Paternal behavior by *Peromyscus leucopus* in enclosures

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Male *Peromyscus leucopus* are known to exhibit well-developed paternal behavior in confined cages, but electrophoresis indicates promiscuity in this species. One explanation for this paradox is that the documented paternal behavioral patterns are laboratory artifacts. We made nocturnal observations of parental behavior in 14 families of *P. leucopus* in large enclosures and observed no paternal care. Males rarely entered the natal nest and when they did, remained in the nest for less than 2 min. Thus, we consider direct paternal care such as licking, retrieving, and huddling unlikely. We also failed to observe any indirect paternal investment such as nest building or food caching. The female in each of five pairs was very aggressive towards the male, continuously chasing him throughout most of the observation periods. Another three females actively prevented their mates from entering the natal nest. Paternal care probably does not contribute to the growth and survivorship of the young under natural conditions.

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Les mâles de *Peromyscus leucopus* ont des comportements paternels très évidents en cage, mais l'électrophorèse indique qu'il y a promiscuité chez cette espèce. Ce paradoxe peut s'expliquer si les comportements paternels observés chez les animaux en captivité sont en fait des artéfacts expérimentaux. Nous avons observé les comportements parentaux durant la nuit chez 14 familles de *P. leucopus* gardées dans de grandes enceintes et les mâles n'ont manifesté aucun comportement paternel : ils pénétraient rarement dans le nid et y restaient d'ailleurs pour moins de 2 min. Il semble donc que les soins paternels directs tels le léchage, le transport et le blotissement, n'existent pas en nature. Nous n'avons pas observé non plus d'investissement paternel indirect comme la participation à la construction du nid ou au stockage de la nourriture. Les femelles de cinq couples se sont avérées agressives envers leur mâle, le pourchassant presque continuellement. Trois autres femelles empêchaient leur partenaire de pénétrer dans le nid des nouveau-nés. Les soins paternels ne contribuent donc probablement pas à la croissance ou à la survie des jeunes dans des conditions naturelles.

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Introduction

Captive male *Peromyscus leucopus* and *Peromyscus maniculatus* have been observed to provide a great deal of parental care (Horner 1947; McCarty and Southwick 1977; Hartung and Dewsbury 1979). Because juveniles are vulnerable to ectoparasites (Whitaker 1968) and low temperatures (Hill 1972), the adaptive value of parental behavior, such as licking, retrieving, and huddling, seems obvious. Electrophoresis, however, indicates that both species are promiscuous (Birdsall and Nash 1973; J. O. Wolff, personal communication). There are two explanations for this paradox. Either paternal care is a laboratory artifact or these mice are monogamous during some period in the breeding season. All previous experiments on paternal care in *Peromyscus* have been conducted in small cages in which the male shared a nest with the female and the young. A large enclosure provides the male with the option of living elsewhere and should approximate natural conditions more closely than do confined cages. In this paper we examine relationships among the male, his mate, and his offspring in large enclosures.

Materials and methods

An in-room enclosure (2.4 m long, 1.8 m wide, and 0.8 m high, open at the top), constructed of wood partitions, contained four numbered nest boxes (21.5 × 14.5 × 13.5 cm, inside dimensions) occupying the four corners of the enclosure. Water and Purina rat chow were provided *ad libitum*; cotton batting was scattered on the floor. A light regime of 17L:7D was used, with lights off at 6:00 p.m. Dawn and dusk were simulated by manually decreasing or increasing the resistance of the light bulb circuit for about 0.5 h. A dim red light was used for nocturnal observations. The mice could leave the enclosure by climbing up one corner of the enclosure, which gave them access to a 3.2 × 4.5 m room. Neither food nor water was provided ....ice could easily reenter the enclosure by

climbing one of several support struts. It was easier to get into the enclosure than to get out.

Wild-caught mice were maintained in 28 × 16 × 12 cm cages, and provided with hardwood sawdust and cotton batting, and *ad libitum* Purina rat chow and water. These mice (15 males and 13 females) were used in the experiment after they had been held in captivity for more than 50 days; their field-conceived offspring were used when they were older than 90 days. Adult males and females were paired at random. The extra two adult males were paired with two randomly selected offspring females. These 15 pairs were maintained in standard cages until females were in the late stages of pregnancy or had given birth. At that time, pairs were transferred to the enclosure in the cages in which they had been housed, with the cover removed to allow access to the enclosure. One field-caught female was barren and thus only 14 pairs were used for our experiment. Seven pairs of mice (group 1) were transferred when their young were 4 to 7 days old, and another seven pairs (group 2) were transferred when the female was still pregnant. The second group of females gave birth after 2–4 days in the enclosure. Each of the 14 pairs was tested separately. Males were ear-tagged to distinguish male and female under the dim red light.

