interactions influence activity or the location of individuals in populations. Although two studies compared solitary individuals to mice in social situations by measuring the amount of activity, there is little information concerning effects of social factors on activity (Falls, 1968). Kavanau (1963) in a one trial experiment found that two adult female Peromyscus maniculatus influenced each other's level of

behavior, whereas Orr (1959) found no difference in activity level whether one or six adult male P. leucopus were present. From the results of trapping, tracking, and nest-box utilization studies it has been hypothesized that the recorded movement of individuals in natural populations is restricted by the presence of other members of the population. This hypothesis cannot be tested by recording the gross movements of individual population members (see Stickel, 1968) because a single individual's own pattern of space utilization cannot be determined independently when other population members are always present. Nor can the reinvasion of an area made void by the removal of the resident (Stickel, op. cit.) show that the removed individual has excluded the others from its area because there is no way of determining if the other population members would not have moved in anyway. Also, other individuals may regularly travel through the removed individual's area but avoid entering traps while the resident is present. The logical extension of the removal type of experiment is to re-introduce the individual to its former area and determine if the other population members leave. This was attempted once in an artificially structured island population but the results are equivocal. The removed individual disappeared from the population shortly after being re-introduced (Sheppe, 1966a). Clearly, the evidence purported to show exclusion of other population members from studies of natural and semi-natural populations is circumstantial at best. A direct test would require comparison of

space utilization data of solitary individuals with similar data of individuals in social situations.

Our lack of quantified data not only on the influence of social interactions upon space utilization, but on every aspect of space utilization gave rise to the accompanying study. To determine the influence of social interactions, the utilization of space by solitary individuals was compared to that of pairs of individuals. A variety of dependent variables were measured as indices of space utilization to determine patterns of space use as completely as possible. These variables included, amount and location of two types of activity, amount and location of food and water consumption, and choice of nest site. Further, two species were examined in order to gain some insight into the generality of the results.

METHODS

Animals

A total of 160 mice, 80 *Peromyscus maniculatus bairdi*, and 80 *P. leucopus noveboracensis* was used. All mice were decendants of wild-caught stocks which had been bred in the laboratory for no more than five generations. This avoided variability in behavior which may result from domestication of the stock (Price, 1967). Variation in behavior due to effects of age was avoided by using only young adults, 90-150 days of age, and by setting a maximum age difference of twelve days for those individuals that met in experimental social encounters. To avoid the influence of previously established social bonds, siblings never met in experimental social encounters.

From weaning at 21 days all mice were held in 11 x 5 x 6 in plastic laboratory cages as bisexual sibling groups of two to six individuals. Four weeks before being used in the experiment, two individuals of opposite sex were selected from the sibling groups according to the following criteria: litters consisted of both sexes, only males with scrotal testes and females with perforate vagina, and neither pregnant nor nursing females were chosen. Non-sibling pairs of the opposite sex were housed on either side of a $\frac{1}{4}$ in mesh

hardware cloth partition positioned in the center of one of the above cages. Such a partition enabled the members of a pair to see, hear, smell and touch each other, but it prevented pregnancy which would have increased the variation in behavior of the females. These pairs served only to keep the mice socialized. The members of such pairs did not meet each other, nor did they meet a sibling of their partner in an experimental social encounter.

Experimental animals were selected from the non-sibling pairs. Each individual was weighed, ear-punched and had an area of fur clipped from one hip to facilitate identification.

The above treatment of individuals provided similar conditions for all mice prior to their use in the experiment. Thus most of the observed variability in behavior was due to a combination of the genetic heterogeneity within the population and to the effects of the experimental treatments.

Apparatus

Four 12 x 6 ft experimental enclosures were used. Each was constructed of plywood panels 3 ft high and rested on a concrete floor. The enclosure was partitioned into quadrants of 3 ft x 6 ft each in a separate corner (Figure 1). Adjacent compartments were connected by one 1.5 in diameter hole. A vertically swinging plastic door covered each hole and, by means of a micro-switch, recorded passages by the mouse on an

Figure 1. Floor plan of experimental enclosures indicating the location of food and water stations, running wheels, nest boxes, screen covers, and doors between compartments.

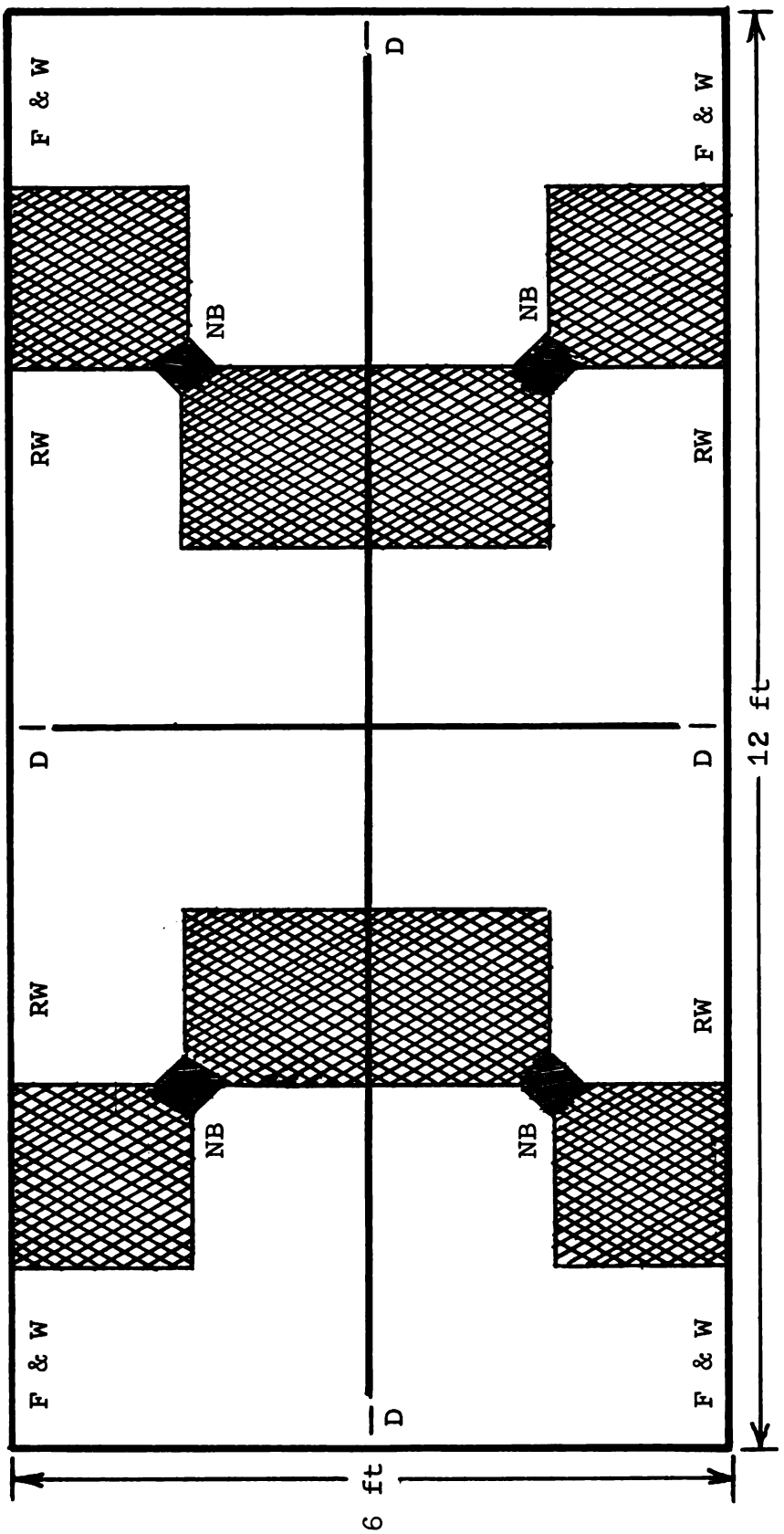
F & W
D
NB
RW
12 ft
6 ft
F&W - Food & Water
RW - Running Wheel
D - Door
NB - Nest Box
- Shelter

Figure 1

event recorder and electric counter. Each hole could be closed with a sliding metal door.

Each compartment was equipped with a food hopper, water bottle, running wheel, nest box, and overhead cover. The food hoppers were made of ¼ in mesh hardware cloth and were filled at the beginning of each experiment with Purina Mouse Breeder Chow. Water was available from 100 ml glass graduated cylinders mounted up-side-down outside each compartment. Each cylinder was equipped with a one hole rubber stopper and a metal drinking tube. The tube fitted into a hole drilled through the wall of the enclosure. Each running wheel was wired to an electric counter. The nest box was positioned in the center of each compartment in association with two 1.5 ft squares of ¼ in mesh hardware cloth, held on 4 in high lengths of wood, which provided overhead cover (Figure 1).

