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Paternal Care in the Social and Diurnal Striped Mouse (*Rhabdomys pumilio*): Laboratory and Field Evidence

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Paternal care is rare in mammals, occurring mainly in carnivores and neotropical primates, in which the difficulties of long generation time and large individuals lead to small sample sizes. Here, the authors show that paternal care can be easily studied in the four-striped mouse (*Rhabdomys pumilio*) because (a) captive males show all the patterns of parental care as do females, with the obvious exception of nursing; (b) in the field, wild males act amicably toward juveniles and retrieve pups experimentally presented to them; (c) the striped mouse facilitates experimental approaches in captivity because it has a short generation period and can be kept in large numbers; and (d) the striped mouse is diurnal, not only making observations in captivity easier but also enabling direct observations in the field.

Direct paternal care, in which fathers actively engage in behaviors such as infant carrying and feeding, is relatively uncommon yet can be found in a variety of animal taxa (Beck, 1998; Gross & Sargent, 1985; Ketterson & Nolan, 1994; Zeh & Smith, 1985). Kleiman and Malcolm (1981) have estimated that paternal care occurs in only 7% of the mammal species studied, mainly in rodents, carnivores, and neotropical primates. Although the social organization of carnivores has been intensively studied (Lewis & Pusey, 1997; Moehlman & Hofer, 1997; Packer, Lewis, & Pusey, 1992), the focus has normally not been on paternal care. Carnivores have long interbirth intervals and most are relatively large (except for mongooses; e.g., Clutton-Brock et al., 2000; Luca & Ginsberg, 2001; Rood, 1990), thus making it difficult to observe more than one group in the field and to keep several groups in captivity under simulated natural conditions. The same holds for neotropical primates that exhibit extensive amounts of paternal care, such as callitrichids, titi monkeys (genus *Callicebus*), and owl monkeys (genus *Aotus*; Vogt, 1984). Although callitrichids have been intensively studied for their communal infant rearing including paternal care (e.g., Bales, O'Herron, Baker, & Dietz, 2001; Koenig, 1995; Schradin & Anzenberger, 2001a, 2001b), New World monkeys also impose the difficulties of large body size and long interbirth intervals, especially when compared with some other mammals such as rodents.

Several rodent species show paternal care in captivity (Dewsbury, 1985). In Mongolian gerbils (*Meriones unguiculatus*), fathers spend time in the nest with the pups and lick and groom them (Elwood, 1975). In prairie voles (*Microtus ochrogaster*; Lonstein & De Vries, 1999), volcano mice (*Neotomodon alstoni*; Laconi & Castro-Vazquez, 1999), and California mice (*Peromyscus californicus*; Gubernick & Alberts, 1987a) males show the same parental behavior patterns and exhibit them to the same extent, with the exception of nursing, as females. Male rodents have often been used to investigate ultimate and proximate reasons for paternal care (for reviews, see Brown, 1993; Schradin, 2001, 2002), such as increased pup survival as a result of the presence of the father (e.g., Dudley, 1974; Gubernick & Teferi, 2000; Wynne-Edwards, 1987) or endocrine regulation of paternal care (e.g., Gubernick & Nelson, 1989; Reburn & Wynne-Edwards, 1999; Wang, Ferris, & De Vries, 1994).

Paternal behavior in rodents has rarely been confirmed by field studies. In several rodent species, males might show paternal behavior under favorable laboratory conditions but not in the field (Dewsbury, 1985). For example, extensive paternal care has been described for captive Djungarian hamsters (*Phodopus campbelli*), whereas only anecdotal evidence for paternal care exists in nature. In fact, it is mainly rodents' nocturnal activity that prevents direct observations in the field (Wynne-Edwards, 1995), and most rodent species thus far studied for paternal care are nocturnal (apart from the dwarf hamsters cited above, the voles of the genus *Microtus* [Dolby & Rozenfeld, 2000; Getz & McGuire, 1997; Webster & Brooks, 1981] and the California mouse [Marten, 1973]).

