SOCIABILTY AND INDIVIDUAL DISTANCE IN FOUR SPECIES OF RODENTS

Bedford M. Vestal*

Department of Biology, University of Missouri-St. Louis

Male *Rattus norvegicus*, *Mus musculus*, *Peromyscus leucopus*, and P. *maniculatus* were paired with conspecific strangers in a 1-m diameter open field for 5-min social tests. The average distance between individuals, latency to make contact, and number of 10-sec periods containing contacts were recorded. *Rattus* were most sociable, followed by *Mus.* The two *Peromyscus* species were least sociable and not different from each other. In *Rattus* and *Mus* average distance was less than a baseline distance calculated from the behavior of animals alone in the arena. *Rattus* were attracted to each other, *Peromyscus* individuals actively avoided each other, and *Mus* were intermediate in contact and avoidance. The differences in individual distance of these species in this situation may be related to the dispersion patterns in their natural populations.

INTRODUCTION

Understanding the relative sociability of a species can be critical to analysis of its social systems. The intraspecific social interactions of individuals within a population may lead to a characteristic social organization for a given species. The quantity and quality of interactions vary widely, but the sum of interactions may be described as attraction or repulsion among animals. When these sums or forces are in balance, we may see a characteristic dispersion pattern. Dispersion may also be considered in terms of the individual distance (1, 2) of animals. Dispersion becomes greater as individual distances increase. Social behavior thus involves space as a component. When animals maintain wide spacing, we consider them unsociable, and when close together, more sociable or gregarious.

Species of rodents vary widely in their sociability. The sociability associated with each species may, however, be a function of the situation in which they are observed. For example, wild Norway rats are gregarious in the field but intolerant of strangers (3). Laboratory rats have been considered less sociable, but, when given an opportunity for contact, exhibit considerable sociability (4) and do not exhibit differential reactions to familiar or strange animals (5).

I am interested in effects of various environmental and genetic factors on sociability in different species of *Peromyscus*. My results on *Peromyscus* (Vestal, unpublished data) are different from those on rats in terms of relative distance maintained between individuals, change in behavior over repeated encounters, and effect of familiarity in the testing arena (4, 5, 6). These species differences led me to compare four different species of rodents in the same social testing situation: *Peromyscus leucopus*, *P. maniculatus*, and laboratory strains of *Rattus norvegicus* and *Mus musculus*.

The basic questions asked were: (a) What is the relative sociability of different species tested in the same social situation? (b) Do various measures of sociability such as average distance maintained between individuals, latency to make contact, and number of contacts provide similar estimates of sociability?

MATERIALS AND METHODS

Peromyscus leucopus noveboracensis, the white-footed mouse, is a semi-arboreal form found in open-upland forests throughout the northeastern and midwestern United States. *Peromyscus maniculatus bairdi*, the prairie deermouse, is found in midwestern grasslands and is terrestrial in its habits. Reviews of the social behavior of these species are in Hill (7).

The *Peromyscus* were born and raised in the laboratory at the University of Missouri—St. Louis. They were descended (four to five generations removed) from mice wildtrapped in the vicinity of East Lansing, Michigan. Animals were left with parents

*Present Address: Department of Zoology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019

Proc. Okla. Acad. Sci. 57: 98-102 (1977)

until weaning at 21 days of age. Thereafter, they were housed as litters or in unisexual groups until experimental manipulation. At ages ranging from 80 days to 6 months of age, 20 males of each species were transferred to fresh cages (clear plastic, mesh top, 28 × 22 × 15 cm high, wood chip bedding, water and Purina mouse breeder chow *ad lib.*). The subjects were housed as pairs of strangers of approximately the same age for 9 to 28 days before testing. Pilot tests indicated that after 6 to 7 days together, the time together had no effect on test results.

The *Mus musculus* were derived from a Swiss-Webster albino strain and were laboratory born and raised. Twenty males were paired under the same conditions as the *Peromyscus* at 21 to 28 days of age and tested at 90 to 100 days of age.

Twenty male *Rattus norvegicus* of a University of Missouri—St. Louis laboratory strain of Sprague-Dawley origin were housed as pairs in hanging wire cages. The animals were paired at weaning (30 days of age) and tested at 60 to 75 days of age.

The range of age at testing differed for each species but did not appear to be a primary variable in this study. The *Peromyscus* and *Mus* were fully sexually mature while the *Rattus* were in early stages of maturity. The behavior of rats in this study did not differ appreciably from that described for 105-day-old rats (4).

All rodents were housed in a reverse-light cycle room for a minimum of 9 days before testing and tests were conducted during the dark part of the light cycle.

