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Author(s): Sunny K. Boyd and Andrew R. Blaustein

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# FAMILIARITY AND INBREEDING AVOIDANCE IN THE GRAY-TAILED VOLE (*MICROTUS CANICAUDUS*)

SUNNY K. BOYD AND ANDREW R. BLAUSTEIN

Department of Zoology, Oregon State University, Corvallis, OR 97331

**ABSTRACT.**—The role of familiarity in inbreeding avoidance was tested in captive gray-tailed voles (*Microtus canicaudus*) in the laboratory. Individuals that were familiar with one another, regardless of relatedness, produced fewer litters than unfamiliar pairs. There were no apparent differences in litter size or pup viability between siblings versus non-siblings. Recognition of kin was based on familiarity. Individuals that were separated for 5 or 12 days from potential partners with whom they had been reared retained their mating avoidance. In the field, familiarity of voles may increase in low density populations and reproductive behavior may decline as a result. Thus, familiarity, kin recognition, and inbreeding avoidance may play important roles in vole population cycles.

Degree of familiarity with other individuals may influence an animal's social behavior, including its use of space and its mating behavior. Thus, the concept of familiarity (*sensu* Bekoff, 1981a), as related to social behavior, has received theoretical attention (e.g., Bekoff, 1981a; Holmes and Sherman, 1982). In addition, experimental investigations have shown that familiarity may play an important role in specific kin-oriented behaviors such as kin recognition (Alexander, 1979; Bekoff, 1981a; Blaustein, 1983; Holmes and Sherman, 1982). Kin-oriented behaviors may influence various aspects of the ecology of a species. For example, kin recognition based on familiarity is probably the mechanism used in some species of larval anuran amphibians to form aggregations in nature (O'Hara and Blaustein, 1982) and it probably plays a role in how individuals behave toward others in various social contexts such as in mate-choice situations and parent-offspring relationships in many mammalian species (see Bateson, 1983; Bekoff, 1981a; Colgan, 1983; Holmes and Sherman, 1982 for discussion). Familiarity and recognition may be especially important in the social interactions of small mammal species that undergo population cycles (Bekoff, 1981b; Charnov, 1981; Charnov and Finerty, 1980).

Familiarity with potential mates seems to play an important role in the mating behavior of some species of small mammals but is less important in other species. For example, there is decreased reproductive output among sibling pairs in several species of *Microtus* and *Peromyscus* (Batzli et al., 1977; Dewsbury, 1982; Gavish et al., 1984; Hasler and Nalbandov, 1974; Hill, 1974; McGuire and Getz, 1981; Schadler, 1983), whereas some microtines show no such inhibition of reproduction (Batzli et al., 1977). Similarly, familiarity may be the main mechanism of kin recognition in some small mammals but not others (see discussions by Bekoff, 1981a; Blaustein, 1983; Holmes, 1984; Holmes and Sherman, 1982).

Our study was designed to investigate the importance of familiarity in the reproductive performance of gray-tailed voles (*Microtus canicaudus*), a species that exhibits population fluctuations similar to the cycles described for other microtine species (Blaustein, pers. observ.). Specifically, we tested the hypotheses that (1) reproductive output by sibling pairs differs from that of non-sibling pairs, (2) that reproductive success is influenced primarily by the probability of breeding, rather than litter size, litter production rate, or rearing success, and (3) that probability of breeding is based on familiarity in this species. Elucidating the role of familiarity in the reproductive biology and ecology of microtine rodents can add potentially valuable information to our understanding of microtine population cycles.

## METHODS AND MATERIALS

*Microtus canicaudus* (= *M. montanus canicaudus*; Hall, 1981) individuals used in our experiments were taken from a laboratory colony established in 1973 with wild-captured animals from Benton Co., Oregon. The colony was periodically outbred by adding recently-trapped animals to the laboratory population. Voles

TABLE 1.—*Reproductive characteristics of Microtus canicaudus related to rearing condition. NSRA = non-sibs reared apart; NSRT = non-sibs reared together; SRA = sibs reared apart; SRT = sibs reared together; SRT - 5 = sibs reared together for 45 days but separated for 5 days before pairing; SRT - 12 = sibs reared together for 38 days but separated for 12 days before pairing. SE = standard error of the mean. N = total number of pairings.*