Whole-night (7-h) observations were made from behind a blind after the mice were transferred to the enclosure, with two breaks of 20 min each night. Thus, total observation time per night was 6 h, 20 min. Observation over five consecutive nights was made for group 1, and over five to seven consecutive nights for group 2 (all prepartum nights and three consecutive postpartum nights). The movement patterns of the male and the female among nest boxes were recorded. Data that were recorded include (*i*) nest location of the male, female, and nestlings during the test; (*ii*) frequency with which different nest boxes were entered by the male and the female, excluding entrances made to cache food, build new nests, or avoid aggression by the other adult; (*iii*) frequency with which nest material and young were carried by the male and by the female; (*iv*) frequency of caching food by the male and by the female; and (*v*) time spent (nearest 10 s) by the male in the female's nest. To avoid confusion, a nest in this paper is defined as a nest box containing cotton batting deposited by the tested

TABLE 1. Nest sharing in relation to the female's reproductive status

Nest sharing	Female's reproductive status		
	Pregnant	Lactating (group 1)	Lactating (group 2)
Yes	7	0	0
No	0	7	7

NOTE: χ^2-test with Yates' correction, df = 1, $p < 0.0001$.

TABLE 2. Relationship between male desertion* and female reproductive status

Male desertion	Female reproductive status		
	Pregnant	Lactating (group 1)†	Lactating (group 2)‡
Yes	0	5	3
No	7	2	4

NOTE: χ^2-test with Yates' correction, df = 1, $p < 0.039$.
*The male nested outside the enclosure.
†Data of first two nights after introduction to enclosure.
‡Data of first two nights after parturition.

animal and structured into a cavity and one or more entrances (or exits), which serves as day shelter or home for young. Nest sharing by the adult pair means the use of one nest by the two adults.

Results

General description

Adults admitted to the enclosure started exploring the enclosure around 6:15 p.m. Exploration involved checking the four edges of the enclosure, the four nest boxes, and food and water containers over a period of 50–190 min. Nest building followed exploration and involved carrying an average of 49 ($N = 14$, SE = 5.3) mouthfuls of nesting material into a nest box. The whole process of nest building required an average of 53 ($N = 14$, SE = 4.7) min of concentrated effort, after which the mice carried nesting material into a nest only sporadically. In group 1, males came out of the cage 5–30 min earlier than females ($p < 0.01$). Young were transferred by the female into a nest box during either the first ($N = 6$) or second ($N = 1$) night, after nesting material was collected. Six females shifted their nests during the second night and one female did this during the third night. During nest shifting, the cotton from the natal nest was transferred into the new nest, with new nesting material being added later. This new nest was used during the remaining observation periods and no other nest was built. Males in group 1 built their nests after the females built their first nest. The quantity of cotton batting in a male's nest was less than a quarter of that of a female's nest. Males did not shift their nests unless the female happened to shift her nest to his. This occurred twice. In both cases the male built a new nest in another nest box.

In group 2, males and females started exploration at similar times and there was no detectable difference in which sex came out of the cage first. Two of the seven group 2 males initiated nest building 20–25 min after introduction to the enclosure. In all seven pairs, males and females shared the first nest. However, all seven females in group 2 gave birth in a different nest box and transferred the young either back to the old nest box ($N = 5$) or to a third nest ($N = 2$). All births occurred during the day and postpartum estrus occurred the same evening about 10–25 min after "sunset." The mating lasted an average of 43 ($N = 7$, SE = 8.2) min during which the male continuously chased the female; an average of 23 ($N = 7$, SE = 3.8) copulations (mountings) were observed outside of nest boxes. No copulation longer than 10 s was observed. Copulation may also have occurred within the nest boxes because the male occasionally chased the female into one of the nest boxes (except for the female's nest) for up to 40 s, which is much longer than required for a copulation.

Two females in group 1 and three females in group 2 were their mates and, except during

postpartum estrus, actively searched for and chased them throughout most of the observation period. Another three females in group 1 were aggressive only when the males attempted to enter their nests at dawn. These females either blocked the entrance of the nest box with their forefeet or rushed out of the nest box. They did not actively search for and chase the male. No male was aggressive towards females.

Paternal care

Males shared nests with females when they were pregnant, but not when they were lactating ($p < 0.0001$, Table 1). Each male in group 2 built his own nest within 2 days of postpartum copulation. Eight males left the enclosure, built nests outside, and stopped visiting nest boxes in the enclosure. Only twice did we observe these males entering the enclosure for water in the evening; these mice may have entered the enclosure for food and water during the day. This "male desertion" occurred only after the postpartum estrus of the female. The relationship between male desertion and female reproductive status (χ^2-test with Yates' correction, $p = 0.039$) is shown in Table 2. No pregnant females left the enclosure, but two lactating females did. The latter returned to the enclosure within 20 min.