The circular testing arena was 1 m in diameter with 51-cm high walls. The wooden floor and sheet metal walls were painted flat white. The arena floor was divided by radians and circles into 49 sections of approximately equal area, patterned after Latané (4) (Figure 1). Each area was assigned a different number, 1-49, for use in recording animal locations. Light was provided by two 15-W frosted incandescent bulbs overhead and measured 29 to 32 lux on the floor of the arena.

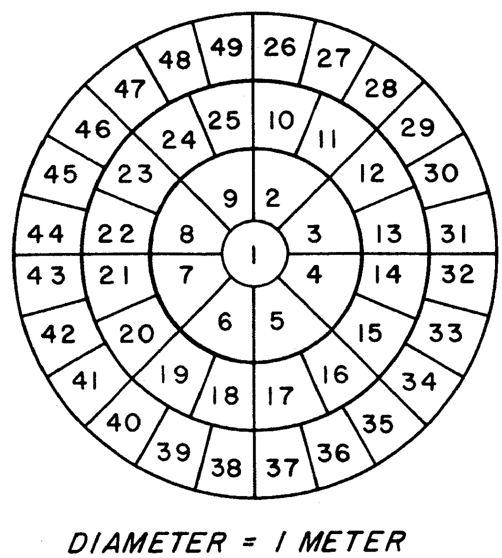

FIGURE 1. Diagram of the floor of the test arena.

Ten pairs of each species were tested, each pair consisting of strangers. Each animal was tested once. The rodents were taken from their cages, immediately placed under inverted cans 42 cm apart in the arena, and after approximately 30 sec were released for a 5-min test period. After each test the arena was thoroughly cleaned with a dilute vinegar solution.

At 10-sec intervals (30 per 5-min trial) each animal's location was noted by section number to provide 30 records of the simultaneous locations of the pair. If the animals had made at least one physical contact during the preceding 10-sec period, it was recorded. General behavior observations were noted at the end of each trial.

Distance between animals was calculated from the known distances between the centers of the sections in which the animals were simultaneously located. Distance ranged from 0 to 86.3 cm. To find the effects of animals on each other's movements, the average distance maintained between animals needs to be compared to some measure of "random" distance. The random or baseline distance would be that which resulted if animals moved about the arena without influencing each other. To obtain the baseline, on the day preceding the test, each member of a pair was placed alone in the arena. Its location was noted at 10-sec intervals for 5 min. The arena was cleaned after each animal. The location records for each pair member while alone were combined. These data for the pair members while alone were treated *as if* the animals

TABLE 1. *Mean and standard error of distance maintained between individuals, of baseline distance, and of deviation of observed distance from baseline during a five-min test period for various species.*[a]

	Rattus	*Mus*	*P. leucopus*	*P. maniculatus*
Distance (cm)	28.3 ± 1.7	40.0 ± 2.8	55.2 ± 3.0	57.2 ± 3.7
Baseline distance (cm)	51.4 ± 1.4	51.5 ± 1.2	52.9 ± 2.7	51.2 ± 1.6
Deviation from baseline (cm)	23.3[b] ± 2.4	11.5[b] ± 2.9	− 2.3 ± 4.0	− 6.0 ± 4.0

[a] Means not connected by common underline differ at $p < 0.05$
[b] Observed differences differ from baseline at $p < 0.05$.
N = 10 per species

had been together to provide a baseline distance measure (4). For each pair the distance while together was compared to the pair's own baseline record to control for position effects. Records of a single observer were used for analysis. Interobserver reliability was high, with an average deviation between observers for thirty pairs of 0.2 cm.

For determining changes in behavior over time the test period was divided into three 100-sec periods. Each of these contained ten records of location and is called a 10-record period.

Species differences in average distance maintained over the entire test period may reflect relative differences in the individual distance of the species. Changes in mean distances during the first through the third 10-record periods indicate any changes in behavior over time. Differences between observed distance and baseline distance estimate how much the animals repel or attract each other. Number of periods containing at least one contact (0-30) and the first period containing a contact (latency to first contact) can be compared with distance measures of sociability. If no contacts were made, it was assumed for purposes of analysis that one would occur in the next period (the thirty-first) after the test was completed. Comparisons were made by the appropriate analysis of variance or t-tests. For analysis of variance, significant differences between means were determined by the Least Significant Range Test (8) or, in the case of the three 10-record periods, by the Newman-Keuls procedure (9).

RESULTS

Average distance between individuals was lowest in *Rattus*, next highest in *Mus*, and highest in the two *Peromyscus* species (Table 1).