Rearing condition	N	Pairs producing litters (%)	Mean (SE) litters per pair	Mean (SE) number of pups per litter	Mean (SE) days latency to first litter
NSRA	16	11 (69)	0.88 (0.18)	4.2 (0.2)	51.4 (4.0)
NSRT	11	1 (9)	0.18 (0.18)	3.0	50
SRA	11	8 (73)	1.09 (0.25)	4.2 (0.3)	44.4 (5.3)
SRT	15	4 (27)	0.27 (0.12)	4.8 (0.9)	50.3 (3.7)
SRT - 5	11	3 (27)	0.36 (0.20)	3.8 (0.9)	50.7 (11.3)
SRT - 12	11	4 (36)	0.55 (0.25)	5.5 (0.6)	29.5 (3.1)

were maintained on a phase-shifted photoperiod of 16L:8D (lights out at 1500 h) and at a controlled temperature of 20 to 22°C. Animals were housed in clear plastic cages (20 by 35 by 17 cm) containing hardwood shavings. Rat chow, rabbit chow, and water were available *ad libitum*.

A total of 150 voles (75 pairs) was assigned to one of six treatment groups. The animals were randomly assigned as individuals to pairs within groups. Animals within any one litter were distributed across as many treatments as possible. One treatment group consisted of 15 pairs of siblings from nine litters that had been reared together from birth (SRT) and another of 16 pairs of non-siblings from 10 litters that had been reared apart (NSRA) until pairing. Two other groups were composed of pairs of voles cross-fostered within 6 h of birth. Two or three pups in one litter were randomly exchanged for two or three pups in another litter and toe-clipped for later identification (young from a total of 12 litters were cross-fostered). All were subsequently raised until pairing within the reconstituted litter group. This generated pairs composed of siblings reared apart (SRA;  $n = 11$  pairs) and non-siblings reared together (NSRT;  $n = 11$  pairs). In the final two groups, siblings were reared together for 45 days, then separated and housed singly for 5 days before pairing (SRT - 5;  $n = 11$  pairs from 6 different litters) or reared together for 38 days, then separated and housed singly for 12 days before pairing (SRT - 12;  $n = 11$  pairs from 5 different litters). The last two tests were designed to investigate whether the ability of voles to recognize siblings decreases with separation.

All animals were housed with mothers or foster-mothers until weaning at 15 days of age. They were then maintained as litter groups until pairing or separation. Pairing was done by introducing a male and female, between 48 and 51 days of age, simultaneously into a clean cage. Pairs were then left undisturbed for 65 days except for transfer to clean cages every other week. Cages were checked daily for the presence of young. If pups were present, litter birth dates, pups per litter, and pup survival until weaning were recorded. Cannibalism was not observed in this study.

Fisher's Exact test (Siegel, 1956) was used to statistically compare numbers of pairs producing litters. Mean number of pups per litter and mean days latency to first litter were compared across all groups (except NSRT where a single litter was born) using a one-way analysis of variance.

## RESULTS

Individuals that had been reared together, regardless of genetic relatedness, produced fewer litters than individuals reared apart (Table 1; 12 of 48 pairs reared together produced litters versus 19 of 27 pairs reared apart;  $P = 0.001$ ; Fisher's Exact test). Importantly, sibs reared apart produced a greater number of litters than sibs reared together (Table 1;  $P = 0.023$ ; Fisher's Exact test), and non-sibs reared apart produced a greater number of litters than non-sibs reared together (Table 1;  $P = 0.003$ ; Fisher's Exact test). These results support the hypothesis that familiarity plays an important role in *M. canicaudus* reproduction. The proportion of pairs

producing litters after voles were reared together, separated for 5 or 12 days, and then reintroduced was not significantly different from unseparated siblings reared together (Table 1). The mean number of pups produced per litter (one-way ANOVA,  $F = 2.06$ ,  $P > 0.05$ ) and the latency to the first litter (one-way ANOVA,  $F = 2.25$ ,  $P > 0.05$ ) were similar in pairs reared together and pairs reared apart (Table 1). There were no differences in survival of pups to weaning (all pups survived) or number of litters per reproductive pair ( $\bar{X} \pm SE = 1.35 \pm 0.24$  litters per pair).