The objective of the present study is to demonstrate that paternal care occurs in the four-striped mouse (*Rhabdomys pumilio*; as this genus is monotypic, this species will from now on be simply called *Rhabdomys*) under both captive and natural circumstances. *Rhabdomys* is a diurnal rodent with adults weighing over 40 g and reaching over 70 g in some free-living individuals. At our field site in the succulent karoo of South Africa, the social structure of *Rhabdomys* is best described as territorial group-living solitary

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foragers with communal breeding (Schradin & Pillay, in press). Groups contain up to 3 breeding females, 1 or 2 breeding males, and sometimes more than 30 adult individuals after the breeding season (i.e., the breeding individuals and their adult offspring). Each group has a nest in a dense bush, from which the group emerges after sunrise with group members basking in the morning sun and often sitting in body contact or grooming each other. Group members forage alone but may meet during foraging, sniffing at each other and feeding in close proximity. In contrast, encounters with mice from different groups are typically aggressive (Schradin, 2003). In the evening, group members meet again in front of the nest, basking together in the evening sun before withdrawing into the nest for the night (Schradin & Pillay, in press).

Anecdotal evidence for paternal care was reported in one study in captivity (Choate, 1972) but not in the field studies. *Rhabdomys* offers all the advantages of a rodent species such as small size and short interbirth interval, and because it is a diurnal species (Choate, 1972; Christian, 1977), observations can be easily made in captivity (Dewsbury & Dawson, 1979) and in the field (Krug, 2002; Schradin, 2003; Schradin & Pillay, in press). This study had three aims: (a) to describe paternal care of captive *Rhabdomys* from two different populations in South Africa that are 1,300 km apart and to test whether paternal care occurs in *Rhabdomys* and is a common pattern found in this species, (b) to compare paternal care with maternal care, and (c) to investigate whether paternal behavior also occurs in free-living *Rhabdomys* of one population.

Method

Laboratory Study

Animals. All animals used were adult wild-born four-striped mice (*Rhabdomys pumilio*) trapped in Goegap Nature Reserve near Springbok, South Africa, and in Suikerbosrand Nature Reserve near Johannesburg, South Africa. Trapping was performed using metal traps (26 × 9 × 9 cm) baited with a mixture of bran flakes, sea salt, and salad oil. Traps were checked at least every hour and closed during the hot part of the day. Whereas the habitat in Goegap Nature Reserve consists of arid succulent karoo with an annual rainfall of approximately 160 mm that occurs mainly in winter (Acocks, 1988), the Suikerbosrand Nature Reserve habitat comprises moist grasses with an annual rainfall of about 740 mm that mainly occurs during summer (Acocks, 1988).

Mice were brought to the laboratory in Johannesburg, South Africa, and kept under standard laboratory conditions with a 14:10-hr light–dark cycle with lights on at 6 a.m., a room temperature of 20–24 °C, and 30%–60% relative humidity. Epol mouse cubes (Epol, Pretoria West, South Africa) and water were provided ad libitum, and seeds (parrot food) were provided daily after pairing. Mice were paired in the laboratory in 40 cm long × 12 cm high × 25cm wide Lab-o-tec cages (Labotec, Halfway House, South Africa) with coarse wood shavings as litter and hay as nesting material. Altogether, 17 pairs of Springbok mice and 12 pairs of Johannesburg mice were established. Of these, 12 pairs from Springbok and 6 pairs from Johannesburg produced litters and were used for study. Each pair raised a first litter in the Lab-o-tec cage without being observed. This was done to ensure that all individuals had experience in infant rearing (mice were wild trapped and we did not know their previous reproductive history). When the first litter was weaned at an age of 16 days (Brooks, 1982), the parents were moved into a glass tank (45 × 30 × 30 cm) without their offspring; the next birth was expected approximately 7 days thereafter (the minimum interbirth interval is 23 days; Dewsbury, Ferguson, & Webster, 1984). The floors of the tanks were covered with wood shavings, and each tank was equipped with a brick (22 × 7 × 10 cm) at its back that gave access to a drinking bottle hanging at the back wall of the tank. Food was provided in food dishes. No hay was provided in these tanks, but in each tank, two nest boxes (13 × 9 × 10 cm) made of polyvinyl chloride were placed in the front corners. Nest boxes were open on two sides, one side allowing access for the mice and the opposite side facing toward the front wall of the tank. The opening in the front was covered by a black piece of paper that was attached to the outside of the tank. Two nest boxes were provided because fathers might have stayed with pups in one nest box not because they intended to stay with their offspring but because no alternative nest box was available.

Observations. Once the second litter of a pair was born in the glass tank, observations were performed daily from the day of birth (Day 0) until Day 9. Pups start leaving the nest around Day 8, and at Day 10, they spend significant time outside the nest (Brooks, 1982). Observations were performed either in the morning (between 7 a.m. and 10 a.m.) or in the afternoon (between 4 p.m. and 7 p.m.), as *Rhabdomys* is known to be most active during these times of the day (Dewsbury & Dawson, 1979). To test whether parents increased the time they spent in the nest after the birth of pups (which would indicate that parents alter their behavior directly as a response to the presence of offspring), we made control observations of each pair six times either before birth of the second litter ($n = 8$) or after the second litter was weaned and removed ($n = 10$). During these control days, the time that parents spent in the nest was recorded.

