

Sex-related dispersion of breeding deer mice in the Kananaskis Valley, Alberta

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Snap trapping of small mammals in the Kananaskis Valley, Alberta, during the breeding seasons of 1982 and 1983 provided data used to analyse sex-related dispersion patterns of adult *Peromyscus maniculatus*. A dispersion pattern of regular alternation of males and females, within-sex avoidance, and strong between-sex association was found. Within-sex exclusion was better exhibited by females than by males. These data are consistent with what would be expected for a promiscuous mating system. Intraspecific resource partitioning between different sexes may occur through adjustments in spatial relationships.

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L'installation de pièges à ressorts pour les petits mammifères dans la vallée de Kananaskis, Alberta, durant les saisons de reproduction de 1982 et 1983 a permis d'analyser la dispersion en fonction du sexe chez les adultes de *Peromyscus maniculatus*. L'analyse a révélé que les mâles et les femelles se dispersent en alternances régulières, que les individus d'un même sexe s'évitent et qu'il existe d'étroites associations entre individus de sexes opposés. Les femelles s'évitent plus entre elles que les mâles. Ces données semblent indiquer un système d'accouplement par promiscuité. Le partage des ressources entre les sexes chez cette espèce semble se faire par des ajustements des relations spatiales.

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Introduction

Sex-related dispersion of the deer mouse, *Peromyscus maniculatus*, has seldom been studied, although within-sex avoidance has been suggested in some species of *Peromyscus* (Nicholson 1941; McCabe and Blanchard 1950; Stickel 1968; Metzgar 1971; Myton 1974; Fairbairn 1977, 1978). Questions as to whether the dispersion of each sex is independent of each other, whether the dispersion is clumped or regular with respect to sex, and whether females avoid each other more than they do males, remain unanswered. Harland et al. (1979) found evidence for within-sex avoidance and between-sex association in breeding *P. leucopus*, and Metzgar (1979) found that adult male and female *P. maniculatus* showed between-sex association, had a loose social organization, and that "new" adults aggregated strongly with other new same-sex adults. Metzgar's (1979) conclusions, however, were based on the assumptions that the habitat was spatially and temporally homogeneous, and that all the traps had the same probability of catching mice. These assumptions likely were not met. For example, Metzgar (1979) reasoned that if females occurred at 0.5 of the stations and males at 0.2 of them, both males and females should be found at 0.1 ($= 0.5 \times 0.2$) of the stations under the null hypothesis of random male-female association. This is incorrect as traps located in favourable microhabitats would catch more deer mice than traps located in less favourable microhabitats. A strong association of both males and females with favourable habitat would be interpreted by Metzgar (1979) as strong male-female association.

Spacing patterns of animals are determined by the interaction between animals and their environment (Connell 1975; Cormack 1979) and tend to reflect different ways that animals partition essential resources for survival and reproduction (Lack 1954; Wynne-Edwards 1962; Crook 1965; Brown and Orians 1970). Among deer mice, dispersion of individuals of the same sex, particularly the female, is not likely to be independent of the opposite sex, for the following reasons. First, deer mice live in habitats with sporadic shortages of resources (*Gashwiler* *latus* exhibits differential resource

use between the sexes (Bowers and Smith 1979). It should be disadvantageous for individuals with similar resource use to live together. Therefore, an optimization hypothesis would predict that they should evolve behavioural characteristics that position individuals of different sexes as close to each other as possible, to save energy in mate searching activity, to increase the chances of mating, and to reduce the risk of predation. Secondly, breeding females have very high energy requirements for reproduction (Millar 1979), and at least in the Kananaskis Valley, Alberta, all adult females breed each year (Millar and Innes 1985). They should, therefore, avoid each other so as to reduce competition for food. It has been found that adult males tolerate each other better than adult females (Stickel 1968). Blair's (1942) intensive livetrapping data also revealed that, although adult males and females, immature males, and subadult males were sometimes caught in the same trap, no females were ever trapped together.

Snap-trapping data have some advantages over livetrapping data in studying animal dispersion patterns. Snap traps are easy to carry and monitor. Given the same manpower, snap traps can be spread over a larger area and produce a larger instantaneous capture than live traps. Snap traps achieved higher first-night trappability than did live traps when both were used to trap the house mouse, *Mus musculus*, at different locations (personal observation). All these suggest that snap trapping has a higher resolution power in reflecting natural spatial distribution of animals than does livetrapping. Snap-trapping data are amenable to the application of some statistical tests, such as the runs test and the blocks test (Pielou 1979), in detecting small-scale nonrandom dispersion patterns. The runs test and blocks test become powerless when there is a large proportion of animals not caught while present, and are of little value if samples are small or sex ratio seriously biased. As a result, the two tests are usually used to deal with large samples collected in habitats with relatively continuous distributions of animals.