Table 3 presents the number of entries made by males and females into the male's nest box, the female's nest box (with young), and the other two nest boxes. Because of the tendency to move nests, data in Table 3 were recorded only on the third and fourth nights after the introduction for group 1, and on the second and third nights after parturition for group 2. Males rarely entered the female's nest with young (Table 3, $N = 6$, mean = 0.58 times; the upper limit of 95% of confidence interval was 1.35 times), which precluded paternal care such as licking, retrieving, or huddling with the young. Moreover, even if a male did enter his female's nest box (7 times altogether; Table 3), the duration of his stay never exceeded 2 min; the three periods long enough to permit recording were 10, 30, and 90 s.

These results show that direct paternal care did not occur, but that males could still make indirect parental investments by building new nests or caching food for the female. Seventeen cases of nest shifting, involving 13 pairs (4 pairs moved nests twice) were recorded when both the male and the female were in the enclosure. In all cases the female did all of the nest building and transferred all of the young.

There were great differences in food caching behavior between males and females when both the male and the female were in the enclosure (Table 4). While all females were active food hoarders, males rarely hoarded. There was no indication that the male cached food for the female.

TABLE 3. Mean frequency (no. of times per night) of the male and female entering different nest boxes (only pairs in which the male did not desert the enclosure are included)

	Male's nest		Female's nest		Other nests		
	Male	Female	Male	Female	Male	Female	No. of nights
Group 1							
Pair 1	14	8.5	0.5	8.5	22	27	2
Pair 2	7	28	1.5	7.5	11	47	2
Group 2							
Pair 3	6.5	24	1.5	7.5	6	22.5	2
Pair 4	4	10	0	11.5	2	8	2
Pair 5	2.5	9	0	10	1	5.5	2
Pair 6	4	9	0	8	1	10	1*
Mean	6.3	14.2	0.6†	8.4	7.3	20	

*Male deserted the following night.
†Upper limit of 95% confidence interval was 1.35.

TABLE 4. Differences between sexes in food-caching activity

		No. of caching trips by:		
Pair No.	Female reproductive status	male	female	No. of nights
1	Lactating	0	70	2
2	Lactating	0	89	3
3	Lactating	1	87	2
4	Pregnant	0	123	3
5	Lactating	0	122	2
6	Lactating	0	13	1
7	Lactating	2	84	1

Discussion

Whether a male should provide paternal care depends on fitness gained by such behavior relative to fitness gained by extra matings (Trivers 1972; Emlen and Oring 1977; Kleiman and Malcolm 1981; Elwood 1983; Dewsbury 1985). Our experimental setup favored paternal care in two ways relative to natural conditions. First, the males in our experiment sired all nestlings in each litter, which is highly unlikely in the field because of promiscuity. Second, in our experiment there were no females available to the males other than their mates, which is also unlikely under natural conditions. Because males in our experiment showed no paternal care, even with full paternity and no chance of extra matings, we infer that paternal care is very unlikely in nature. The fact that 5 of 14 females were aggressive towards their mates and another 3 actively prevented their mates from entering their nests suggests that females do not tolerate paternal involvement in raising the young. Thus the opportunity for the male to increase fitness by providing paternal care appears to be trivial; males should seek extra matings instead of providing paternal care.

Why some females were aggressive towards their mates is not clear. Wolff (1985) found infanticide by conspecific *P. leucopus* when young were 1−12 days old, and suggested that maternal aggression was protection against infanticide. However, aggression persists well past the first 2 weeks of lactation. Wolff (1985) found that young older than 17 days were not susceptible to infanticide, yet Gleason et al. (1980) found a high degree of maternal aggression when young were 20 days old. If maternal aggression is protection against infanticide,

when there is no point to maternal aggression when young are no longer susceptible to infanticide. Alternatively, maternal aggression may also be explained in terms of resource defence for securing a sufficient energy supply during lactation. The male may incur a cost to the female by consuming food cached by her. This cached food may serve to buffer the unpredictability of dispersed food resources in natural environments and may be important in meeting the high energy demands of breeding females (Millar 1978, 1979).

Sex differences in food caching by *P. leucopus* are logical, given the behavior of males and females. First, caching food is for future use, which implies that the cacher is a long-term resident. Second, cachers must be able to defend the cached food against theft (Smith and Reichman 1984), which implies that the cacher is territorial. Nel (1975) found that caching behavior was associated with solitary, territorial habits when he compared the hoarding behavior of nine species of Kalahari Desert rodents. Several studies indicate that adult female *P. leucopus* are solitary and territorial, while adult males are not (Nicholson 1941; Stickel 1968; Metzgar 1971). This observation may be related to the fact that females must secure a stable energy supply for raising young; males in a promiscuous mating system should shift their home ranges according to the location of females approaching estrus. Thus, females should be the food-caching sex in *P. leucopus*.