For observations, the black pieces of paper covering the back of the nest boxes were removed temporarily to enable videotaping of the nest. Videotaping was performed for 20 min with no observers inside the animal room. To give the mice 5 min to recover from the disturbance, we analyzed only the last 15 min of the 20 min recorded. The following behavioral patterns were recorded for both the mother and the father: presence in nest (duration), huddling pups (duration), licking pups (duration), and carrying pups in the mouth (frequency). Carrying pups included manipulation of pups in the nest by taking a pup in the mouth as well as retrieving pups (i.e., carrying a pup that had moved outside the nest in the mouth and bringing it back into the nest). The data for manipulation and retrieving were combined, as both behaviors were observed infrequently.

These behavior patterns are not mutually exclusive, as time in the nest includes time spent huddling and licking pups (which never occurred outside the nest) and parents could huddle some pups and lick others simultaneously. Sometimes a parent in the nest was hidden by the other parent or had its back to the camera, obscuring videotaping. In these cases, it was not possible to see whether parents huddled pups and whether they licked pups or themselves. Therefore, these cases were recorded as time spent in the nest.

Pup retrieval test. On Day 3, a pup retrieval test was performed with all fathers. To minimize disturbance—which could otherwise lead to infanticidal behavior (Elwood, 1991)—we performed only one test per father, and no tests were performed with the mothers. To control for the influence of the mother, we temporarily removed her from the tank for the duration of the test. Two pups were placed in the right back corner of the tank, and 2 in the left back corner. Surplus pups (when the litter was larger than 4 pups) were placed with the mother. Ten minutes of video recording was performed without any observers present in the animal room. During videotaping, the black pieces of paper covering the two nest boxes were removed. After 10 min, the test was terminated and the female and the remaining pups were returned to the tank. Videotapes were analyzed by recording whether the father retrieved pups and after what interval he retrieved the 1st, 2nd, 3rd, and 4th pup. Sometimes not all pups were retrieved, but instead, 2 pups were brought to the other 2 in one corner and the male started nest construction there.

Field Study

Study area and period. A field study was performed from September 2001 to January 2002 in the Goegap Nature Reserve near Springbok in

northwest South Africa. The vegetation here consists of succulent karoo; that is, the main vegetation is bushes of the species *Zygophyllum retrofractum* with the sandy areas between bushes occupied by different succulents and wild flowers in spring (September–October). An area of 80 × 60 m was used as the study area.

Trapping and marking of animals. *Rhabdomys* was live trapped using metal traps (26 × 9 × 9cm). Traps were placed at bushes where mice had been observed previously. Trapped mice were sexed, weighed, and individually marked with hair dye; we used Wella Viva (Modern Hairdressing Supplies, Cape Town, South Africa) color for blond, red, and violet and Inecto Rapid (Rapido, Pinetown, South Africa) for black. The practice of marking wild *Rhabdomys* by writing numbers with hair dye on their backs has previously been successfully used by Krug (2002), and we had previously practiced hair dying with colors on captive striped mice. There was no indication that hair dying made mice more conspicuous to predators, as a field trip 3.5 months after termination of the field study revealed very high survival rates for the study groups (mean survival of 73% for five groups at the end of the dry season with low food abundance). Mice were retrapped about every 5 to 6 weeks to refresh the marking of hair dye as well as to mark juveniles.

Observations. We observed marked individuals in the field by eye and by using binoculars. As *Rhabdomys* is mainly active during the morning and afternoon (see Dewsbury & Dawson, 1979) and not during the middle of the day in the field (personal observation) when temperatures can reach over 40 °C, observations were performed during the morning (3.5 hr starting after sunrise) and afternoon (3.0 hr before sundown). Every time a mouse was spotted that could be identified, it was observed by focal-animal sampling and carefully followed for a distance of 5–10 m. When the focal mouse disappeared inside a bush, the observation was terminated after 3 min, as it was not known whether the mouse remained in the bush or had exited undetected through another side. Focal observations had a duration of 1–45 min. Additional observations were performed during mornings and afternoons in front of nests, when mice showed many social interactions before leaving for foraging (morning) or withdrawing into the nest (afternoon). All social behaviors of adults directed toward juveniles were recorded: Aggressive interactions included chasing, jumping on the juvenile (attack), and biting; affiliative interactions included sniffing at the juvenile, sitting in body contact, and grooming. All behaviors were recorded as events, as the complex situation in the field made measurement of time impractical, imposing the risk of losing focal individuals. After nests of groups were found, we recorded whether the same adult males always stayed at these nests and whether they were observed entering the nest in the evening and emerging in the morning, giving an indication of whether males stayed overnight in the nest.

