PARENTAL BEHAVIOR OF THE VOLCANO MOUSE, *NEOTOMODON ALSTONI* (RODENTIA: MURIDAE), IN CAPTIVITY

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Paternal behavior of the volcano mouse (*Neotomodon alstoni*) was studied and its role in the care of young compared with that of the female. Paternal behavior of this rodent under laboratory conditions consisted of direct and indirect activities, such as huddling, grooming, sniffing, and retrieving young as well as maintenance and vigilance of the nest. The male volcano mouse exhibited all components of parental behavior displayed by mothers, except suckling. However, the male participated significantly more than the female in huddling, grooming, and sniffing. The existence of paternal behavior in this rodent suggests that under natural conditions this species exhibits a monogamous mating system because monogamy in rodents is often associated with paternal care.

Key words: captivity, Mexico, monogamy, Muridae, *Neotomodon alstoni*, paternal behavior, Rodentia, volcano mouse

Paternal care is not common in mammals. Internal fertilization followed by lengthy pregnancy and a feeding strategy in which offspring are fed milk produced by the mother determine to a great extent that the male stays with the female only during mating. However, in some species of primates, carnivores, insectivores, and rodents, the male remains with its mate and provides care to its offspring (Elwood 1983; Kleiman and Malcolm 1981; Mitchell and Brandt 1972). In rodents, paternal care can be classified into 2 broad categories: direct paternal investment involvement activities that have a direct effect on the offspring, such as feeding, grooming, huddling, and retrieving the pup, and indirect paternal investment consisting of activities that indirectly benefit the offspring, such as resource acquisition, territory defense, nest vigilance, and maintenance (Kleiman 1977). Paternal care in rodents is thought to vary as a function of social organization and mating system. Biparental care seems to occur in species with monogamous mating systems, and single-parent care is usually associated with promiscuous mating. In *Meriones unguiculatus, Microtus ochrogaster,* and *M. pinetorum,* a female and male share a nest and males exhibit parental care (Elwood 1983; Getz et al. 1981; Oliveras and Novak 1986). *Peromyscus californicus* is monogamous, and wild males and females invest similar amounts of time in the nest during lactation (Ribble 1991; Ribble and Salvioni 1990). Fathers exhibit all components of parental behavior displayed by mothers, except nursing (Dudley 1974).

Little is known about parental behavior and social structure of the volcano mouse.
(Neotomodon alstoni), a mouse closely related to Peromyscus (Carleton 1985). The volcano mouse is endemic to the mountain range named Transversal Neovolcanic Axis of México at 2,600–4,500 m above mean sea level (Aranda et al. 1980). This rodent is found in forests dominated by Pinus with an understory of bunch grasses such as Muhlenbergia macroura and Stipa ictize. Observations on reproduction of volcano mice in captivity suggest that males may display paternal behavior (Granados and Hoth 1989). When volcano mice were mated in a monogamous system, the reproductive output and survival of young were higher than in those of promiscuous and polygynic arrangements. Aggression levels also were lower in monogamous systems. These observations suggest that male volcano mice may be involved in parental care. However, that hypothesis has not been directly tested. Therefore, we conducted a study of paternal behavior of the volcano mouse in captivity to assess the role of males in parental care.

MATERIALS AND METHODS

Volcano mice were trapped during September–December 1995 with folding Sherman traps baited with oat flakes in the mountains of the range Volcano Ajusco Sierra, at 1.5 km SE from Parres, Delegación Tlalpan, México, D.F. The mice were transported to a laboratory of the University of Mexico, Mexico City, and kept at ambient temperature (18–22°C) and a photoperiod of 14L:10D (onset light at 0600 h). Two mice of the same sex were placed in acrylic cages (17 by 15 by 12 cm) with sawdust as bedding. They were fed Purina nutricubes for small rodents and tap water ad lib. After a 30-day adaptation period, they were paired. The male remained with the female until young were weaned.

Observations on paternal care of 19 adult pairs with their offspring (families) were performed during January–December 1996. Each family was observed daily during 30-min periods between 2000 and 0200 h under red light in a transparent nesting acrylic cage (17 by 15 by 12 cm) from the day of birth to 30 days postpartum. Observations were performed at night, when animals show more activity. The male was depilated in a small dorsal region to distinguish it from the female. Observations were performed directly by 1 observer, who kept 50 cm away from the nesting cage.