In this paper, the following hypotheses were tested. First, the dispersion of each sex is not independent of the other. Secondly, the dispersion pattern reflects within-sex avoidance and

between-sex association, i.e., the probability for an adult having an adult of the opposite sex as its neighbour should be greater, and the probability of having a same-sex neighbour should be less than expected under the null hypothesis of random association. A pattern of regular alternation between the sexes might exist. Thirdly, as breeding females likely require a greater energy budget than males, the probability of an adult female having a same-sex neighbour should be less than that of an adult male, i.e., the observed frequency of females being neighbours should deviate more from random association than that of males being neighbours.

Materials and methods

Snap trapping of small mammals was done during the summer months of 1982 and 1983. Trap lines consisted of random lines of single traps with approximately 10-m spacing (for a detailed description of trapping and data collecting methods see Millar and Innes, 1985). Forty trap lines in 1982 and 30 trap lines in 1983 yielded 460 and 384 deer mice, respectively. Mice were sexed, weighed, and aged on the basis of size, pelage characteristics, and eye lens weights (Millar and Iverson 1976). Only samples collected from the beginning of May to the end of July were used in this study because later samples contained many juveniles and few adults. The data used in this analysis consisted of 14 of the largest samples (6 in 1982 and 8 in 1983), a sample being defined as all adults caught in a trap line the first night. Only the adults (overwintered adults in breeding condition) trapped on the first of three consecutive nights were used in the analysis because the individuals caught on the last two nights might not reflect the natural dispersion pattern. We assumed that adults trapped on the first night adequately reflected the position of deer mice along the trap line. If some deer mice were present but not caught, any test based on capture sequence would tend to be conservative in rejecting a hypothesis of random dispersion. To pool the data from the 2 years, a heterogeneity χ^2 test was used to test whether different samples had different sex ratios. A runs test above and below the median (Sokal and Rohlf 1981) was also performed to examine independence of sampling at different times during the 2 years.

There were 23 couplets of deer mice, a couplet being defined as two deer mice caught next to each other with no trap between them. These data were analysed with a χ^2 test against the expected frequency of combinations of different sexes, based on a binomial distribution. The largest sample, which had 23 adults, was used for a runs test to see whether there was a regular alternation of males and females along the trap line. A blocks test was used for comparison. There were 48 males and 53 females having neighbours, a neighbour of an individual being defined as an adult caught closest to that individual with no more than three unproductive traps between them. The numbers of same-sex neighbours and opposite-sex neighbours of these males and females were recorded. These data were also tested against the expected values calculated under the null hypothesis of random association of different sexes. The pooled sex ratio (males/females = 0.9389) was used to calculate all expected values.

Statistics followed Pielou (1979) and Sokal and Rohlf (1981).

Results

The heterogeneity χ^2 test showed that the samples collected at different times of the 2 years were homogenous with respect to sex ratio ($\chi^2 = 6.7824$, $p > 0.90$). No single sample had a sex ratio deviating significantly from the pooled sex ratio (minimum $p_i > 0.10$, $i = 1, 2, \dots, 14$). The runs test above and below the median supported the assumption of independence of observations ($r = 11$, $0.05 < p < 0.95$).

The adult males and females caught in the largest sample showed the following sequence, where F represents female and M represents male. The runs have been underlined. Numbers indicate number of traps at the two ends of the trap line and adjacent individuals.

TABLE 1. χ^2 test on 23 couplets of deer mice. A couplet consists of two deer mice caught in sequential traps. Expected values were calculated using the pooled sex ratio on the basis of a binomial distribution ($p = 0.4843$, $q = 0.5157$). The female-female category made the greatest contribution to the rejection of the null hypothesis of random association between different sexes

Association	Frequency		χ^2 value	df†
	Observed	Expected		
Male-male	5	5.393	0.029	
Male-female	17	11.489	2.644	
Female-female	1	6.118	4.281	
Sum	23	23	6.954*	2

* $p < 0.05$.

†Since p and q were calculated from the pooled sample, not from the 23 couplets, the df should be 2.