Pup retrieval experiment. One- to 3-day-old pups were presented to males (Elwood, 1991, advocates the use of young pups in such experiments because older pups with a more well-developed nervous system experience greater stress). Pups were obtained from six breeding pairs kept in cages at the Goegap Nature Reserve. Pups were presented about 2 m away from nests in which it was assumed that pups of approximately the same age were present, calculated from the first time small juveniles were observed at the nest (estimated as being 10 days old, the age when pups start leaving the nest) and the interbirth interval of approximately 23 days (Brooks, 1982). Thus, when 10-day-old pups were observed at a nest, the pup retrieval experiment was performed 13–15 days later. From cross-fostering experiments, we know that striped mice do not distinguish between their own and strange pups as long as pups are younger than 10 days, probably because under natural circumstances encounters with strange pups that are too young to leave their nest are unlikely to occur, making the evolution of kin recognition of pups of 10 days of age or younger unnecessary (Pillay, 2000; Schwaibold & Pillay, 2001). Pups were presented in front of nests, and resident mice were enticed from the nest with bait to reduce the time necessary to perform the experiment. Not more than 2 pups were presented at each nest to avoid increasing litter size to one that would be too large for wild mice to rear. Only 1 pup was presented at one time (for ethical considerations that suggest using as few pups as possible, see Elwood, 1991), and observations were performed from a distance of 5 m. As only adult males were to be tested and only a limited number of pups were presented at each nest, group members other than adult males were chased away from the pup. The behavior of adult males toward the pup was recorded as neutral (no reaction apart from sniffing), retrieving of pup for some distance but not into nest, and retrieving into nest. If an attack occurred, the attacking mouse was immediately chased away and the pup was examined and euthanized if it was alive (a case that never occurred; for ethical concerns concerning this procedure, see Elwood, 1991). If pups were not retrieved into the nest within 10 min, they were returned to their parents. Before being placed in front of nests, stimulus pups were marked with hair dye to enable us to identify these pups once they emerged from recipient nests; this was to allow us to gauge whether wild mice reared them.

Statistical Analyses

All tests used were nonparametric (Siegel & Castellan, 1988) and two-tailed. For comparisons within individuals or pairs, the Wilcoxon matched-pairs signed-ranks test was used, abbreviated as Wilcoxon test (test statistic given as T). For comparisons between groups, the Mann–Whitney U test was used. When multiple comparisons were performed to test for one null hypothesis, the sequential Bonferroni method was applied (Rice, 1989).

Results

Laboratory Study

Comparison of paternal care between populations. Males of both populations showed paternal care, spending time with the pups in the nest, huddling, licking, and retrieving pups (see Table 1). In the retrieval experiment, 17 of 18 males retrieved pups (1 Springbok male did not retrieve). There were no differences in paternal response between males from the Springbok population and males from the Johannesburg population (see Table 1).

Comparison between paternal and maternal care. As no population differences were found in paternal response, paternal care and maternal care were compared using pairs from both populations ($n = 18$). There were no differences between fathers and mothers in the time spent in the nest with the pups, time spent huddling pups, and time spent licking pups (see Table 2). However, mothers carried pups in the mouth significantly more often than did fathers (see Table 2).

Direct parental care. We compared the time parents spent in the nest box containing the pups with the time spent in the nest box during control days. In both conditions, observations were made at the same time of the day; that is, of the 10 days of pup rearing, we used data for only the 6 days when data were collected at the same time as control days. All fathers and mothers spent more time in the nest box during pup rearing than during control days (Wilcoxon test): for both comparisons, $T(N = 18) = 0.0$, $p = .0002$ (see Figure 1). They even spent more time in the nest box with the pups than in both nest boxes combined during control days: for fathers, $T(N = 18) = 4.0$, $p = .004$; for mothers, $T(N = 18) = 12.0$, $p = .028$.