An enclosure was lighted by four 7.5 watt white, incandescent bulbs each suspended over the center of a compartment, and by one 100 watt bulb over each half of the enclosure. The light cycle was 16 hours of "daylight" (100 watts) and 8 hours "dark" (7.5 watts) with the latter from 7:30 p.m. to 3:30 a.m. The levels of illumination were approximately 16 foot candles for daylight and 0.5 foot candles for dark.

The experimental enclosure was designed to observe the movements and social interactions of mice. An observer positioned on a platform over the center of each enclosure could see individually identifiable mice throughout all four

compartments. A much larger or more complexly structured enclosure would have interfered with identification of individuals, and a much smaller enclosure would have restricted the movements of the mice. Indoor enclosures avoided variability in behavior due to changes in weather and habitat conditions.

Prior to experimental testing individuals were held in activity cages (2 x 1 x 1 ft with a $\frac{1}{4}$ in mesh screen floor). Each cage was divided into two compartments. Passage between compartments was possible through a vertically swinging door which activated an electric counter. A running wheel wired to an electric counter was positioned in one compartment of each cage. The other compartment contained a food hopper, water bottle, and nest box. The light cycle and levels of illumination in the cages were the same as those in the experimental enclosures.

The experimental enclosures were housed in the subbasement of the Chemistry Building on the Michigan State campus. The activity cages were housed in small chambers in the Biology Research Center. Both buildings were air-conditioned. Over the year, the temperature in the Chemistry Building varied between 60° and 75° F. Temperatures in the Biology Research Center ranged about five degrees higher.

Experimental Design

The experiment investigated the influence of social interactions on space utilization by comparing space utilization

of solitary individuals to that of pairs. To adjust for individual variation every individual supplied its own base-line data for comparison to those obtained during experimental manipulation. Base-line data were obtained during one week when each individual had private access to two adjacent compartments of an experimental enclosure. The various experimental treatments were applied during the following week when all four compartments in an enclosure were made available. The design in Table 1 shows that an individual experienced one of the following experimental treatments: 1. It had access to the whole enclosure without meeting another individual. 2. It met a conspecific individual of the same sex with the same experience. 3. It met a conspecific individual of the opposite sex with the same experience.

Table 1. Experimental Design, Showing the Number of Replicated Trials for Each Species-Social Treatment Combination.

Treatment	Sex	Species	
		P.m.b.	*P.l.n.*
Solitary	M	10*	10
	F	10	10
Social	M v M	10	10
	M v F	10	10
	F v F	10	10

* = number of replicates

Prior to testing in the experimental enclosures all mice were maintained as solitary individuals in activity cages. This period of 13 days acquainted the mice with running wheels, door, food hoppers, water bottles, and nest boxes similar to those in the experimental apparatus. This familiarization period was included since it has been shown that activity, as measured by running wheels, stabilizes only after several days of exposure (Dice and Hoslett, 1950; Kavanau, 1967). Thus the first week in the experimental enclosures was expected to supply relatively stable base-line data for comparison to those when the experimental treatments came into effect during the second week.

Procedure

An individual experienced the following sequence: 1. It was selected from the stock maintained in the segregated pair cages, ear-punched, fur-clipped, examined for external signs of sexual maturity (i.e., scrotal testes in males and perforate vagina in females), and weighed. 2. It was maintained in an activity cage for 13 days. Body weights were obtained on day 13. 3. It was then introduced into one half of the experimental enclosure. 4. It was weighed at the end of the week and returned to the compartment from which it was taken. 5. At the beginning of the second week the experimental treatments (Table 1) were applied by opening all of the doors between the four compartments. 6. At the end of

this second experimental week it was removed from the enclosure and weighed. 7. Males were returned to the colony or discarded. Females that had met males were held alone for 3 weeks to record if they had a litter. Those females that did not produce litters were examined for the condition of the ovaries and for evidence of embryo resorption.

Measures (dependent variables)

Food and Water Consumption. Food consumption was determined by weighing to the nearest 1/10 gm each food hopper once per day. No correction for spillage of food was made because the mice ate most of the food that spilled from the hoppers, and the amount remaining was too small to be measured reliably. A daily correction was made for changes in relative humidity with control food hoppers. Weight changes in the control hoppers were added to or subtracted from the weights of hoppers available to the mice.

Water consumption was also determined once per day. Water levels were estimated to the nearest 1/10 ml and subtracted from the prior days reading. The amount of water consumed was adjusted by an evaporation factor: the mean daily water loss measured over weekly intervals from control bottles. Since one ml of water weighs approximately one gm, water consumption was expressed in gms to facilitate comparison to food consumption.

To provide a standard measure for comparisons between the species, the datum used for analysis was the mean amount consumed daily per gram body of weight during each week of the experiment. The mice were weighed only at the beginning of each week so the mean body weight per week was used. When two individuals were present consumption was calculated as the total grams consumed per grams of mice present.

Each day the food hopper and water bottle from which the largest amount had been consumed were noted. The number of changes of these preferences was analysed as a measure of the strategy employed by each species in exploiting its environment.

Activity. Each morning between 8:00 and 9:00 a.m. the number of wheel and door counts from the preceding 24 hours was recorded. In addition, the number of counts occurring between the morning data collection and 5:00 p.m. each afternoon was also recorded as an estimate of diurnal activity.

The wheel with the greatest number of revolutions was noted each day so that changes in preference could be determined. Shifts in running wheel preference were analysed in conjunction with shifts in the location of food and water consumption preferences to provide an over-all measure of the strategy employed by each species. Door usage was analysed on the basis of the mean number of door counts per day for each week per door available per individual present. Daytime activity was analysed as the number of days per week during which any measurable daytime activity occurred.

Choice of Nest Site. The nest site occupied by each individual was recorded every day. Occupancy of a nest box was observed by blocking the entrances to the nest box and removing the sliding top far enough to identify any occupants. Use of a nest site other than a nest box was recorded, as was the mutual occupancy of a nest site. The nest site data were analysed with regard to the number of shifts of location, and the frequency and duration of mutual nest site use. Also, the location of the nest site occupied mutually was recorded to determine if that nest site had been the preferred site of one of the two individuals prior to their nesting together. The sex and relative social position of the individual that moved in to share the nest site of the other were the data compiled for analysis.

Observation of Social Interactions. In the social treatments dominance was ascertained during the first night when all doors were opened. The doors were opened just prior to the night phase of the light cycle and the mice were observed until one had clearly become established as the social dominant or until four hours had elapsed. The dominant individual was the one whose activities caused the other individual to assume a subordinate posture (Eisenberg, 1968) or to move away. More aggressive manifestations of dominance included attacking and chasing of the subordinate individual.

On nights two, three, four, and seven, of the week, observations were made between 7:30 and 9:00 p.m. because

the mice were very active during this period. At 15 second intervals the location and activity of both individuals in an enclosure were recorded during two non-sequential 10 minute sample periods on all four nights. Data analysed included the frequency of simultaneous occupancy of the same compartment, the frequency of social interactions and the frequency of aggressive interactions. Also, the number of times each individual moved from one compartment to another was analysed with regard to the sex and social status of that individual. An estimate of the proportion of time spent in social activities was obtained from the frequency of social encounters data.

Analysis of Data

The data were analysed with a repeated-measures design analysis of variance (Bruning and Kintz, 1968). The various significant factors were further analysed with Duncan's New Multiple Range tests (Li, 1964). All data met the assumption of variance homogeneity, as tested by maximum variance divided by total variance (Bliss, 1967) or were transformed prior to analysis. All data were also examined for any relationship between the means and variances (Bliss, 1967). In those instances where non-parametric statistics were used the procedures followed were those of Seigel (1956).

RESULTS

Food and Water Consumption

Food and water consumption were examined to determine any effect of doubling the available space of one mouse in the presence or absence of another individual. Doubling the space significantly increased the amounts of food and water consumed, however, the presence or absence of another individual did not affect consumption (Table 2). Most of the increase in consumption associated with doubling the space was contributed by *P. leucopus* (see ratios in Table 3). This suggests that *P. leucopus* was influenced more by the space increase than was *P. maniculatus*. Although *P. maniculatus* consumed significantly more over-all than *P. leucopus*, most of this difference was due to the former's greater consumption of food prior to the doubling of space. Because consumption was determined on a per gram of body weight basis it provided a crude measure of relative metabolic rates. Therefore, after space was doubled, all animals had a higher metabolic rate which undoubtedly reflects an over-all increase in activity.

Table 2. Analysis of Variance of Food and Water Consumption in Grams per Gram of Body Weight.