A working ethogram was constructed in which the following activities were recorded: time that male and female huddled with young and frequency and duration of grooming, sniffing, retrieving young, and nest maintenance; time that male and female spent in the nest; surveillance of the nest; and nursing. Descriptions of paternal behaviors were huddling of young by leaning on its forelimbs, keeping its body bowed, while the young lie under its abdomen; grooming of young by holding young with its forelimbs, licking throughout its body, mainly at the genital region; sniffing of young by approaching its snout to young until touching it, rhythmically moving the nose and the vibrissae; retrieving young by holding young with its mouth, bringing it back to the nest; maintenance of nest by pulling bedding material with its forelimbs to make the nest more concave; and vigilance whereby the male keeps an alert position after any strange noise or in response to the observer’s presence.

Data were grouped in 3-day observation periods because behaviors from daily observation were scarce. Statistical analyses performed were analysis of variance with repeated measures, Student’s t-test, and simple linear regression. Means ± SD are presented.

RESULTS

Nineteen pairs of volcano mouse shared single nests throughout the 30-day study period. Each nest consisted of sawdust piled up with a top central concavity. Male volcano mice exhibited paternal behavior, which consisted mainly of huddling, grooming, sniffing, retrieving young, nest maintenance, and vigilance.

During the observation period, males spent more time huddling with young than did females ($F = 23.2$, $d.f. = 1, 10$, $P = 0.0000$). Females stopped huddling with young at day 27 postpartum, whereas males continued displaying this behavior up to day 30 (Fig. 1a). However, both parents invested considerably less time in huddling...
Fig. 1.—Parental care per 30 min of observation by male and female volcano mice (*Neo-
tomodon alstoni*) under captive conditions in relation to age of young: a) mean time of huddling
with young, b) mean frequency of grooming young, and c) mean frequency of sniffing young.

with young between days 18 and 27. As the lactation period progressed, time spent in
huddling also decreased for both parents (males, $F = 12.5$, $d.f. = 9$, 153, $P < 0.0001$; females, $F = 4.8$, $d.f. = 9$, 153, $P < 0.0001$) as revealed by a significant negative correlation ($P < 0.0001$) between huddling time and age of young (males, $r = -0.61$; females, $r = -0.44$).

Males and females exhibited grooming behavior during the whole observation period (Fig. 1b). Males groomed young more frequently than did females ($F = 19.2$, $d.f. = 1$, 9, $P < 0.0001$). Grooming frequencies did not differ during the 3-day observation period for males ($F = 1.2$, $d.f. = 9$, 154, $P = 0.29$), whereas those for females did differ ($F = 2.8$, $d.f. = 9$, 154, $P = 0.004$); that variation, however, was not consistent. Mean time of grooming was similar ($t = -0.23$, $d.f. = 643$, $P = 0.81$) for males (29.2 s ± 23.2 $SD$) and females (29.6 s ± 24.1).

Pup sniffing was displayed by males more frequently than by females during the 30-day observation period ($F = 6.3$, $d.f. = 1$, 9, $P = 0.01$; Fig. 1c). Frequency of sniffing by males and females did not vary during nursing periods (males, $F = 1.3$, $d.f. = 29$, 156, $P = 0.23$; females, $F = 1.7$, $d.f. = 29$, 156, $P = 0.08$). Mean duration of young sniffing by males (4.9 s ± 3.6 $SD$) and females (4.5 s ± 4.9) did not significantly differ ($t = 0.73$, $d.f. = 290$, $P = 0.46$).

Retrieving frequency by males did not differ from that of females ($F = 1.65$, $d.f. = 1$, 9, $P = 0.19$). Variations in retrieving frequency through the nursing period were not statistically different in males ($F = 1.3$, $d.f. = 9$, 157, $P = 0.20$) or females ($F = 0.8$, $d.f. = 9$, 157, $P = 0.56$).

There were no differences between sexes in time allocated to nest maintenance ($F = 3.9$, $d.f. = 1$, 9, $P = 0.06$). Variations per 3 days of observation were not significant for females ($F = 0.7$, $d.f. = 29$, 136, $P = 0.77$) on females for males ($F = 1.7$, $d.f. = 29$, 136, $P = 0.02$), although no pattern was observed. Mean times invested in nest maintenance by males (3.4 s ± 6.2 $SD$) and females (3.4 s ± 5.3) were not different ($t = -0.03$, $d.f. = 125$, $P = 0.97$). During the 30-day observation period, males (26.07 min ± 6.08 $SD$) remained at the nest longer than females (19.42 min ± 12.31; $F = 39.8$, $d.f. = 1$, 9, $P < 0.0001$). Time spent by females nursing was shorter than that for remaining at the nest and not nursing ($F = 39.8$, $d.f. = 1$, 9, $P < 0.0001$).