Males tended to spend more time without the mother in the nest box during the time of pup rearing ($Mdn = 16.6$ min/150 min, 1st quartile = 7.9 min, 3rd quartile = 24.9 min) than during control days ($Mdn = 8.2$ min/150 min, 1st quartile = 2.6 min, 3rd

Table 1
Comparison of the Amount of Paternal Care Shown by Male Striped Mice From Springbok, South Africa (n = 12), and From Johannesburg, South Africa (n = 6)

	Springbok			Johannesburg				
Behavior pattern	*Mdn*	1st quartile	3rd quartile	*Mdn*	1st quartile	3rd quartile	*U*	*p*
Presence in nest (min)[a]	113	93	135	119	112	124	29	.51
Huddling pups (min)[a]	43	30	57	43	29	55	35	.93
Licking pups (min)[a]	2.0	1.0	5.1	3.6	1.8	5.8	32	.71
Carrying pups (no. of times)[a]	2.0	0.0	3.3	1.5	1.0	5.0	35	.92
Retrieval of 1st pup (s)[b]	18	13	115	18	7	35	28	.45
All 4 pups brought together (s)[b]	148	105	225	292	143	358	66	.40

[a] During the total observation time of 150 min. [b] Results of the retrieval test, measured as the time from the beginning of the test until completion of retrieval behavior.

quartile = 20.7 min), $T(N = 18) = 43.0$, $p = .0642$. Males spent the same percent of their time in the nest together with their female partner during control days (*Mdn* = 75%, 1st quartile = 44%, 3rd quartile = 89%) as during the time of pup rearing (*Mdn* = 78%, 1st quartile = 60%, 3rd quartile = 86%), $T(N = 18) = 75.5$, $p = .66$.

To establish whether males and females showed time sharing in parental care duties, which means that one parent looks after the pups while the other is out (e.g., to feed), we compared the percentage of time the male spent in the nest relative to the total time (150 min) with the percentage of time he was alone in the nest relative to the time the female was not in the nest. If time sharing existed, males would have been more likely to be found in the nest when the female was out (time alone in nest relative to time female not in nest) compared with baseline (time in nest relative to total time). In contrast to the time-sharing prediction, the percentage of time males spent in the nest relative to the total time was significantly higher (*Mdn* = 77.6%, 1st quartile = 71.4%, 3rd quartile = 86.5) than compared with the time the female was absent (*Mdn* = 68.7%, 1st quartile = 43.8%, 3rd quartile = 79.2%), $T(N = 18) = 0.0$, $p = .0002$.

Field Study

Nest attendance. A total of seven nests were located during the study. In six of seven nests, individually marked adult males entered in the afternoon before sunset and left the same nest the next morning after sunrise. The seventh nest was only observed during mornings, and the same males were seen at this nest several mornings, but no data are available about whether these males had entered this nest the previous afternoon. The ratio of the nests that were observed both afternoons and mornings with males entering in the afternoon and leaving the next morning was 6:0, which differs significantly from chance (binomial test, $N = 6$, $p < .05$).

Direct observations. A total of 38 interactions of 6 breeding males belonging to six different groups with juveniles were observed. Of these, 2 were aggressive, and the other 36 were amicable (see Figure 2). One male chased 2 juveniles that were relatively old (30 days) and probably belonged to another group. This male was not observed to show amicable behavior, whereas the other 5 males showed only amicable and never aggressive behavior. Adult males were not significantly more likely to show amicable than aggressive behavior toward juveniles, $T(N = 6) = 3.0$, $p = .11$.

Interactions between adult females and juveniles were observed on 31 occasions; 2 of these were aggressive and the other 29 were amicable (see Figure 2). Interactions of a total of 8 adult females from five different groups were observed; 2 of the females showed aggressive behavior (1 of these also showed amicable behavior) and 6 showed only amicable behavior. All of these females were reproductively active, as indicated by body weight (range 40–84 g) typical of pregnant females and prominent nipples indicative of lactation. Adult females were significantly more likely to show

Table 2
Comparison of the Amount of Paternal and Maternal Care Shown by 18 Pairs of Mice During 150 min of Total Observation Time

	Fathers			Mothers					
Behavior pattern	*Mdn*	1st quartile	3rd quartile	*Mdn*	1st quartile	3rd quartile	*T*	*p*[a]	Adjusted *p*[b]
Presence in nest (min)	116.7	106.5	132.4	99.1	90.8	112.0	44.0	.07	> .3
Huddling pups (min)	42.8	28.9	56.5	55.2	39.3	70.5	55.0	.18	> .3
Licking pups (min)	2.8	1.1	6.0	5.0	3.0	6.5	69.0	.47	> .4
Carrying pups in mouth (no. of times)	2.0	0.3	3.8	10.5	5.0	18.5	11.5	.0021	< .01

Note. The 18 pairs were combined from the Springbok population and the Johannesburg population.
[a] Wilcoxon test. [b] Sequential Bonferroni.