We assumed in our experiment that food abundance would not alter paternal behavior, but this assumption requires justification. Scarce food can have two consequences. First, lactating females may be energetically stressed, increasing the benefits of paternal care. Second, estrous females are spatially

and temporally rare. Both of these consequences could favor monogamy and paternal care. We do not know if males are able to adjust their behavior according to the need for paternal care. If they are, then the *ad libitum* food supply in our experiment may have provided males with a cue that paternal care was not needed. Two lines of evidence, however, favor our assumption. First, in paternal care studies with caged mice, food was also provided *ad libitum*, but paternal care was common, i.e., *ad libitum* food did not inhibit paternal behavior. Second, food resources for these mice may indeed be abundant during the breeding season because supplementary food did not increase breeding activities (Hansen and Batzli 1978; Wolff 1986).

In conclusion, our results suggest that paternal care in *Peromyscus leucopus* documented in small cages is very likely an artifact of the caged condition.

Acknowledgements

BIRDSALL, D. A., and NASH, D. 1973. Occurrence of multiple insemination of females in natural populations of deermice (*Peromyscus maniculatus*). Evolution (Lawrence, Kans.), **27**: 106–110.

DEWSBURY, D. A. 1985. Paternal behavior in rodents. Am. Zool. **25**: 841–852.

ELWOOD, R. W. 1983. Paternal care in rodents. *In* Parental behavior of rodents. *Edited by* R. W. Elwood. John Wiley & Sons, Toronto. pp. 235–258.

EMLEN, S. T., and ORING, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. Science (Washington, D.C.), **197**: 215–223.

GLEASON, P. E., MICHAEL, S. D., and CHRISTIAN, J. J. 1980. Aggressive behavior during the reproductive cycle of female *Peromyscus leucopus*: effects of encounter site. Behav. Neural Biol. **29**: 506–511.

HANSEN, L., and BATZLI, G. O. 1978. The influence of food availability on the white-footed mouse: populations in isolated woodlots. Can. J. Zool. **56**: 2530–2541.

HARTUNG, T. G., and DEWSBURY, D. A. 1979. Paternal behavior in six species of muroid rodents. Behav. Neural Biol. **26**: 466–478.

HILL, R. W. 1972. The amount of maternal care in *Peromyscus leucopus* and its thermal significance for the young. J. Mammal. **53**: 774–790.

HORNER, B. E. 1947. Parental care of young mice of the genus *Peromyscus*. J. Mammal. **28**: 31–36.

KLEIMAN, D. G., and MALCOLM, J. R. 1981. Evolution of male parental investment in mammals. *In* Parental care in mammals. *Edited by* D. J. Gubernick and P. H. Klopfer. Plenum Press, New York. pp. 347–388.

McCARTY, R., and SOUTHWICK, C. H. 1977. Patterns of parental care in two cricetid rodents, *Onychomys torridus* and *Peromyscus leucopus*. Anim. Behav. **25**: 945–948.

METZGAR, L. H. 1971. Behavioral population regulation in the woodmouse, *Peromyscus leucopus*. Am. Midl. Nat. **86**: 434–448.

MILLAR, J. S. 1978. Energetics in reproduction in *Peromyscus leucopus*: the cost of lactation. Ecology, **59**: 1055–1061.

——— 1979. Energetics of lactation in *Peromyscus maniculatus*. Can. J. Zool. **57**: 1015–1019.

NEL, J. A. J. 1975. Aspects of the social enthology of some Kalahari rodents. Z. Tierpsychol. **37**: 322–331.

NICHOLSON, A. 1941. The home and social habits of the wood-mouse (*Peromyscus leucopus nebrascensis*) in southern Michigan. Am. Midl. Nat. **25**: 196–223.

SMITH, C. C., and REICHMAN, O. J. 1984. The evolution of food caching by birds and mammals. Annu. Rev. Ecol. Syst. **15**: 329–351.

STICKEL, L. F. 1968. Home range and travels. *In* Biology of *Peromyscus* (Rodentia). *Edited by* J. A. King. Spec. Publ. Am. Soc. Mammal. **2**: 373–411.

TRIVERS, R. L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine, Chicago.

WHITAKER, J. O., JR. 1968. Parasites. *In* Biology of *Peromyscus* (Rodentia). *Edited by* J. A. King. Spec. Publ. Am. Soc. Mammal. **2**: 254–311.

WOLFF, J. O. 1985. Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. Anim. Behav. **33**: 117–123.

——— 1986. The effects of food on midsummer demography of white-footed mice, *Peromyscus leucopus*. Can. J. Zool. **64**: 855–858.