Source	DF	MS	F	P
Total	399			
Between Subjects	99			
Species	1	1,284,142	5.02	<0.05
Treatments	4	192,139	0.75	NS
Species x Treatment	4	349,016	1.36	NS
Error	90	255,986		
Within Subjects	300			
Space	1	4,604,458	92.38	<0.005
Measures	1	32,503,681	652.13	<0.005
Space x Measures	1	762,653	15.30	<0.005
Space x Species	1	563,550	11.30	<0.005
Space x Treatment	4	167,404	3.36	<0.01
Species x Measures	1	1,644,293	32.99	<0.005
Treatment x Measures	4	123,830	2.48	<0.05
Space x Species x Measures	1	91,325	1.83	NS
Space x Species x Treatment	4	6,732	0.14	NS
Space x Treatment x Measures	4	108,476	2.18	NS
Species x Treatment x Measures	4	37,593	0.75	NS
Space x Species x Treatment x Measures	4	26,272	0.53	NS
Error	270	49,842		

Table 3. Consumption Data in Grams per Gram Body Weight.

Species	*P. maniculatus*				*P. leucopus*			
Measures	Food		Water		Food		Water	
Space	2	4	2	4	2	4	2	4
Mean	0.153	0.162*	0.192	0.212*	0.125	0.142*	0.183	0.224*
(Std. error)	(0.003)	(0.003)	(0.004)	(0.005)	(0.003)	(0.007)	(0.003)	(0.007)
$\frac{\text{4 Space}}{\text{2 Space}}$[a]	1.05		1.10		1.14		1.22	

a = Ratio indicates relative consumption with increased space, i.e., $\frac{0.162}{0.153} = 1.05$.

* = Significant change with space increase.

Activity

Three measures of activity were examined to determine if the amount of activity was influenced by doubling space in the presence or absence of another individual.

Wheel Running. P. maniculatus exhibited significantly more wheel running activity than P. leucopus, however, only the latter species was influenced by the increase in space. This was shown by the reduction in wheel running activity by P. leucopus after the space was doubled (Tables 4 and 5). Amongst the treatments, only the solitary females of both species showed a significant reduction in wheel running when space was increased (Table 5). This result suggests that, to females of both species the presence of another individual, regardless of sex, is a significant factor. Females in the presence of another individual did not react as solitary females did by decreasing their running wheel activity when space was doubled. Running wheel activity in males of both species was not influenced by either an increase in space or by the presence of another individual of either sex.

Door Counts. P. maniculatus moved between adjacent compartments of the enclosures significantly more often than P. leucopus (Tables 6 and 7). The difference between the species was further emphasized in that only P. maniculatus reacted to the doubling of space by significantly reducing the number of movements between adjacent compartments. The presence of another individual was an important factor related

Table 4. Analysis of Variance of Wheel Running Activity.

Source	DF	MS	F	P
Total	199			
Between Subjects	99			
Species	1	727,665,471	12.87	<0.005
Treatments	4	37,806,291	0.67	NS
Species x Treatments	4	40,235,365	0.71	NS
Error	90	56,523,008		
Within Subjects	100			
Space	1	6,705,854	14.87	<0.005
Space x Species	1	1,834,762	4.07	<0.05
Space x Treatments	4	21,140,490	46.88	<0.005
Space x Treatments x Species	4	51,027,830	113.15	<0.005
Error	90	450,989		

Table 5. Daily Means of Wheel Running Activity.

Treatment		Species				Treatment Means (Species Pooled)	
		P. maniculatus		P. leucopus			
		2 Space	4 Space	2 Space	4 Space	2 Space	4 Space
Solitary	M	7172	7832	1475	1114	4324	4473
	F	5976	4244*	2193	1228*	4084	2736*
Social	MvM	3747	3482	2625	2258	3186	2870
	MvF	5038	5149	2423	1919	3730	3534
	FvF	7991	8343	3092	2500	5542	5421
Space Means		5985 (1046)	5810 (990)	2361 (385)	1804* (258)	4173 (586)	3807* (549)
Species Means		5897.5 (720)		2082.5[a] (233)			

* = Significant change with space increase.

[a] = Significant species difference.

( )= 1 Standard Error.

Table 6. Analysis of Variance of Square Root of Number of Door Counts per Door Available per Individual Present.

Source	DF	MS	F	P
Total	199			
Between Subjects	99			
Species	1	551	27.40	<0.005
Treatments	4	57	2.82	<0.05
Species x Treatments	4	11	0.55	NS
Error	90	20		
Within Subjects	100			
Space	1	46	7.36	<0.01
Space x Species	1	92	14.78	<0.005
Space x Treatments	4	23	3.66	<0.01
Space x Treatments x Species	4	12	1.90	NS
Error	90	6		

Table 7. Daily Means of the Square Root of the Number of Door Counts per Door Available per Individual Present.

Treatment		Species				Treatment Means (Species Pooled)	
		P. maniculatus		P. leucopus			
		2 Space	4 Space	2 Space	4 Space	2 Space	4 Space
Solitary	M	9.4	7.0	4.9	3.4	7.15	5.20*
	F	10.2	6.3	5.7	3.8	7.95	5.05*
Social	MvM	8.3	8.4	5.8	7.7	7.05	8.05
	MvF	13.1	9.6	5.6	8.6	9.35	9.10
	FvF	9.8	7.9	5.4	5.9	7.60	6.90
Space Means		10.16 (0.80)	7.84 (0.45)	5.48 (0.14)	5.88 (0.51)	7.82 (0.47)	6.86* (0.69)
Species Means		9.00 (0.47)		5.68[a] (0.27)			

* = Significant change with space increase.

a = Significant species difference.

( )= 1 Standard error.

to the number of times that members of both species moved between adjacent compartments. When only solitary individuals of either sex were present, there was a significant reduction in door usage per door available (Table 7). When two individuals were present there was no significant change in number of door counts per door per individual present when space was doubled. This indicates that the presence of another individual promoted an increase in movement throughout an enclosure compared to situations where only one individual was present.

Daytime Activity. P. leucopus was active during the daylight phase of the light cycle on a significantly greater number of days than P. maniculatus (Tables 8 and 9). Daytime activity significantly increased with doubled space only among social treatments (Table 9). This shows that for both species only the presence of another individual, regardless of sex, contributed to the increase in daytime activity.

Shifting of Preference Sites

The number of times individuals, or social pairs, shifted their preference (most used in one 24 hour period) among the available running wheels, food hoppers, and water stations provide a measure of the strategy employed by each species in exploiting its environment. P. leucopus shifted its preference sites more frequently than P. maniculatus, but exhibited no difference between the number of shifts of wheel,

Table 8. Analysis of Variance of Daytime Activity.

Source	DF	MS	F	P
Total	199			
Between Subjects	99			
Species	1	370	67.62	<<0.005
Treatment	4	10	1.74	NS
Species x Treatment	4	4	0.71	NS
Error	90	5		
Within Subjects	100			
Space	1	40	30.38	<<0.005
Space x Species	1	0.5	0.38	NS
Space x Treatment	4	7	5.36	<0.005
Space x Species x Treatment	4	0.4	0.30	NS
Error	90	1.3		

Table 9. Mean Number of Days of Daytime Activity.

Treatment		Species				Treatment Means (Species Pooled)	
		P. maniculatus		*P. leucopus*			
		2 Space	4 Space	2 Space	4 Space	2 Space	4 Space
Solitary	M	1.20	1.30	3.00	3.10	2.10	2.20
	F	0.60	0.60	3.00	3.00	1.80	1.80
Social	MvM	0.40	2.40	3.35	5.30	1.88	3.85*
	MvF	0.90	1.90	3.95	5.10	2.42	3.50*
	FvF	0.25	1.10	3.15	4.90	1.70	3.00*
Space Means		0.67 (0.16)	1.46 (0.27)	3.29 (0.29)	4.28 (0.31)	1.98 (0.21)	2.87* (0.25)
Species Means		1.065 (0.162)		3.785[a] (0.217)			

* = Significant change with space increase.

a = Significant species difference.

( ) = 1 Standard error.

food, and water preference sites (Tables 10 and 11). The over-all species difference probably resulted because P. maniculatus displayed significant differences in the number of shifts of the three types of preference site (Table 11). Both species reacted to increased space, and consequently, to the doubled number of potential preference sites, by shifting their preferences more frequently (Table 11). The presence of another individual did not significantly influence the number of shifts of preference.

Nesting

Number of Nest Sites. The number of nest sites occupied by an individual measures the frequency at which the nest site is shifted in response to the presence of another individual and to the availability of more nest sites. P. leucopus shifted its nest site more frequently than P. maniculatus. Both species used more nest sites when more nest sites became available with the doubling of space. The difference between the species and that due to the space increase resulted largely from the proportionately greater number of nest sites used by P. leucopus after space was doubled (Tables 12 and 13). Therefore, P. leucopus was most influenced by the space increase. Neither the presence, nor the sex, nor the relative social status ("Hierarchy", in Table 12) of another individual had any influence on the number of nest sites used.

Table 10. Analysis of Variance of Number of Wheel, Food, and Water Preference Sites.