TABLE 2. G test on frequencies of same-sex neighbours and opposite-sex neighbours of 48 males and 53 females. Neighbours were defined as deer mice caught within four sequential trap sites. The tests were run separately on 72 neighbours of 48 males and 74 neighbours of 53 females. See text for the calculation of the expected values

	Sex of neighbour	Frequency		G test	df
		Observed	Expected		
48 males	Male	24	34.87		
	Female	48	37.13		
	Sum	72	72	6.714*	1
53 females	Male	48	35.84		
	Female	26	38.17		
	Sum	74	74	8.100**	1

* $p < 0.05$.

** $p < 0.01$.

6 F5 M2 F1F2 M1 F7 M4 F4 M1M F4F3 M2 F M2 F M5
F7F1F M13 F4 M3

A runs test rejected the hypothesis that adults of the two sexes were randomly dispersed and accepted the hypothesis that the adult males and females were arranged in an alternating sequence ($r = 18$, $n_1 = 10$, $n_2 = 13$, $r(0.025) = 7$, $r(0.975) = 18$). A blocks test rejected the hypothesis at a more significant level (females as "cuts," $p = 0.017$; males as "cuts," $p = 0.002$). We therefore conclude that adult deer mice are spatially arranged in a regular alternation, at least when population density is high (70 mice, including juveniles, were caught on this trap line with 100 traps over three consecutive nights).

The results of the analysis on the 23 couplets are presented in Table 1. The observed frequency of couplets being of the same sex was lower, and the observed frequency of couplets being of different sexes was higher, than the expected values. The observed frequency of couplets being females made a much greater contribution to the rejection of the null hypothesis than did the observed frequency of couplets being males, indicating a stronger within-sex avoidance in females than in males.

A G -test was carried out on the last set of data, the numbers of same-sex neighbours and opposite-sex neighbours of the 48 males and 53 females. The probability of an adult having a male neighbour was 0.48425, and a female neighbour, 0.51575,

according to the pooled sex ratio under the null hypothesis of random association. A total of 48 males had 72 neighbours which were expected to consist of $72 \times 0.48425 (= 34.866)$ males and $72 \times 0.51575 (= 37.134)$ females. The expected values for 53 females, which had 74 neighbours, were calculated in the same manner. The results were consistent with the previous analysis (Table 2). The observed frequency of neighbours being of the same sex was much lower than the expected value, and the observed frequency of neighbours being of the opposite sex was higher than the expected value. Both sets of data rejected the null hypothesis, indicating strong within-sex avoidance and between-sex association of both males and females.

Discussion

This study revealed a regular alternation of adult males and females, a strong association between adult females and males, and a strong within-sex exclusion of adult females. The minimization, through the regular alternation of males and females, of the average distance between different sexes maximizes the probability that two adults meeting are of different sexes, thus increasing mating and mate-searching efficiency. Taking differential habitat use of males and females into consideration (Bowers and Smith 1979), this regular alternation reduces local similarity in resource use. Consequently, intrasexual competition in females for such resources as food and intrasexual competition in males for mates are reduced, increasing the carrying capacity of the habitat. Through this dispersion pattern, intrasexual interference is minimized.

Metzgar (1967) found that familiarity with the habitat is important in reducing predation in *Peromyscus leucopus*. This suggests that predation may serve to limit travelling distance of deer mice and may reinforce the regular alternation of adult males and females. If risk of predation is high, an adult male may benefit by tracking the reproductive status of females around him, rather than venturing out into unfamiliar habitats searching for females of uncertain reproductive status.

Our study of this deer mouse population does not provide evidence in favour of the existence of a polygynous mating system with discrete social units, as suggested for some small mammals such as *Apodemus sylvaticus* (Brown 1966) and *Peromyscus leucopus* (Myton 1974). The regular alternation of adult males and females is unlikely to be the product of social dominance of certain individuals. The short breeding season, the short life span, the limited resources, and predation may preclude complex social interactions. These findings contrast with some other studies of *Peromyscus*. Mihok (1979) thought that multiple captures of *Peromyscus maniculatus* reflected a long-term association between individual mature males and a few mature females living within their territories. This is a conclusion that was not supported by his data. His data showed more triplets consisting of two males and one female and fewer triplets containing one male and two females than expected under a null hypothesis of random association. What is interesting in Mihok's (1979) study is that no within-sex association or between-sex avoidance was evident in his multiple capture data. Perhaps his 25-m spacing between traps prevented the detection of the real dispersion pattern of a highly clumped population of deer mice.