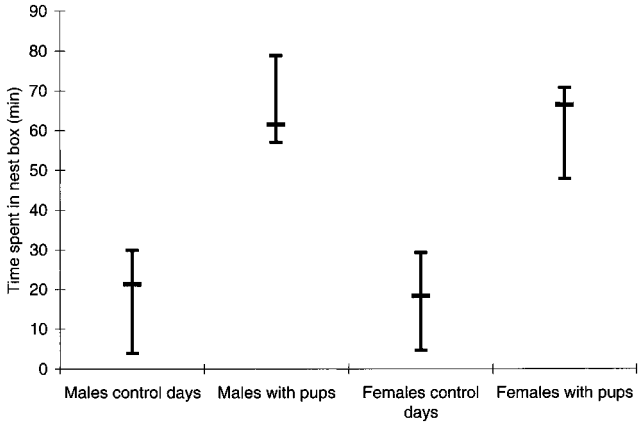

Figure 1. Time spent in the nest box (out of 90 min of observation) during the period of infant rearing (with pups) and during control days for both males and females. Medians and first and third quartiles (bars) are shown.

amicable than aggressive behavior toward juveniles, $T(N = 8) = 2.0$, $p = .02$.

The ratio of aggressive to amicable males (1:5) did not differ significantly from the ratio in females (1:6, with the 1 female showing both aggressive and amicable behavior being scored as 0; Fisher exact test, $p > .99$).

Pup retrieval experiment. Table 3 summarizes the results of the pup retrieval experiment. The table distinguishes between old adult males that were considered to be the breeding males of the group and young adult males born in the same breeding season and probably offspring of the breeding females of the groups observed (Schradin & Pillay, in press). Five of the 7 old adult males retrieved the pup for at least some distance, although only 2 of them carried the pup directly into the nest. A ratio of paternal to nonpaternal males of 0:7 would be expected if males were not paternal. The observed ratio of 5:2 differs significantly from this expectation (Kolomogorov–Smirnov one-sample test), $D(N = 7) = .714$, $p < .01$. One of the males that retrieved the pups for some distance without taking it into the nest was also observed licking and huddling the pup in front of the nest, thus showing paternal behavior.

Further observations were made of nests to ascertain whether nest inhabitants were rearing their own pups during retrieval experiments. If pups had been present, we expected to see very young juveniles at the nest a few days later. These observations revealed that at the nests of the 2 retrieving old adult males, pups had been present during the experiment. In nests of the 3 males that retrieved for some distance but not into the nest, no juveniles were observed outside two nests, indicating that during the experiment no pups were present; at the third nest, juveniles were observed 6 days later. No juveniles were observed at the nest of the nonreacting male. With regard to the infanticidal male, it became evident later that he was no longer a group member of the nest where he was tested and that he had been displaced by another male.

Other group members were also attracted to the pups presented at nests, and it was not always possible to keep them away from pups. These coincidental results are also included in Table 3 for comparison. Similar to the breeding males, 1 breeding female showed infanticide: Both pups were bitten in the head resulting in their immediate death. It is of further interest to note that 2 young adult males that approached a pup showed no reaction, whereas 3 juveniles of unknown sex retrieved the pups.

It was not possible to determine whether the recipient groups reared the retrieved pups because the hair dye used to mark the pups had faded. The fading of the hair dye was noticed on pups that were not retrieved and were returned to their parents.

Discussion

Paternal care was studied in captive *Rhabdomys* of two populations that live 1,300 km apart in extremely different ecological conditions: One population inhabits arid succulent karoo, and the other inhabits moist grasslands. However, captive male *Rhabdomys* of both populations exhibited extensive amounts of paternal care, indicating that paternal care is the normal reaction of captive male *Rhabdomys*. With the exception of nursing, males show the same patterns of parental behavior as females. Males spend as much time with the pups in the nest as females, and both sexes huddle and lick pups for similar lengths of time. Sexes differed only in carrying of pups, with mothers performing this behavior more often than fathers. However, males do carry pups, and in the retrieval experiment, 17 of 18 fathers retrieved their pups in the absence of the mother. In several other rodent species that exhibit paternal care, such as Mongolian gerbils (Weinandy & Gattermann, 1999), fathers huddle and lick pups under captive conditions but do not retrieve pups (Dewsbury, 1985).