Source	DF	MS	F	P
Total	599			
Between Subjects	99			
Species	1	22.04	7.28	<0.01
Treatments	4	5.96	1.97	NS
Species x Treatments	4	0.57	0.19	NS
Error	90	3.03		
Within Subjects	500			
Space	1	171.70	114.45	<<0.005
Measures	2	5.63	3.75	<0.05
Space x Measures	2	2.57	1.71	NS
Space x Species	1	2.04	1.36	NS
Space x Treatment	4	0.72	0.48	NS
Species x Measures	2	18.28	12.18	<0.005
Treatment x Measures	8	0.65	0.43	NS
Space x Species x Treatment	4	0.83	0.55	NS
Space x Species x Measures	2	0.92	0.61	NS
Space x Treatment x Measures	8	0.43	0.28	NS
Species x Treatment x Measures	8	2.27	1.51	NS
Space x Species x Measures x Treatment	8	1.87	1.25	NS
Error	450	1.50		

Table 11. Mean Number of Preference Sites

	P. maniculatus			*P. leucopus*			
	Wheel	Food	Water	Wheel	Food	Water	Space Means
2 Space	1.75	2.58	2.15	2.73	2.12	2.43	2.29 (0.06)
4 Space	2.62	3.66	3.06	3.52	3.60	3.72	3.36* (0.09)
Measure Mean	2.18 (0.13)	3.12 (0.15)	2.60[b] (0.13)	3.12 (0.14)	2.86 (0.15)	3.08[c] (0.15)	
Species Mean	2.64 (0.08)			3.02[a] (0.08)			

* = Significant change with space increase.

a = Significant species difference

b = Measure means for *P. maniculatus* all differ at p = 0.05.

c = Measure means for *P. leucopus* do not differ at p = 0.05.

( ) = 1 Standard error.

Table 12. Analysis of Variance of Number of Nest Sites.

Source	DF	MS	F	P
Total	319			
Between Subjects	159			
Hierarchy	3	2.21	1.11	NS
Sex	1	1.65	0.82	NS
Species	1	53.63	26.92	<<0.005
Hierarchy x Sex	3	5.14	2.58	NS
Hierarchy x Species	3	3.68	1.85	NS
Species x Sex	1	2.28	1.14	NS
Hierarchy x Species x Sex	3	0.88	0.44	NS
Error	144	1.99		
Within Subjects	160			
Space	1	87.15	47.93	<<0.005
Space x Hierarchy	3	2.10	1.16	NS
Space x Sex	1	0.53	0.29	NS
Space x Species	1	22.58	12.42	<0.005
Space x Hierarchy x Sex	3	2.09	1.15	NS
Space x Hierarchy x Species	3	0.04	0.02	NS
Space x Sex x Species	1	4.28	2.35	NS
Space x Hierarchy x Species x Sex	3	0.13	0.07	NS
Error	144	1.82		

Table 13. Number of Nest Sites Occupied.

Species	*P. maniculatus*		*P. leucopus*	
Space	2 Space	4 Space	2 Space	4 Space
Mean	1.80	2.31	2.09	3.66
(Std. Error)	(0.13)	(0.15)	(0.15)	(0.18)
$\frac{\text{4 Space}}{\text{2 Space}}^{a}$	1.29*		1.75*	

a = Ratio indicates relative number of nest sites used with increased space.

* = Significant change with increased space.

Use of Nest Boxes. P. maniculatus nested in the nest boxes more frequently than P. leucopus. This difference is illustrated in Table 14. Because P. maniculatus almost always occupied the nest boxes (i.e., 1109 out of 1120 possible occasions) it was not included in further analyses. When not occupying nest boxes, P. maniculatus nested in a corner of one of the shelters. P. leucopus also nested in the shelters, but was also found nesting in the plastic tunnels leading to the doors between compartments and was even found sleeping on the running wheels. With the doubling of space, P. leucopus occupied nest boxes more frequently than before (Tables 15 and 16). Of the 80 P. leucopus tested, only eight, four males and four females, did not occupy a nest box on at least one morning during the two weeks of measurement.

Table 14. Use of Nest Boxes: Mean Days per Week.

	P. maniculatus	P. leucopus
Mean	6.93	4.43
(Std. error)	(0.04)	(0.23)

Table 15. Analysis of Variance of Use of Nest Boxes by *P. leucopus*.

Source	DF	MS	F	P
Total	159			
Between Subjects	79			
Sex	1	0.01	0.0004	NS
Treatment	3	14.86	1.0047	NS
Sex x Treatment	3	1.87	0.1266	NS
Error	72	14.79		
Within Subjects	80			
Space	1	45.16	25.2143	<0.005
Space x Sex	1	0.06	0.0313	NS
Space x Treatment	3	3.12	1.7437	NS
Space x Treatment x Sex	3	1.66	0.9247	NS
Error	72	1.79		

Table 16. Use of Nest Boxes by P. leucopus: Mean Days per Week Both Sexes Pooled.

	Solitary	Heterosexual Pairs	Unisexual Pairs		Space Means
			Dominant	Subordinant	
2 Space	3.90	3.60	3.25	4.85	3.90 (0.34)
4 Space	4.25	5.20	4.65	5.75	4.96* (0.29)
Treatment Means	4.08 (0.49)	4.40 (0.43)	3.95 (0.46)	5.30 (0.39)	

* = Significant change with space increase.
( ) = 1 Standard error.

Mutual Nesting. The number of days that two animals nested together was taken as a measure of their readiness to establish a social relationship. Heterosexual pairs of P. maniculatus were together on a significantly greater number of days than were pairs of all other groups (Tables 17 and 18). Heterosexual pairs of P. leucopus were together no more frequently than were members of unisexual pairs of both species.

If two individuals nested together on at least one day they were considered to have moved together and were scored as such in the totals columns of Table 19. All heterosexual pairs of P. maniculatus nested together and nine of the ten P. leucopus heterosexual pairs eventually nested together.

Table 17. Analysis of Variance of Days of Mutual Nesting.

Source	DF	MS	F	P
Total	59			
Species	1	6.02	1.21	NS
Treatment	2	49.40	9.93	<0.005
Species x Treatment	2	16.07	3.23	<0.05
Error	54	4.98		

Table 18. Duncan's Test on Mean Days of Mutual Nesting.

Species	*P. leucopus*			*P. maniculatus*		
Treatment	MvM	FvF	MvF	MvM	FvF	MvF
Mean	2.50	2.80	3.80	2.00	2.50	6.50
(Std. error)	(0.79)	(0.49)	(0.79)	(0.80)	(0.83)	(0.17)

Those means subtended by the line do not differ at p = 0.05.

Table 19. Mutual Nesting: Sex and Social Rank of Intruder.

		Unisexual Pairs			
				Totals	
		Dominant Moved In	Subordinant Moved In	Moved Together	Remained Separate
P. maniculatus	Males	0	4	4	6
	Females	3	3	6	4
	Total	3	7	10	10
P. leucopus	Males	1	5	6	4
	Females	2	7	9*	1*
	Total	3*	12*	15*	5*

	Heterosexual Pairs			
			Totals	
	Male Moved In	Female Moved In	Moved Together	Remained Separate
P. maniculatus	1*	9*	10*	0*
P. leucopus	4	5	9*	1*

* = Deviation from expected binomial frequency of 0.5 significant at $p < 0.05$.

P. leucopus females eventually nested with other females as frequently as they nested with males. This suggests that P. leucopus females did not respond with regard to the sex of their nesting partners.

The location of the mutual nest site was examined with regard to the location of the preferred nest site of the two individuals. All pairs that nested together did so in a nest site that one of the individuals had occupied alone on the preceding day. The results are summarized in Table 19 with regard to the social status and sex of the individual that moved in to share the other individuals preferred nest site. Among unisexual pairs, only in P. leucopus, when both sexes were considered simultaneously, did a significant pattern emerge where the subordinate individual moved in to share the nest site of the dominant. Among heterosexual pairs, only in P. maniculatus was there a significant pattern where the female moved in with the male. These data show that the two species differ greatly in their mutual nesting habits.

Observations of Social Interactions

Occurrences Together. The frequency of the simultaneous presence of two individuals in the same compartment was examined for species, social treatment, and temporal differences. The species and social treatments showed no significant differences (Table 20). The difference between days was due to the more frequent simultaneous occupancy of a compartment

Table 20. Analysis of Variance of Occurrences Together in the Same Compartment.

Source	DF	MS	F	P
Total	191			
Between Subjects	47			
Species	1	275.5	0.57	NS
Treatment	2	1,149.2	2.39	NS
Species x Treatment	2	807.2	1.68	NS
Error	42	480.7		
Within Subjects	144			
Days	3	1,239.2	6.11	<0.005
Days x Species	3	54.7	0.27	NS
Days x Treatment	6	197.1	0.97	NS
Days x Species x Treatment	6	73.6	0.36	NS
Error	126	202.9		

on day 7 (Table 21). The means in Table 21 are expressed in Figure 2 as percentages. In both species individuals avoided each other at the beginning of the week but by day 7 they began to spend a significant portion of time together.