Deviation of average distance from the baseline distance for each pair showed that rats were again most socially attracted, with observed distances significantly lower than baseline. The *Mus'* observed distance was also significantly lower than their baseline. The deviation between observed and baseline values was not different from that of the rats. The *Peromyscus* species' deviations were significantly different from the *Rattus* and *Mus*, and observed values were greater than baseline, although not significantly so. Mean distance changed over the test period in all species (Table 2). In *Rattus*, distance in the second 10-record period was lower than in the first and third. The *Mus* distance decreased significantly over the three

TABLE 2. *Mean and standard error of distance (cm) maintained between individuals of* Rattus (R), Mus (M), Peromyscus leucopus (Pl), *and* P. maniculatus (Pm) *over three consecutive (A, B, C) 10-record periods.*[a]

R^B	R^A	R^C	M^C	M^B	M^A	Pl^C	Pl^B	Pm^C	Pm^B	Pm^A	Pl^A
23.3 ±3.8	30.3 ±2.4	31.4 ±2.6	33.7 ±2.5	39.7 ±3.6	46.5 ±4.0	51.6 ±2.3	52.4 ±4.0	53.9 ±4.4	56.6 ±3.9	61.2 ±5.3	61.7 ±5.3

[a] Means not connected by common underline differ at $p < 0.05$
N = 10 per species

periods. For both *Peromyscus* species distances were highest in the first period but did not decrease from second to third periods.

Essentially the same pattern of sociability emerged with latency to the first contact (Table 3). *Rattus* and *Mus* made contact significantly earlier than did the *Peromyscus*. Rats also made contacts with each other in significantly more periods than did the other species (Table 4). *Mus* made fewer contacts than *Rattus* but not significantly more than *P. maniculatus*. The *P. maniculatus* were not different from *P. leucopus* in number of periods containing contacts.

Correlations of the variables with each other also indicate their consistency as social indicators. In both *P. maniculatus* and *P. leucopus*, average distance was positively correlated with latency to first contact (r = 0.66, 8df, and r = 0.80, 8df, p<0.05) and negatively correlated with the number of contacts (r = –0.86, 8df, and r = 0.88, 8df, p<0.01), while latency was negatively correlated with the number of contacts (r = –0.79, 8df, and r = –0.85, 8df, p<0.01). The only significant correlation in either *Rattus* or *Mus* was a negative one between distance and number of contacts in *Mus* (r = –0.77, 8df, p<0.02). The lack of correlation in the latter species may be due to the lesser variation in their responses.

TABLE 3. *Mean and standard error of number of first ten-sec periods in which a contact occurred.*[a]

Rattus	*Mus*	*P. leucopus*	*P. maniculatus*
1.6	4.5	14.9	15.2
± 1.2	± 0.2	± 3.6	±13.5

[a] Means not connected by common underline differ at $p < 0.05$
N = 10

TABLE 4. *Mean and standard error of number of ten-sec periods containing contacts.*[a]

Rattus	*Mus*	*P. maniculatus*	*P. leucopus*
22.8	14.8	8.6	7.5
± 1.5	± 0.8	±2.7	±1.8

[a] Means not connected by common underline differ at $p < 0.05$
N = 10

DISCUSSION

In this testing situation laboratory *Rattus* are obviously the most sociable of the four species in all measures used. Laboratory *Mus* are next, followed by the two *Peromyscus* species, which did not differ from each other.

Distance measures of *Rattus* and *Mus* were significantly smaller than those expected by chance and indicate attraction of individuals to each other. Observation of the rats clearly indicated this. Once contact had been made the rats tended to remain in contact for long periods. They explored the arena with their heads while maintaining contact, or ventured apart for short periods to explore, followed by renewed contact. The rats were very active in sniffing and crawling over and under each other. Exploration of each other often seemed to take precedence over exploration of the arena.

Mus in the arena appeared less reactive to each other than did *Rattus*, spending less time in contact and more in exploration of the arena. Contact duration was not measured but three observers noted that contact durations of *Mus* were shorter than in *Rattus* and were longer than in *Peromyscus*. *Mus* did not crawl over and under as did rats but one often followed another nose-to-rear around the arena. The *Mus* did not appear to react to each other at distances of greater than 10 to 15 cm and would sometimes pass each other without overt reaction.

The *Peromyscus* appeared to actively avoid each other for long periods of time. On many occasions one mouse watched the other from across the arena (1 m) and followed the other's movements with its head. In many cases *Peromyscus* appeared to maintain the greatest possible distance between themselves by deliberate movements. If one mouse was exploring around the arena wall, the other often moved in the opposite direction to a point approximately 180° opposite. Contacts between *Peromyscus* appeared briefer than in *Rattus* and *Mus* and were primarily naso-nasal and naso-anal sniffing. Once initial contact had been made the mice often returned for brief bouts of sniffing.