#### DISCUSSION

The likelihood of reproduction by *M. canicaudus* individuals reared together was significantly less than that of individuals reared apart, regardless of genetic relatedness. Such avoidance of sibling matings has been previously reported in *M. ochrogaster* (Hasler and Nalbandov, 1974; McGuire and Getz, 1981; see also Gavish et al., 1984), *M. pinetorum* (Batzli et al., 1977; Schadler, 1983), *M. californicus* (Batzli et al., 1977), *P. maniculatus* (Dewsbury, 1982; Hill, 1974), and *P. eremicus* (Dewsbury, 1982). *M. pennsylvanicus* does not show such avoidance however (Batzli et al., 1977). In microtines, siblings may adversely affect reproduction of their partners indirectly or directly. For instance, there is evidence that male *M. ochrogaster* may fail to induce estrus in their sisters (McGuire and Getz, 1981). In *M. pinetorum*, however, presence of a sibling male directly decreases rate of conception even when females are in estrus and are housed with a non-sibling stud male (Schadler, 1983).

The decrease in reproduction observed here in *M. canicaudus* is due to a decreased propensity to produce young rather than changes in litter size, pup viability, or apparent parental care. There was no evidence of inbreeding depression as has been reported for *P. maniculatus* (Hill, 1974).

Familiarity is an important parameter affecting litter production in *M. canicaudus*. Because there is a high probability that members of different litters (kin groups) do not mix (see discussion below), familiarity can be used as a general kin recognition mechanism (see Bekoff, 1981a; Blaustein, 1983 for discussion) and as an inbreeding avoidance mechanism specifically. Other species of small mammals that also seem to use familiarity to some extent for kin recognition are spiny mice (*Acomys cahirinus*) (Porter et al., 1978; Porter and Wyrick, 1979), house mice (*Mus musculus*) (Kareem, 1983; Kareem and Barnard, 1982), and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) (Holmes, 1984). However, other mechanisms of kin recognition could be operating in conjunction with familiarity in these and other species of small mammals (see discussions in Blaustein, 1983; Holmes and Sherman, 1982).

Holmes and Sherman (1982) suggested that species displaying kin recognition through familiarization (social learning) are those with a low probability of mixing with relatives of varying degrees of relatedness or non-relatives during development. Furthermore, they suggested that this recognition mechanism is likely if young can be successfully cross-fostered early in development (Holmes and Sherman, 1982). Although no comprehensive data concerning the social behavior of *M. canicaudus* exist to support these points, information available for a closely related species, *M. montanus*, suggests that pregnant females of the latter species do not move to new nests and only travel short distances (Jannett, 1980). This implies that the likelihood of nestlings of various coefficients of relatedness ( $r$ ) coming together is not great. Moreover, successful intraspecific cross-fostering was accomplished in our study, and interspecific cross-fostering between *M. canicaudus* and *M. montanus* has been achieved (McDonald and Forslund, 1978). Thus, the general statements of Holmes and Sherman (1982) concerning familiarity and social behavior are supported by this study.

The social and ecological parameters in which different species evolved probably greatly influence the shaping of kin recognition abilities. Differences between species in how familiarity affects kin recognition are apparent. In our study, *M. canicaudus* still showed tendencies to mate with non-kin over kin after 5 or 12 days of isolation. Perhaps these periods of isolation were not sufficient to diminish the recognition ability or *M. canicaudus* may have a tendency

to retain kin recognition after it is learned. Development of kin recognition in the house mouse is influenced by familiarity in the nest, but it can develop without postnatal association between the animals involved or with parents (Kareem, 1983). Spiny mice, however, seem to need constant exposure to siblings for maintenance of their kin-recognition abilities because after 8 days of isolation kin-recognition tendencies are diminished (Porter and Wyrick, 1979).

Our study supports the hypothesis that familiarity in voles may be of importance in influencing vole population cycles. Charnov and Finerty (1980) suggested that when vole populations are low, close relatives probably interact most frequently and aggressive encounters are probably diminished because of the high  $r$  value. Therefore, demographic fluctuations could be influenced by changes in behavior as manifested in reproductive behavior or in aggressive encounters. Bekoff (1981b) suggested that voles in small (low dispersal) populations are more familiar with one another and therefore fighting is diminished. Subsequent behavioral changes ensuing are the result of increasingly familiar individuals living in small populations regardless of changes in  $r$ . Although we did not test changes in aggressive behavior with familiarity we suggest that voles in small, low-dispersing populations may become increasingly familiar with one another and, as the coefficient of familiarity ( $f$ ; *sensu* Bekoff, 1981a) increases, reproduction may decrease. Increased reproduction and subsequent population growth may occur only after sufficient emigration takes place.

Our results suggest that the role of familiarity is important in the reproductive biology of a species that undergoes population cycles similar to those described previously (Krebs and Myers, 1974). The importance of familiarity and kinship in cycling small mammal species should be investigated further because such studies may help elucidate the problem of cycling small mammal populations.