Location of Meeting. For all observation periods, the number of simultaneous occupancies per compartment was examined to determine if these meetings were spatially organized. For both species the distribution of meetings was not random as both met in only one of four compartments a disproportionate number of times (Table 22). P. maniculatus met relatively more frequently in one compartment than did P. leucopus (Table 23).

The compartment within which an individual appeared most frequently as the sole occupant was called the preferred compartment of that individual. The number of simultaneous occupancies of each compartment was then examined with regard to whether the meeting occurred in a compartment preferred by either of the two individuals. In both species there is a significant bias toward meeting in a compartment that at least one of them prefers to occupy when alone (Table 24). Neither sex nor social position was a significant factor in determining the location of meetings.

Occurrence of Social Interactions. The number of overt social interactions occurring while both mice were in the same compartment was examined as a direct measure of social organization. As used here social interactions included acts

Table 21. Duncan's Test on Means of Occurrences Together Across Days.

Day	2	3	4	7
Mean[a]	15.69	17.98	17.06	26.90

a = Means subtended by the line do not differ at p = 0.05.

Table 22. Mean Percent of All Meetings in Compartment of Most Meetings.

Species	P. maniculatus	P. leucopus
Mean[a]	71.14%	59.93%
(Std. error)	(3.26)	(3.50)

a = Random expectation = 25.0%

Figure 2. Percentage of time two individuals were simultaneously present in the same compartment.

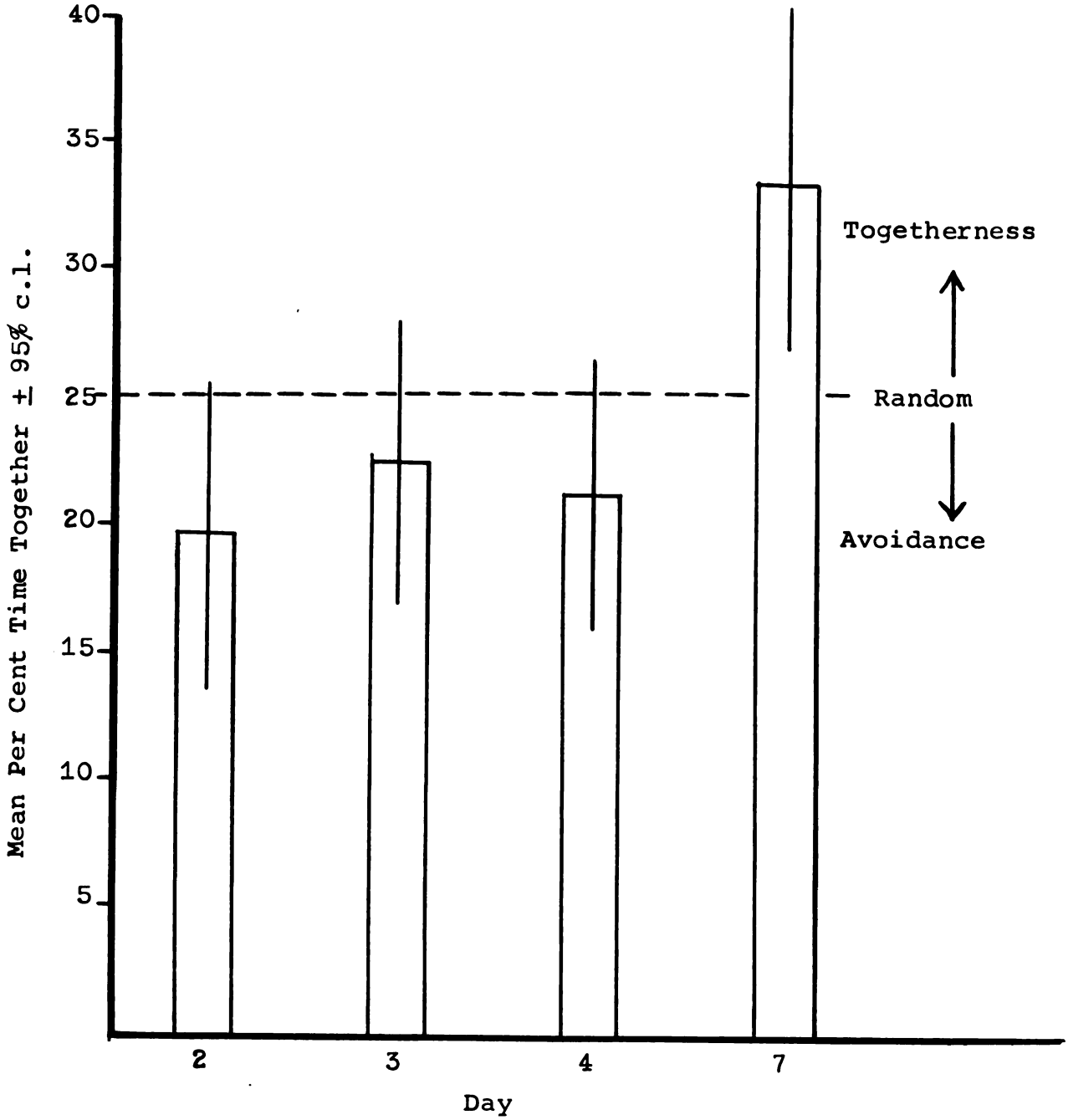
40
35
30
25
20
15
10
5
Mean Per Cent Time Together ± 95% c.l.
Togetherness
Random
Avoidance
2
3
4
7
Day

Figure 2

Table 23. Analysis of Variance of Number of Meetings in Compartment of Most Meetings.

Source	DF	MS	F	P
Total	47			
Species	1	731.64	5.39	<0.025
Treatment	2	97.41	0.72	NS
Species x Treatment	2	44.62	0.33	NS
Error	42	135.76		

Table 24. Relationship of Compartment of Most Meetings to Individual Preferences.

Meet in Individuals' Preference	*P. maniculatus*			*P. leucopus*			Total
	MvM	MvF	FvF	MvM	MvF	FvF	
Yes	6	8	8	6	7	6	41*
No	2	0	0	2	1	2	7

* = Deviation from expected equal distribution in all four compartments (2,2,2,2) significant at $p < 0.001$.

of aggression, such as fighting and chasing, and other instances where the behavior of one individual was obviously influenced by the other individual. If the two individuals entered a nest box at the same time or if both ran on the same running wheel at the same time these acts were scored as social interactions. Unlike the number of mutual occupancies of a compartment, the number of social interactions was significantly greater in heterosexual pairs than in the other social treatments (Tables 25 and 26). The increased number of interactions on day 7 (Table 27) is undoubtedly related to the greater frequency of simultaneous occupancy of the preferred compartment on that day (Table 20).

Occurrence of Aggressive Interactions. The number of aggressive interactions was examined for species and social treatment differences. The significant treatment effect was due to P. leucopus male-male pairs which engaged in significantly more aggressive interactions than all other groups (Tables 28 and 29). The over-all frequency of aggressive interactions was low.

Movement. The number of times each individual moved between compartments revealed the effect that the sex and social status of one individual had upon the movements of the other individual. The only difference was between species with P. maniculatus moving more frequently than P. leucopus (Tables 30 and 31). This agrees with the difference in over-all use of doors shown in Tables 6 and 7. These results show

Table 25. Analysis of Variance of Number of Social Interactions.

Source	DF	MS	F	P
Total	191			
Between Subjects	47			
Species	1	35.02	0.60	NS
Treatment	2	240.30	4.09	<0.025
Species x Treatment	2	28.55	0.49	NS
Error	42	58.72		
Within Subjects	144			
Days	3	202.70	3.28	<0.025
Days x Species	3	110.20	1.78	NS
Days x Treatments	6	43.82	0.71	NS
Days x Species x Treatments	6	40.94	0.66	NS
Error	126	61.80		

Table 26. Duncan's Test on Means of Social Interactions of Treatments.

Treatment	FvF	MvM	MvF
Mean	4.09	4.38	7.66

Means subtended by the line do not differ at p = 0.05.

Table 27. Duncan's Test on Means of Social Interactions Across Days.

Day	2	3	4	7
Mean	4.85	4.50	3.79	8.40

Means subtended by the line do not differ at p = 0.05.

Table 28. Analysis of Variance of Number of Aggressive Encounters.

Source	DF	MS	F	P
Total	191			
Between Subjects	47			
Species	1	4.08	1.10	NS
Treatments	2	32.63	8.50	<0.005
Species x Treatments	2	9.29	2.50	NS
Error	42	3.72		
Within Subjects	144			
Day	3	2.50	1.82	NS
Day x Species	3	2.36	1.71	NS
Day x Treatment	6	1.53	1.11	NS
Day x Treatment x Species	6	0.79	0.58	NS
Error	126	1.37		

Table 29. Duncan's Test on Mean Number of Aggressive Encounters per Day.