Paternal care can be divided into direct and indirect paternal care. Indirect paternal care is shown independently of the presence of young (e.g., defending a nest or a territory including critical resources), whereas direct paternal care is shown as a direct response to the presence of offspring (Kleiman & Malcolm, 1981). In *Rhabdomys*, retrieving, huddling, and licking pups are patterns of direct paternal care. Additionally, both parents also increase the time spent in the nests during the period of pup rearing, indicating that they are attracted to their offspring.

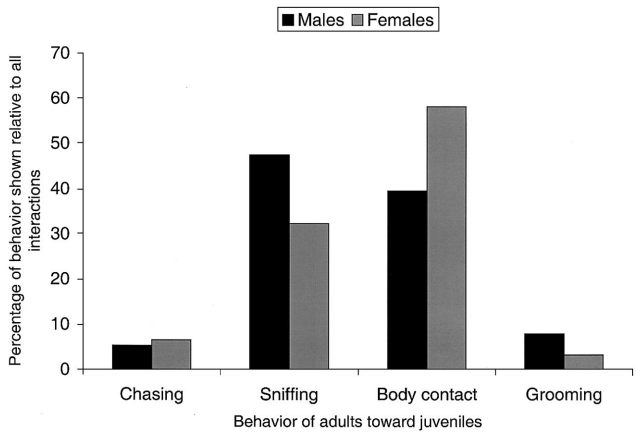

Figure 2. Interactions between wild adult male (black bars) and female (gray bars) *Rhabdomys* and juveniles. The occurrence of each behavioral category is given as a percentage of all interactions observed (for males, $n = 38$; for females, $n = 31$).

Table 3
Responses of Male Striped Mice Toward Pups Presented in the Field and Responses of Females and Juveniles That Approached the Pups

Subjects	No reaction apart from sniffing	Attack	Carrying in mouth but not into nest	Retrieving into nest
Old adult males	1	1	3	2
Young adult males	2			
Old adult females	1	1		3
Juveniles[a]				3

[a] Sex unknown.

It could be that males increase the time spent in the nest because they are attracted to the female rather than the pups. Indeed, males spent the same percentage of time together with the female in the nest during both control days and the period of pup rearing. This also indicates that *Rhabdomys* parents do not show time sharing during pup rearing; that is, males were not more likely to be found in the nest when the female was outside the nest. We cannot distinguish whether the male was attracted to the female or whether there was mutual attraction between the sexes. Nevertheless, extensive amounts of parental care by both parents demonstrate that they directly reacted to the presence of pups. Furthermore, males tended to spend more time alone in the nest during pup rearing than during control days ($p = .06$).

Rhabdomys fathers show an extensive amount of direct paternal care in captivity. However, this does not automatically mean that they also show paternal investment; that is, increasing their pups' survival probability by reducing their possible investment in future litters (Trivers, 1972). Licking of pups probably does not constitute parental investment because parents ingest liquid, and it is important to note that lactating females compensate for salt loss by obtaining saline-rich urine from licking pups (Friedman, Bruno, & Alberts, 1981; Gubernick & Alberts, 1987b). Therefore, it is surprising that female *Rhabdomys* did not lick pups more often than did males, as found in Mongolian gerbils (Elwood, 1975) and prairie voles (Solomon, 1993). Huddling with pups might also not involve parental investment because parents might gain thermoregulatory benefits. It seemed that parents preferred to sit over the warm pups, a possible proximate mechanism leading to huddling behavior. Both males and females often used a certain huddling position (kyphotic posture), with stretched legs to make space for the pups under their abdomen, instead of simply sitting on pups. The kyphotic posture is very likely to be energetically expensive and thus a form of parental investment. Retrieving pups can be regarded as parental investment, as it is likely to reduce predation risk and to be energetically costly. The highest investment by fathers is probably the enormous increase (nearly threefold) in time spent in the nest during the period of infant rearing. This time could alternatively be invested in searching for food or additional mates. With only one pair in a tank, however, males could not search for additional females; therefore, it is difficult to assess paternal investment in captivity.