In general the social behavior of the species conformed to other descriptions in the literature. The *Rattus* were gregarious and spent considerable time in contact with no overt aggression observed, as found by Barnett (3) and Latané (4). The *Mus* were somewhat more aggressive (overt aggression in 3 pairs of 10) than *Peromyscus* (2 pairs of 20 aggressive) as noted by King (10). However, the *Mus* avoided each other less than did *Peromyscus*. Hill (7) noted that the same two species of *Peromyscus* in a social situation exhibited avoidance behavior.

The differences in sociability may be genuine species differences but two of the groups tested were domesticated strains. The domestic rat, however, shows many of the social tendencies of wild forms (3, 11). Scott (11) indicates that aggressive patterns in wild *Mus* are similar to those of laboratory strains. The Swiss-Webster strain of *Mus* used in this experiment were albinos, with concomitantly poor eyesight, and seemed much less violently reactive to their environment than wild *Mus* (personal observation). Certainly we need to compare the behavior of wild *Rattus* and *Mus* in a similar situation to determine the effects of domestication on their sociability. Wild *Rattus* and *Mus* typically live in groups and might be expected to exhibit a relatively small individual distance. *Peromyscus* typically range over a much larger spatial area than do individuals of the other two species and their populations are more dispersed (12). The individual distance of *Peromyscus* should be greater as population dispersion may be maintained by mutual avoidance (7). The relative scale of sociability and individual distance in this study would probably be maintained if wild strains of *Mus* and *Rattus* were tested.

The measure of individual distance can be important in understanding the organization of populations, since organization may have a strong spatial component. However, many factors can cause variations in the individual distance of an animal (1). For example, male wild rats which are territory holders typically drive away other males (13) and might exhibit a greater individual distance than subordinate males. Longer term, more comprehensive measurements are needed on many species before phylogenetic and ecological patterns can be determined. In addition, quantitative measures and analysis of the reactive patterns between animals may be important. For example, the *Peromyscus'* habit of orienting to each other and moving to reestablish a maximum distance was striking, and has been noted in these and similar experiments by several observers. The *Mus* and *Rattus* did not exhibit these patterns. If such behaviors can be measured, we will have a tool for analyzing how one rodent perceives and subsequently determines its reaction to another.

ACKNOWLEDGMENTS

Susan Klages, Raana Rashidian, and Michael Ponstingle helped collect and compile the data. Don Grogan provided the rats. Lee Drickamer, Jenna Hellack, John King, Beth Leuck, and James Gillingham critically read an earlier version of the manuscript. Ginna Davidson provided the figure. Financial support was provided by the Biology Department of the University of Missouri—St. Louis. Carolyn Vestal provided advice and encouragement and critically read the manuscript.

REFERENCES

1. G. McBRIDE, Univ. Queensl. Pap., Fac. Vet. Sci. 1: 73-110 (1964).
2. H. HEDIGER, *Wild Animals in Captivity*, Dover Publications, Inc., New York, 1964. (Reprint of 1950 Edition).
3. S. A. BARNETT, *The Rat,* Aldine Publishing Co., Chicago, 1963.
4. B. LATANÉ, J. Exp. Soc. Psychol. 5: 61-69 (1969).
5. B. LATANÉ, E. SCHNEIDER, P. WARING, and R. ZWEIGENHAFT, Psychon. Sci. 23: 28-29 (1971).
6. J. ECKMAN, J. D. MELTZER, and B. LATANÉ, J. Personal. Soc. Psychol. 11: 107-114 (1969).
7. J. L. HILL, *Space Utilization of Peromyscus: Social and Spatial Factors,* Ph.D. Dissertation, Michigan State University, East Lansing, 1970.
8. R. R. SOKAL, and F. J. ROHLF, *Biometry*, W. H. Freeman and Co., San Francisco, 1969.
9. B. J. WINER, *Statistical Principles in Experimental Design,* McGraw-Hill, New York, 1962.
10. J. A. KING, Ecology 38: 355-357 (1957).
11. J. P. SCOTT, Am. Zool. 6: 683-701 (1966).
12. L. F. STICKEL, *in:* J. A. KING (ed.), *Biology of* Peromyscus *(Rodentia),* Am. Soc. Mammal. Spec. Pub. No. 2, 1968, pp. 373-411.
13. J. B. CALHOUN, *The Ecology and Sociology of the Norway Rat*, Public Health Service Publ. No. 1008, U. S. Dept. Health, Educ., Welfare, Bethesda, Md., 1963.