Species	P.m.b.	P.l.n.	P.l.n.	P.m.b.	P.m.b.	P.l.n.
Treatment	FvF	FvF	MvF	MvF	MvM	MvM
Mean	1.16	1.16	1.53	1.81	1.97	3.13

Means subtended by the line do not differ at p = 0.05.

Table 30. Analysis of Variance of Number of Moves During Observations of Social Animals.

Source	DF	MS	F	P
Total	383			
Between Subjects	95			
Species	1	664.13	4.5	<0.05
Sex	1	370.13	2.5	NS
Hierarchy	2	390.54	2.6	NS
Species x Sex	1	120.38	0.8	NS
Species x Hierarchy	2	227.95	1.5	NS
Sex x Hierarchy	2	114.39	0.8	NS
Species x Sex x Hierarchy	2	270.70	1.8	NS
Error	84	149.16		
Within Subjects	288			
Days	3	102.22	1.6	NS
Days x Species	3	118.80	1.9	NS
Days x Sex	3	39.82	0.6	NS
Days x Hierarchy	6	38.69	0.6	NS
Days x Species x Hierarchy	6	47.23	0.7	NS
Days x Sex x Hierarchy	6	46.57	0.7	NS
Days x Species x Sex	3	38.08	0.6	NS
Days x Species x Sex x Hierarchy	6	13.86	0.2	NS
Error	252	63.37		

Table 31. Movement During Observations of Social Interactions.

Species	P. maniculatus	P. leucopus
Mean	11.81	9.18
(95% conf.)	(0.73)	(0.59)

that both animals present, regardless of sex and social rank, move between compartments with equal frequency. From direct observations, these movements did not occur in a tandem relationship except when a dominant individual was chasing a subordinant. The species means in Table 31 are higher than those in Table 7 because the observations for the former were made during a peak activity period.

Amount of Time Spent in Social Activities. The number of occurrences of overt social interactions was examined as an index of sociability. Since the species did not differ in either number of occurrences together in the same compartment (Table 20), or in the number of overt social interactions (Table 25), the species totals were pooled. The proportion of time that Peromyscus spends in overt social activities is small (Table 32).

Table 32. Time Spent in Social Interactions.

Time Spent in the Same Compartment	
Number of Occurrences	= 3726
Percent of Total Time	= 24.3%
Time Spent Interacting	
Number of Occurrences	= 824
Percent of Time when in Same Compartment	= 22.6%
Percent of Total Time	= 5.5%

Age and Weight as Determinants of Social Position

Differences in age and weight between individuals that met in unisexual social encounters were examined to determine if either factor was related to social position. There was no significant age or weight difference between dominant and subordinant individuals of either species. The age and weight means on the day two individuals were allowed to meet are presented in Table 33.

Reproduction

The establishment of heterosexual pair bonds was indicated by the production of offspring. Nearly all P. manículatus females produced a litter (Table 34). P. leucopus

Table 33. Age and Weight Means of Dominant and Subordinant Individuals.

Species	*P. maniculatus*				*P. leucopus*			
Sex	Males		Females		Males		Females	
Social Position	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.	Dom.	Sub.
Age (days) Mean	136.7	139.5	135.2	134.9	146.5	148.3	138.8	140.8
(Std. error)	(4.7)	(4.5)	(3.6)	(4.2)	(4.2)	(3.4)	(4.0)	(3.8)
Weight (gm) Mean	17.9	17.6	17.2	15.8	19.7	19.2	19.0	18.0
(Std. error)	(0.6)	(0.6)	(0.3)	(0.8)	(0.7)	(0.6)	(0.8)	(0.6)

Table 34. Reproduction.

Litter Born	P. maniculatus	P. leucopus
Yes	9	0
No	1	10

females never produced litters and apparently never became pregnant since placental scars were never found. This suggests that P. leucopus females failed to come into estrus during their one week of exposure to males. P. maniculatus females came into estrus on about the third day of exposure to males. The gestation period for P. maniculatus is approximately 21 days, and the litters were born a mean of 24.7 ± 0.4 days after the pairs were allowed to meet.

DISCUSSION

The hypothesis tested in this study was that both the amount of space available and social interactions would influence the utilization of space in two species of Peromyscus. Three independent variables, amount of space, social treatment, and species were examined for their influence upon several dependent variables, which served as indices of space utilization. The amount of space and social treatment are discussed here with the intent of establishing which of them most consistently influenced space utilization in the two species. In addition, a discussion of the establishment of social relationships by the two species is presented.

Amount of Space

The utilization of space was influenced by the amount of space available. When the available space was doubled, significant changes occurred in a variety of dependent variables which represented a wide range of behavioral responses on the part of the mice (Table 35). How each of these variables was influenced by the space change has been described in the results section, however, the fact of primary significance here is that all of the variables were influenced as a result of doubling available space.

Table 35. Summary of Main Effects.

Dependent Variable	Analysis Table Number	Independent Variable		
		Space	Treatment[a]	Species
Consumption	2	+	-	+
Wheel Counts	4	+	-	+
Door Counts	6	+	+	+
Day Activity	8	+	-	+
Preference Shifts	10	+	-	+
No. of Nest Sites	12	+	-	+

+ = Significant difference or effect.

- = No significant difference.

a = Includes sex and social status variables when applicable as well as the major social treatments.

All individuals utilized the additional space made available. With access to an increased number of running wheels, food and water stations, and nest sites the mice shifted their preferences more frequently than before (Tables 10, 11, 12, and 13). This agrees with Howard's (1949) observation that when more nest boxes were placed in the home range of P. maniculatus the animals shifted their nest site with increased frequency. That both species often move their nest sites has been described by several authors (Burt, 1940; Nicholson, 1941; Blair, 1948; Howard, 1949) and that P. leucopus shifts its home range in response to changes in

the location of a food hopper has been shown (Sheppe, 1966a). The results of the present study suggest that both species often shift their preferred sites for all their activities and that the frequency at which these shifts occur is directly related to the number of available sites. These results indicate that Peromyscus is very labile in its manner of utilizing available resources. Such a trait would be of high survival value in an environment where the location and amounts of various resources change frequently.

P. maniculatus and P. leucopus utilized space differently. This difference stemmed primarily from the absolute differences between the species within all of the dependent variables listed in Table 35. Also, as shown by the significant interactions between space and species in Table 36, the species frequently differed in the degree to which they responded to the increase in available space. Although both species shifted their preferences with a greater frequency with the increase in space, they each had their particular strategy for exploiting the increased space. P. leucopus shifted its preference sites for food, water, and wheel running at the same frequency but more frequently than P. maniculatus (Tables 10 and 11). P. maniculatus shifted its preference sites for food, water, and running wheels at different frequencies.

It was expected that these two species would utilize space differently, because it was assumed that each species

Table 36. Summary of Two Factor Interaction Effects.

Dependent Variable	Analysis Table Number	Interaction		
		Space x Treatment	Space x Species	Species x Treatment
Consumption	2	+	+	-
Wheel Counts	4	+	+	-
Door Counts	6	+	+	-
Day Activity	8	+	-	-
Preference Shifts	10	-	-	-
No. of Nest Sites	12	-	+	-

+ = Interaction is significant.
- = Interaction is non-significant.

would exhibit a pattern of space utilization most suitable to the type of habitat in which it is found. The determination of whether patterns of space utilization are related to the type of habitat in which a species is found must await further comparative studies. However, it is suggested here that the quantitative analysis of the utilization of space will yield a clearer understanding of the relationship between a particular species and the habitat in which it is found than will any further studies which show that a species tends to prefer one type of habitat to another (Harris, 1952; Wecker, 1963).

There was a marked species difference in daytime activity. P. leucopus was active during the daylight hours on more days

than P. maniculatus (Tables 8 and 9). Also, P. leucopus was often observed sleeping in a running wheel or nesting in some other exposed part of the enclosure. In contrast, P. maniculatus almost always occupied nest boxes (Table 17). The tendency for P. leucopus to be out of nest boxes may have been the factor contributing to its being active during the daylight hours. Animals nesting in exposed locations would be more likely to be disturbed by stimuli exterior to the enclosure (e.g., the experimenter) and become active. That these two species exhibit measurable daytime activity has been reported by several authors (see Falls, 1968), however, the direct comparison of these species has not been made previously.

Social Treatments

The two species responded similarly to the various social treatments. This is indicated in that all of the species-treatment interactions in Table 36 are non-significant. Therefore, despite differences between the species and differences in their use of space, the influence of the presence or absence of another individual had the same general effect upon both species. Perhaps social factors have the same general influence upon space utilization throughout the genus Peromyscus. The validity of this speculation can be established through further comparative studies.