Although males of several rodent species are known to display paternal behavior in captivity, often little or no evidence of paternal care exists in nature. Our field study demonstrates that the results obtained in captivity are not artifacts. In the succulent karoo of northwest South Africa, *Rhabdomys* is a highly social species, and each social group contains 1 or 2 breeding males (Schradin & Pillay, in press). These males clearly stay with the group, meeting other group members in the evening at the nest, which is the time and place when most social interactions between group members occur (Schradin & Pillay, in press). The same males were observed in front of these nests the following morning, sitting in body contact with other group members, suggesting that these males spent the night in the nest and potentially show paternal care. Ad libitum sampling showed that males also visited nests during the day (personal observation). Furthermore, nearly all social interactions observed between males and juveniles were amicable, whereas aggressive interactions were rare. Exactly the same pattern of amicable interactions was found for breeding females. However, it was not possible to observe the behavior of the occupants inside nests because nests were located in very dense bushes (Schradin & Pillay, in press). Instead, pup retrieval experiments demonstrated that wild males readily retrieve pups, but we were unable to show that retrieved pups were actually raised by the group because their markings faded. It is possible that mice simply carried pups away to eat them, as occurs in captive gerbils (Elwood, 1977), but the behavior observed during retrieval in the field resembled that of captive studies: Males that retrieved pups for only a short distance did not treat pups as food but sniffed, licked, and huddled pups, indicating paternal motivation. There are other reasons why our results might have to be interpreted cautiously: (a) Presented pups did not have a familiar odor to nest inhabitants; (b) pups were presented at a distance from the nest where pups never had been observed, such that the selective advantage of males retrieving pups at this distance is not clear; (c) males were attracted by presenting bait, which might have confounded motivation of males; and (d) other group members were chased away, such that adult males could have been alarmed. However, if these reasons are of crucial importance, they would work against males showing paternal-like behavior. Thus, our results are in agreement with the interpretation that wild *Rhabdomys* males can be paternally motivated, and the results from captivity are not incidental but need special explanations at both the proximate and ultimate level.

There was some difference in the response of wild males. One male showed infanticide, 1 showed no reaction, 3 retrieved for a short distance but not into the nest, and 2 retrieved into the nest. The simplest explanation is that males were differently motivated because of different social stimuli in their own nests. It became evident later that the 2 retrieving males had pups in their nest during experiments, whereas 2 of the 3 males who retrieved for only a short distance had no pups. Experiments were performed at the end of the breeding season, and the groups to which these 2

males belonged had presumably terminated breeding. It is important to note that the infanticidal male had been displaced from his group before the experiment.

Although more data are desirable, we have good indication that paternal care occurs also in wild *Rhabdomys*. Nevertheless, paternal care may not occur in free-living *Rhabdomys* males of all populations. Dewsbury (1985) commented on males of several species that readily show paternal care in captivity without any evidence of such behavior from the field, indicating that the results obtained in the laboratory might be artifacts. His alternative explanation was that paternal behavior might also occur in these species in the field but only under particular circumstances. Thus, males may be capable of an adaptive, flexible behavioral response dependent on ecological conditions. This might also apply to *Rhabdomys*, as field studies from different localities, which differ in their ecological conditions, suggest that the social structure of *Rhabdomys* is highly flexible. Social flexibility might be a key factor that led to striped mice inhabiting different habitats throughout southern Africa, such as grassland, marsh, forests, succulent karoo, and deserts (Kingdon, 1974; Nel, 1975; Schradin & Pillay, in press). Whereas *Rhabdomys* inhabiting dry areas are quite social (Krug, 2002; Nel, 1975; Schradin & Pillay, in press), the situation seems to be very different in moist grasslands. Here, *Rhabdomys* is not communal: Instead, females have exclusive territories, which are aggressively defended against other females, with only the last litter staying in the nests, and males occupy separate territories that overlap several female territories (Brooks, 1982; Choate, 1972; Perrin, 1980; Willan & Meester, 1989). Although wild populations of *Rhabdomys* might differ in their social organization and possibly also in the amount of parental care, our study demonstrates that captive males from a dry habitat (Springbok, South Africa) and a grassland habitat (Johannesburg, South Africa) display extensive amounts of paternal care.

Rhabdomys offers an excellent opportunity to understand paternal care in mammals because it has a short interbirth interval and a small body size, making studies in captivity including experimental approaches relatively easy. It has an advantage over other muroid rodents because its diurnal habit permits direct observations in the field. Furthermore, indications of intraspecific social flexibility suggest that ecological factors might influence social behavior: Populations living in dry habitats might show paternal care, whereas males in grasslands might invest more energy in mate searching. More detailed studies are needed in this respect.

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