Males that showed more paternal behavior also showed subordination behavior to females. For example, before an aggressive posture by the female, the male laid down on its back; then the female climbed on top
of him and sniffed and touched his genital region with her snout. During this behavior, males sometimes emitted screeches.

**DISCUSSION**

Male volcano mice, under laboratory conditions, do exhibit direct and indirect paternal behavior (Kleiman 1977), such as huddling, sniffing, grooming, and retrieving young as well as maintenance of and vigilance at the nest. Fathers exhibited all components of parental behavior displayed by mothers, except for nursing, as has been shown for other rodents with biparental care (Elwood 1979, 1983; Gubernick and Alberts 1987; Waring and Perper 1980). Therefore, parental care in the volcano mouse under captive conditions fits that for monogamous species (Elwood 1983; Kleiman and Malcolm 1981; Wittenberger and Tilson 1980). Our results confirmed that reproductive performance of captive volcano mice was successful under monogamous mating conditions (Granados and Hoth 1989).

Differences were found regarding amount of care given by each parent to the young. Males invested significantly more time huddling with young than females. This huddling behavior of male volcano mice may be important in temperature regulation of young, which would be of adaptive value for this species, which dwells in a habitat with temperatures frequently <0°C. Other reports have stated that one of the main contributions of the male to the care of young is maintaining their body temperature (Dudley 1974; Elwood and Broom 1978). For both parents, time spent huddling with young was correlated negatively with age of young. This may be due to gradual acquisition of thermoregulatory capabilities by young; as this develops, young require less huddling. The fact that huddling by both parents decreased between 18 and 27 days suggests that thermoregulatory capability of young may begin during this period.

Male volcano mice participated more than females in huddling, grooming, and sniffing of young, suggesting that, except for nursing, males spend more time in the care of offspring. Similarly, male *Rattus fuscipes* participate more in parental care than females (Elwood 1983). Male volcano mice spent more time in the nest than females, which agrees with data from *Meriones unguiculatus* (Elwood 1975) and *Mus musculus* (Priesnall and Young 1978). In contrast, females of *Peromyscus leucopus*, *Onychomys torridus* (McCarty and Southwick 1977) and those of the monogamous *Microtus pinetorum* and *M. ochrogaster* (McGuire and Novak 1984; Oliveras and Novak 1986; Solomon 1993) remain longer in the nest than males. On the other hand, amount of care given by males of monogamous *P. californicus* is similar to that provided by females (Gubernick and Alberts 1987).

Male volcano mice that exhibited subordination behavior (Granados et al. 1996) to the female were more paternal, suggesting that hierarchical position influences amount of paternal care in this species. Similarly, it has been observed that subordinate males of the Mongolian gerbil (*Meriones unguiculatus*) tend to be more paternal than dominant males (Elwood and Ostermeyer 1984).

Because monogamy is often associated with presence of paternal care, existence of paternal care in the volcano mouse suggests that this species is monogamous under natural conditions (Elwood 1983; Kleiman and Malcolm 1981; Wittenberger and Tilson 1980). Monogamous species tend to dwell in stable environments, give birth to altricial offspring, and have low reproductive potentials and slow postnatal development (Eisenberg 1965; Kleiman 1977). The volcano mouse shares these traits. It dwells in a relatively stable environment, gives birth to altricial offspring, and has 3.2 young/litter and a slow postnatal development; opening of the eyes occurs at 18–20 days; and weaning is not achieved >30 days postpartum (Chavez and Villegas 1993; Martín and
Alvarez 1982). Our laboratory observations showed that suckling behavior took place up to 36 days postpartum. In addition, females remained longer at the nest than the time invested in nursing, suggesting that, besides feeding their young, they carry out other parental activities.

Although monogamy is likely to occur in the volcano mouse, laboratory results could be different from the mating system seen in the wild. For example, males of *Microtus montanus* and *M. pennsylvanicus* exhibit paternal care only when kept in limited space (Hartung and Dewsbury 1979; Wilson 1982). However, field and enclosure data showed that males of these species do not nest with females (Jannett 1982; Olveras and Novak 1986). Conversely, males of *M. pennsylvanicus* are found in the nest with females and young during autumn and winter; in the absence of mothers, fathers spent long periods of time with young and prevented unfamiliar males from gaining access to their young (Madison et al. 1984; McShea 1990; Storey et al. 1994). Therefore, field experiments are needed to confirm whether the volcano mouse is monogamous under natural conditions.

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LITERATURE CITED


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