The over-all influence of the social treatments is not readily apparent. Compared to the effects of space and of

species, social treatment, as a first order variable, appeared inconsequential since it significantly influenced only movement between compartments (Table 25). However, it must be remembered that the social treatments came into effect only with the doubling of space so that any influence of these treatments is most likely to appear in interactions with space. In Table 36 the majority of interactions between space and treatment are significant which gives evidence that social factors do influence space utilization. These statistical interactions were primarily produced by the differences between solitary and social individuals.

Solitary and social animals differed greatly in their movement between compartments. Solitary individuals reacted to the increase in space by moving between adjacent compartments less frequently than previously. Social individuals, in comparison, showed an increase in movement through space (Tables 6 and 7). The difference between these treatment types was so large that it resulted in treatments appearing as a significant first order variable (Table 35). In contrast, Orr (1959) found that the presence of another individual resulted in no change in activity in P. leucopus males held in a large out-door enclosure, however, some activity other than the one measured could have increased and this would have gone undetected. Kavanau (1963) observed that two P. maniculatus females, when together, exhibited a level of activity that was intermediate to the activity levels

exhibited when both were alone. Whether this intermediate level of activity represented the mean of the two individual levels or a net increase in overall activity was not made clear.

Daylight activity increased only in those mice that met other individuals when space was doubled (Tables 8 and 9). With two mice present, those individuals either became more reactive to stimuli exterior to the enclosure or were so reactive to each other's activity that some measurable activity (e.g., wheel or door count) resulted. Although the social individuals increased their consumption of food and water with the doubling of space more than those individuals in solitary trials, these differences were not significant (Tables 2 and 3). The absolute amounts consumed were similar to those summarized for each species by King (1968).

Only solitary females of both species exhibited a significant decrease in wheel running with the doubling of space (Table 36), which indicates that females were influenced more by the presence or absence of another individual than were males (Tables 4 and 5). Such a sex difference may have important consequences in the formation of social relationships. That two P. maniculatus females influence each other's activity level has been suggested from the one trial test of a relatively sophisticated activity measuring apparatus (Kavanau, 1963).

The conclusion to be reached here is that social factors significantly influence the utilization of space by these two

species, and that the two species are influenced in the same general way. Also, since the species reacted differently to the increase in space, social treatment, not the amount of space available, has the most consistent influence upon space utilization. Therefore, the influence of social factors should be more fully examined in further studies of the use of space by Peromyscus.

Because social interactions play such a significant role in influencing space utilization it could be assumed that they would involve a large proportion of the animal's time. However, the two species spend only about five percent of their time in social interactions (Table 32). King (1955) notes that black-tailed prairie dogs spend a similar proportion of their time involved in social interactions. That social interactions involve such a small proportion of time, yet still have a major influence upon space utilization only serves to underscore the statement that social factors are important regulators of patterns of space utilization.

Social Relationships

In this study an attempt was made to determine how social relationships became established in the two species and to determine how sex and social status influenced some of their behavior patterns. The formation of social relationships in the two species is revealed by the patterns of mutual nesting and by the direct observation of social interactions.

When nesting, individuals in social trials avoided each other for at least the first three days of the week, except for heterosexual pairs of P. maniculatus which almost always nested together from the first day (Tables 14 and 15). However, when active, all individuals in social trials avoided each other for the first three days and by the last day of the week they were together in the same compartment more frequently than by random chance (Tables 20 and 21, and Figure 2). Most pairs also nested together by the last day. Since more social interactions occurred during the last day than on previous days temporal factors were involved in establishing social relationships. Also, on the last day of the week, there were significantly more social interactions than during the other days (Table 27).

Although territorial behavior has been suggested to occur in Peromyscus (Burt, 1940), there is no direct evidence to support this suggestion (Blair, 1953). Evidence that individuals tend to avoid each other has been noted in P. leucopus (Sheppe, 1966a) and in P. manciulatus (Terman, 1961). Although social encounters were spatially organized in the present study (Tables 22, 23, and 24), no behavior patterns which could be described as the aggressive defense of mutually exclusive areas were ever observed. In fact, as has been noted previously (King, 1957), the social interactions of Peromyscus were typified by their low frequency of aggression (Table 29). It would seem, therefore, that the

even dispersion patterns observed in natural populations of Peromyscus result more from mutual avoidance than from aggressive defense of specific areas.

Heterosexual pairs of both species exhibit a significant tendency to nest together for at least one day (Table 16). Also, when a male and female of either species were present simultaneously in the same compartment of an enclosure, they interacted significantly more frequently than members of unisexual pairs (Tables 25 and 26). This suggests that sexual recognition occurred in both species, although only P. manículatus pairs produced litters whereas P. leucopus apparently did not even mate (Table 34). A lack of placental scars was taken as indicating mating had not occurred, however, with this criterion it must be remembered that mating may have occurred and the pregnancy was aborted before implantation.

If the failure of P. leucopus to reproduce was due to one of the sexes failing to recognize the other, this lack of sexual recognition may also be reflected in other behaviors. This might give some clue as to which sex failed to recognize the other. Males apparently recognized other males since male-male pairs of P. leucopus engaged in more aggressive interactions than any other social treatment (Table 29). Also, males nested with females more frequently than with other males (Table 16) although the mean length of time of mutual nesting did not differ (Table 15). That females are more reactive than males to the presence of

another individual of either sex has already been noted. However, the females nested as frequently and for as long with males as with females (Table 16). It therefore, appears that the females failed to recognize the males, or it may be that P. leucopus females require a longer exposure to males before they become sexually receptive than do P. maniculatus females. That estrus in P. maniculatus females is induced after about three days of exposure to males has been shown by Bronson and Marsden (1964) and was confirmed by the present reproduction data. No evidence of male induction of estrus in P. leucopus females has been reported.

Among unisexual pairs of both species the relative social position of each member of a pair was not related to any difference in their activity levels (Table 31). Healey (1967) observed that dominant individuals tended to be more active than subordinants. However, he measured activity for only one short period during one 24-hour session and the differences he reports may indicate only relative activity levels upon exposure to a novel situation. Neither a difference in age nor weight influenced the outcome of social encounters (Table 33). This may have been due in part to the relatively small differences between the individuals that met.

This study has shown that both the amount of space available and social interactions influence the utilization

of space in *P. maniculatus* and *P. leucopus*. As was expected, because they occupy different habitat types, the two species utilized space, and reacted to the increase in space, differently. However, both species reacted in the same relative way to the presence of another individual, and this resulted even though the species did display different social relationships. Since social interactions influenced both these species in the same way, it suggests that other species of the genus may be similarly influenced. So that general statements concerning the influence of social interactions on the use of space in *Peromyscus* may be made, further studies with more species are required. However, there is a statement concerning territoriality in *Peromyscus* that can be made at present. *Peromyscus* is not territorial according to the commonly accepted definition of territorial behavior. This definition at least implies an active defense of an area, either by direct aggression or through active advertisement of the possession of the area. The initial reaction of two individuals in the present study was active avoidance which persisted for several days, and there was no evidence of any aggressive defense of an area. However, the distribution of individuals in natural populations of *Peromyscus* is similar to that seen in species that do defend their territories. Therefore, it appears that *Peromyscus* maintains a territorial type of spatial organization without defending territorial boundaries.

The confusion resulting from this argument merely reflects the confusion in the literature because of the word "territoriality." I suggest that we are not concerned with whether a species is "territorial" or not, but rather if the species exhibits some form of social behavior that restricts the space utilization of individuals. The mechanism for socially limiting space utilization may be aggressive defense, active advertisement of possession of an area, or mutual avoidance, and any or all of these mechanisms may be employed by a species./ An important first step in studying social restriction of space use is the determination of whether or not social interactions influence space utilization. The present study has shown that space utilization by Peromyscus is influenced by social interactions and that the typical social interaction is one of initial avoidance.

SUMMARY

1. The hypothesis tested in this study was that both the amount of space available and social interactions would influence the utilization of space in two species of Peromyscus.

2. A total of 160 mice, 80 P. maniculatus bairdi and 80 P. leucopus noveboracensis was used. Individuals were permitted access to two adjacent enclosures of a four-compartment enclosure for a period of one week. For an additional week access to all four compartments was permitted. The two new compartments were either vacant or were occupied by a conspecific individual of similar experience. Within each species both sexes were tested as solitary individuals or they met another individual of the same or opposite sex.

3. Dependent variables measured daily in each compartment were amount of food and water consumed, amount of running wheel activity, and choice of nest site. By comparing these data from each compartment, site preferences and changes in preference could be determined. The number of movements between compartments was also measured daily. In addition, direct observations of social interactions were recorded.

4. The utilization of space was influenced by the amount of space available; the doubling of space was accompanied by changes in all of the dependent variables.

5. All individuals utilized the additional space; with access to an increased number of running wheels, food and water stations, and nest sites the mice shifted their preferences more frequently than before.