Our finding is compatible with Metzgar's (1979) study on dispersion in a deer mouse population. Metzgar found that breeding adults were evenly dispersed; the home range of an adult male usually overlapped those of several adult females, might also overlap those of several

breeding males. This dispersion pattern leaves the mating system open to promiscuity. Birdsall and Nash (1973) provided evidence of frequent multiple male parentage within single litters in natural populations of deer mice. Promiscuity therefore appears to be the mating system in deer mice best supported by the available data.

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- BIRDSALL, D. A., and D. NASH. 1973. Occurrence of multiple insemination of females in natural populations of deermice (*Peromyscus maniculatus*). *Evolution*, **27**: 106–110.
- BLAIR, W. F. 1942. Size of home range and notes on the life history of the woodland deermouse and eastern chipmunk in Northern Michigan. *Am. Nat.* **23**: 27–36.
- BOWERS, M. A., and H. D. SMITH. 1979. Differential habitat utilization by the sexes of the deermouse, *Peromyscus maniculatus*. *Ecology*, **60**: 869–875.
- BROWN, J. L., and G. H. ORIANS. 1970. Spacing patterns of mobile animals. *Annu. Rev. Ecol. Syst.* **1**: 239–262.
- BROWN, L. E. 1966. Home range and movement of small mammals. *Symp. Zool. Soc. London*, **18**: 111–142.
- CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *In Ecology and evolution of communities*. Edited by M. Cody and J. Diamond. Harvard University Press, Cambridge, MA. pp. 460–490.
- CORMACK, R. M. 1979. Spatial aspects of competition between individuals. *In Spatial and temporal analysis in ecology*. Edited by R. M. Cormack and J. K. Ord. International Co-operative Publishing House, Fairland, MD. pp. 151–211.
- CROOK, J. H. 1965. The adaptive significance of avian social organizations. *Symp. Zool. Soc. London*, **14**: 181–218.
- FAIRBAIRN, D. J. 1977. The spring decline in deer mice: death or dispersal? *Can. J. Zool.* **55**: 84–92.
- . 1978. Dispersal of deer mice, *Peromyscus maniculatus*: proximal cause and effects on fitness. *Oecologia*, **32**: 171–193.
- GASHWILER, J. S. 1979. Deermouse reproduction and its relationship to a tree seed crop. *Am. Midl. Nat.* **102**: 95–104.
- HARLAND, R. M., P. J. BLANCHER, and J. S. MILLAR. 1979. Demography of a population of *Peromyscus leucopus*. *Can. J. Zool.* **57**: 323–328.
- LACK, D. 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford.
- MCCABE, T. T., and B. D. BLANCHARD. 1950. *Three species of Peromyscus*. Rood Associates, Publishers, Santa Barbara.
- METZGAR, L. H. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *J. Mammal.* **48**: 387–391.
- . 1971. Behavioural population regulation in the woodmouse, *Peromyscus leucopus*. *Am. Midl. Nat.* **86**: 434–448.
- . 1979. Dispersion patterns of a *Peromyscus* population. *J. Mammal.* **60**: 129–145.
- MIHOK, S. 1979. Behavioural structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus maniculatus*. *Can. J. Zool.* **57**: 1520–1535.
- MILLAR, J. S. 1979. Energetics of lactation in *Peromyscus maniculatus*. *Can. J. Zool.* **57**: 1015–1019.
- MILLAR, J. S., and D. G. L. INNES. 1985. Breeding of *Peromyscus maniculatus* over an elevational gradient. *Can. J. Zool.* **63**: 124–129.
- MILLAR, J. S., and S. L. IVERSON. 1976. Weight of eye lens as an indicator of age in *Peromyscus*. *Can. Field-Nat.* **90**: 37–41.

- MYTON, B. 1974. Utilization of space by *Peromyscus leucopus* and other small mammals. *Ecology*, **55**: 277–290.
- NICHOLSON, A. J. 1941. The home and social habits of the woodmouse (*Peromyscus leucopus noveboricensis*) in southern Michigan. *Am. Midl. Nat.* **25**: 196–223.
- PIELOU, E. C. 1979. *Biogeography*. John Wiley & Sons, New York.
- SOKAL, R. R., and F. J. ROHLF. 1981. *Biometry*. 2nd ed. Freeman Publications, San Francisco.
- STICHEL, L. F. 1968. Home range and travels. *Spec. Publ. Am. Soc. Mammal.* **2**: 1–593.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion*. Oliver & Boyd Ltd., Edinburgh.