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#### LITERATURE CITED

- ALEXANDER, R. D. 1979. Darwinism and human affairs. Univ. Washington Press, Seattle, 317 pp.
- BATESON, P. 1983. Mate choice. Cambridge Univ. Press, London, 462 pp.
- BATZLI, G. O., L. L. GETZ, AND S. S. HURLEY. 1977. Suppression of growth and reproduction of microtine rodents by social factors. *J. Mamm.*, 58:583-591.
- BEKOFF, M. 1981a. Mammalian sibling interactions: genes, facilitative environments and the coefficients of familiarity. Pp. 307-346, in *Parental care in mammals* (D. Gubernick and P. H. Klopfer, eds.). Plenum Press, New York, 1-459 + xix pp.
- . 1981b. Vole population cycles: kin selection or familiarity? *Oecologia*, 48:131.
- BLAUSTEIN, A. R. 1983. Kin recognition mechanisms: phenotypic matching or recognition alleles? *Amer. Nat.*, 121:749-754.
- CHARNOV, E. L. 1981. Vole population cycles: ultimate or proximate explanation? *Oecologia*, 48:132.
- CHARNOV, E. L., AND J. P. FINERTY. 1980. Vole population cycles: a case for kin selection? *Oecologia*, 45:1-2.
- COLGAN, P. 1983. Comparative social recognition. John Wiley and Sons, New York, 281 pp.
- DEWSBURY, D. A. 1982. Avoidance of incestuous breeding between siblings in two species of *Peromyscus* mice. *Biol. Behav.*, 7:157-169.
- GAVISH, L. H., J. E. HOFFMAN AND L. L. GETZ. 1984. Sibling recognition in the prairie vole, *Microtus ochrogaster*. *Anim. Behav.*, 32:362-366.
- HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 2:601-1181 + ii.
- HASLER, M. J., AND A. V. NALBANDOV. 1974. The effect of weanling and adult males on sexual maturation in female voles (*Microtus ochrogaster*). *Gen. Comp. Endocrinol.*, 23:237-238.
- HILL, J. L. 1974. *Peromyscus*: effect of early pairing on reproduction. *Science*, 13:1042-1044.
- HOLMES, W. G. 1984. Sibling recognition in thirteen-lined ground squirrels: effects of genetic relatedness, rearing association, and olfaction. *Behav. Ecol. Sociobiol.*, 14:225-233.
- HOLMES, W. G., AND P. W. SHERMAN. 1982. The ontogeny of kin recognition in two species of ground squirrels. *Amer. Zool.*, 22:491-517.
- JANNETT, F. J., JR. 1980. Social dynamics of the

- montane vole, *Microtus montanus*, as a paradigm. *The Biologist*, 62:3-19.
- KAREEM, A. M. 1983. Effects of increasing periods of familiarity on social interactions between male sibling mice. *Anim. Behav.*, 31:919-926.
- KAREEM, A. M., AND C. J. BARNARD. 1982. The importance of kinship and familiarity in social interactions between mice. *Anim. Behav.*, 30:594-601.
- KREBS, C. J., AND J. P. MYERS. 1974. Population cycles in small mammals. *Adv. Ecol. Res.*, 4:267-399.
- MCDONALD, D. L., AND L. G. FORSLUND. 1978. The development of social preferences in the voles *Microtus montanus* and *Microtus canicaudus*: effects of cross-fostering. *Behav. Biol.*, 22:497-508.
- MCGUIRE, M. R., AND L. L. GETZ. 1981. Incest taboo between sibling *Microtus ochrogaster*. *J. Mamm.*, 62:213-215.
- O'HARA, R. K., AND A. R. BLAUSTEIN. 1982. Kin preference behavior in *Bufo boreas* tadpoles. *Behav. Ecol. Sociobiol.*, 11:43-49.
- PORTER, R. H., AND M. WYRICK. 1979. Sibling recognition in spiny mice (*Acomys cahirinus*): influence of age and isolation. *Anim. Behav.*, 27:761-766.
- PORTER, R. H., M. WYRICK, AND J. PANKEY. 1978. Sibling recognition in spiny mice (*Acomys cahirinus*). *Behav. Ecol. Sociobiol.*, 3:61-68.
- SCHADLER, M. H. 1983. Male siblings inhibit reproductive activity in female pine voles, *Microtus pinetorum*. *Biol. Reprod.*, 28:1137-1139.
- SIEGEL, S. 1956. Nonparametric statistics. McGraw-Hill, New York, 312 pp.

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