6. The two species utilized space differently; they differed in the absolute values of all dependent variables, reacted differently to the increase in space, and exhibited species specific strategies for exploiting the increased space.

7. That the species would use space differently was predicted since it was expected that each species would exhibit a pattern of space utilization most suitable to the exploitation of the habitat in which it is found.

8. The species differed significantly in reproductive success; nine of ten P. maniculatus pairs produced litters while P. leucopus pairs failed to reproduce.

9. Direct observations show that when two individuals are allowed to meet their initial reaction is one of avoidance; no behavior that could be interpreted as defense of mutually exclusive areas was observed.

10. It was concluded that Peromyscus is not territorial, but that the avoidance behavior observed could promote the type of dispersion patterns reported in natural populations.

BIBLIOGRAPHY

BIBLIOGRAPHY

Anderson, P. K. 1961. Density, social structure, and non-social environment in house mouse populations, and implications for the regulation of numbers. Trans. N. Y. Acad. Sci., 23: 447-451.

Anderson, P. K. 1964. Lethal alleles in Mus musculus: Local distribution and evidence for isolation of demes. Science, 145: 177-178.

Anderson, P. K. and J. L. Hill. 1965. Mus musculus: Experimental induction of territory formation. Science, 148: 1753-1755.

Barnett, S. A. 1963. The rat. A study in behavior. Methuen and Co., London.

Blair, W. F. 1948. Population density, life span, and mortality rates of small mammals in the blue-grass associations of southern Michigan. Amer. Midl. Nat., 40: 395-419.

Blair, W. F. 1951. Population structure, social behavior, and environmental relations in a natural population of the beach mouse, Peromyscus polionotus leucocephalus. Contrib. Lab. Vert. Biol. Univ. Mich. No. 48: 1-47.

Blair, W. F. 1953. Population dynamics of rodents and other small mammals. Adv. Gen., 5: 20-37.

Bliss, C. I. 1967. Statistics in biology. Vol. 1. McGraw-Hill, New York.

Bronson, F. H. and H. M. Marsden. 1964. Male-induced synchrony of estrus in deermice. Gen. and Comp. Endocrin., 4: 634-637.

Brown, L. E. 1966. Home range and movement of small mammals. Zool. Soc. London. Symp., 18: 111-142.

Brown, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull., 81: 293-329.

Bruning, J. L. and B. L. Kintz. 1968. Computational handbook of statistics. Scott, Foresman and Co. Glenview, Ill.

Burt, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Mis. Publ. Mus. of Zool. Univ. Mich. No. 45.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mamm., 24: 346-352.

Burt, W. H. 1949. Territoriality. J. Mamm., 30: 25-27.

Calhoun, J. B. 1962a. The ecology and sociology of the norway rat. U.S.D.A.H.E.W., Publ. Health Service, viii+288 pp.

Calhoun, J. B. 1962b. A behavioral sink. In: E. Bliss (Ed.), Roots of behavior, New York.

Calhoun, J. B. 1963. The social use of space. In: W. Mayer and R. VanGelder (Eds.), Physiological mammology, Vol. 1. Academic Press, New York.

Crowcroft, P. 1955. Territoriality in wild house mice (Mus musculus). J. Mamm., 36: 299-301.

Crowcroft, P. and F. P. Rowe. 1963. Social organization and territorial behavior in the wild house mouse (Mus musculus L.) Proc. Zool. Soc. Lond., 140: 517-531.

Davis, D. E. 1958. The role of density in aggressive behavior in house mice. Anim. Behav., 6: 207-210.

Dice, L. R. and S. A. Hoslett. 1950. Variation in the spontaneous activity of Peromyscus as shown by recording wheels. Contrib. Lab. Vert. Biol., Univ. Mich. No. 47.

Eibl-Eibesfeldt, I. 1950. Beitrage sur Biologie der haus und der zhrendmaus neban einigen beobachtungen an anderen nagern. Zeit. fur Tierpsychol., 7: 558-587.

Eisenberg, J. F. 1962. Studies on the behavior of Peromyscus maniculatus gambelli and P. californicus parasiticus. Behavior, XIX: 178-207.

Eisenberg, J. F. 1963a. The behavior of heteromyid rodents. U. C. Publ. in Zool., 69: 1-100.

Eisenberg, J. F. 1963b. The interspecific social behavior of some cricetine rodents of the genus Peromyscus. Amer. Midl. Naturalist, 69: 240-246.

Eisenberg, J. F. 1968. Behavior patterns. In: J. A. King (Ed.), Biology of Peromyscus (Rodentia). Spec. Publ. No. 2 Amer. Soc. of Mamm.

Emlen, J. T., Jr. 1957. Defended area? - A critique of the territory concept and of conventional thinking. Ibis, 99: 352.

Falls, J. B. 1968. Activity. In: J. A. King (Ed.), Biology of Peromyscus (Rodentia). Spec. Publ. No. 2 Amer. Soc. of Mamm.

Fisler, G. F. 1969. Mammalian organizational systems. Contrib. to Sci. Los Angeles County Museum No. 167: 1-32.

Harris, Van T. 1952. An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Contrib. Lab. Vert. Biol. Univ. Mich. No. 56: 1-53.

Healey, M. C. 1967. Aggression and self-regulation of population size in deermice. Ecology, 48: 377-392.

Heape, W. 1931. Emigration, migration and nomadism. W. Heffer and Son. Cambridge.

Howard, H. E. 1920. Territory and bird life. Dutton and Co., New York.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern, Michigan. Contrib. Lab. Vert. Biol. Univ. Mich. No. 43.

Kavanau, J. L. 1963. The study of social interaction between small mammals. Anim. Behav., 11: 263-273.

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

Krushinskii, L. V. 1960. Animal behavior--its normal and abnormal development. Consultants Bureau, New York.

Lack, D. 1944. Early references to territory in bird life. Condor, 46: 108-111.

Li, J. C. R. 1964. Statistical inference Vol. 1 Edwards Bros., Ann Arbor, Mich.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol. Univ. Mich. No. 67.

King, J. A. 1957. Intra- and interspecific conflict of Mus and Peromyscus. Ecology, 38: 355-357.

King, J. A. 1968. Psychology. In: J. A. King (Ed.), Biology of Peromyscus (Rodentia). Spec. Publ. No. 2 Amer. Soc. of Mamm.

Mackintosh, J. H. 1970. Territory formation by laboratory mice. Anim. Behav., 18: 177-184.

McCabe, T. T. and B. D. Blanchard. 1950. Three species of Peromyscus. Rood Associates, Santa Barbara.

Metzgar, L. 1968. Social organization and population regulation in the wood-mouse, Peromyscus leucopus (Fisher) Univ. Mich. Ph. D. Dissertation.

Nice, M. M. 1953. The earliest mention of territory. Condor, 55: 316-317.

Nicholson, A. J. 1941. The homes and social habits of the wood-mouse (Peromyscus leucopus noveboracensis) in southern Michigan. Amer. Midl. Naturalist, 25: 196-223.

Noble, G. K. 1939. The role of dominance in the social life of birds. Auk, 56: 263-273.

Orr, H. D. 1959. Activity of white-footed mice in relation to environment. J. Mamm., 40: 213-221.

Price, E. O. 1967. Behavioral changes in the deermouse, Peromyscus maniculatus bairdi, after seventeen years of domestication: Reaction to novel stimuli. Ph. D. Dissertation, Mich. State Univ.

Reimer, J. D. and M. L. Petras. 1967. Breeding structure of the house mouse, Mus musculus, in a population cage. J. Mamm., 48: 88-99.

Scott, J. P. 1966. Agonistic behavior of mice and rats: A review. Amer. Zool., 6: 683-701.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

Sheppe, W. 1966a. Determinants of home range in the deer mouse, Peromyscus leucopus. Proc. Calif. Acad. Sci., 34: 377-418.

Sheppe, W. 1966b. Social behavior of the deer mouse, Peromyscus leucopus. Wasmann J. Biol., 24: 49-65.

Stickel, L. F. 1968. Home range and travels. In: J. A. King (Ed.), Biology of Peromyscus (Rodentia). Spec. Publ No. 2. Amer. Soc. of Mamm.

Terman, C. R. 1961. Some dynamics of spatial distribution within semi-natural populations of prairie deermice. Ecology, 42: 288-302.

Tinbergen, N. 1951. The study of instinct. Oxford Univ. Press, London.

Vessey, S. 1967. Effects of chloropromazine on wild house mice. Ecology, 48: 368-376.

Wecker, S. C. 1963. The role of early experience in habitat selection by the prairie deermouse, Peromyscus maniculatus bairdi. Ecol. Monogr., 33: 307-325.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Hafner, New York.

Wynne-Edwards, V. C. 1964. Population control in animals. Sci. Amer., 211: 68-74.