

The Striped Mouse (*Rhabdomys pumilio*) From the Succulent Karoo, South Africa: A Territorial Group-Living Solitary Forager With Communal Breeding and Helpers at the Nest

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The authors studied the striped mouse (*Rhabdomys pumilio*) in the semiarid succulent karoo of South Africa. Mice forage alone, but they live in groups that share a common nest. Groups consist of 1 to 4 breeding females, 1 to 2 breeding males, and their offspring of both sexes, which remain in their natal group even after reaching adulthood, participating in territorial defense and nest building without showing signs of reproductive activity. Interactions are typically amicable and take place inside or in front of the nest. In contrast, encounters with mice from other groups are aggressive. Group living in the succulent karoo is possibly due to ecological constraints imposed by habitat saturation because of a year-round stable food supply as well as associated benefits of philopatry.

For researchers of animal behavior, the study of differences in social organization has always been a fascinating topic (Lott, 1991). Closely related species were often studied to find explanations for differences in social behavior (e.g., Crook, 1964; Jarman, 1974; Reburn & Wynne-Edwards, 1999; Schradin, Reeder, Mendoza, & Anzenberger, 2003). Differences in social organization occur, for example, in closely related species of the vole genus *Microtus* (Parker, Phillips, & Lee, 2001). Some species are solitary, such as the California vole (*Microtus californicus*; Salvioni & Lidicker, 1995) and the meadow vole (*Microtus pennsylvanicus*; Parker et al., 2001; Webster & Brooks, 1981), whereas in the common vole (*Microtus arvalis*), females live in groups (Dobly & Rozenfeld, 2000). Differences in social organization can even occur within species, and the social flexibility of a species is often associated with its ability to inhabit different habitats (Lott, 1991). One example is the prairie vole (*Microtus ochrogaster*), which can be monogamous or solitary promiscuous or polygynous depending

on the habitat it occupies (Roberts, Williams, Wang, & Carter, 1998). Another rodent species that inhabits various habitats is the striped mouse (*Rhabdomys pumilio*); as this genus is monotypic, we refer to this species as *Rhabdomys* hereafter; but see also Rambau, Stanyon, & Robinsom, 2003), a diurnal murid rodent with a body weight of 40–80 g. It is widely distributed in southern Africa and can be found in different habitats, such as grassland, marsh, forests, semideserts, and deserts (Kingdom, 1974).

Many field studies have been conducted on *Rhabdomys* (Brooks, 1982; Choate, 1972; David & Jarvis, 1985; Perrin, Ercoli, & Dempster, 2001; Willan & Meester, 1989; Wirminghaus & Perrin, 1993), all of which used the indirect method of capture, mark, and recapture. In the grasslands of Zimbabwe, a female and her pups of the last litter stay in one nest, whereas the males occupy separate areas (Choate, 1972). The same pattern apparently exists in the grasslands of KwaZulu-Natal Province, South Africa, where female *Rhabdomys* have exclusive territories, which are aggressively defended against other females, and male territories overlap several female territories (Perrin et al., 2001; Willan, 1982; Willan & Meester, 1989; Schradin & Pillay, 2003b). Additionally, field studies in grassland areas in several other South African localities, such as Pretoria (Brooks, 1974) and KwaZulu-Natal midlands (Wirminghaus & Perrin, 1993) as well as in *Acacia* habitat near Cape Town (David & Jarvis, 1985), and in semisucculent thorny scrub in the Eastern Cape Province (Perrin, 1980b) indicate that *Rhabdomys* lives solitarily, except for mothers and unweaned pups.

We showed in an earlier study that male *Rhabdomys* exhibit high levels of paternal care in captivity (Schradin & Pillay, 2003d). As a direct response to the presence of pups, fathers increase the time spent in the nest nearly threefold. Males lick and huddle pups in the nest, and they show this behavior to the same extent as females. Also, males retrieve pups that have been positioned outside the nest. These behaviors do not concur with observations that *Rhabdomys* is a solitary species and males associate with females only for mating and are not associated with juveniles in the field (Willan, 1982). Males of many rodent species show

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paternal care under artificial conditions in the laboratory without indications from the field, and these behaviors might be regarded as laboratory artifacts (Dewsbury, 1985). Alternatively, paternal care might be a true alternative strategy shown under special ecological conditions, but not under others (Dewsbury, 1985).

There is some indication that the social structure of *Rhabdomys* is flexible. In the Kalahari, *Rhabdomys* seems to exhibit a more communal than solitary lifestyle (Nel, 1975). For small mammals, group living could be a strategy that provides some benefits in arid environments (Dean & Milton, 1999), but not in more mesic environments. For example, southern Africa squirrels (Sciuridae) living in arid environments are typically group living, probably because of benefits accrued through predator avoidance and thermoregulatory benefits provided by nest sharing, but are solitary in more mesic areas (Waterman, 1995). One reason for *Rhabdomys* being solitary in grasslands but social in dry habitats might be differences in food abundance: In grasslands, most vegetation consists of grass that is apparently not consumed by *Rhabdomys*, which instead feeds on grass seeds and other foods, such as berries and herbs (Curtis & Perrin, 1979; Perrin, 1980b). Thus, *Rhabdomys* in the mesic grasslands may actually be surrounded by mostly unpalatable food, and palatable food is patchily distributed and scarce, which then would demand large home ranges, low population density, and a solitary lifestyle (Ostfeld, 1990). In contrast, food is abundant in spring in the semiarid succulent karoo, and mice gain weight during this period, probably ensuring survival during the forthcoming dry season (summer) when the food availability decreases (Schradin & Pillay, 2003a). Even during the dry summer, mice have access to a stable year-round food source that consists of succulents and *Zygophyllum retrofractum* bushes (personal observation). Similarly, *Acacia* tree seeds are a long-lasting food source of high nutritional value in the Kalahari, and mice here are communal (Nel, 1975; personal observation). A larger food supply might lead to smaller home ranges, higher population density, and possibly sociality (Ostfeld, 1990).

Because of larger food abundance in dry areas, we predict that *Rhabdomys* is more social there than in the mesic grasslands. Furthermore, for paternal care to be an adaptive strategy, males would need to be associated with their potential offspring. To test these predictions, we studied a *Rhabdomys* population in a dry environment, the succulent karoo of South Africa.

Method

Study Area and Period

The study was conducted in Goegap Nature Reserve near Springbok in the Northern Cape Province of South Africa. The area is semiarid, and rainfall, which averages 160 mm per year, falls mainly in winter (Jackson, 1999). The vegetation type is succulent karoo (Acocks, 1988), consisting mainly of *Zygophyllum retrofractum* bushes (see Figure 1A). There are large, open sandy patches, containing different species of small succulents. In spring (August–September), these sandy areas are covered by approximately 600 different species of wild flowers (information provided by Goegap Nature Reserve). There are more than 4,000 species of plants in the succulent karoo (leRoux, Schelpe, & Wahl, 1997), which has been identified as 1 of 25 global biodiversity hotspots (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000).

The study was performed from September 2001 to January 2002, during 2 weeks in April 2002, and from September 2002 to December 2002. The

study area was initially 80 m × 60 m but was enlarged in December 2001 by an additional 60 m × 40 m to include two more *Rhabdomys* groups. In September 2002, the study area was further increased to 200 m × 150 m.

Trapping and Marking of Animals

Rhabdomys was live trapped using metal traps (26 × 9 × 9 cm) baited with a mixture of bran flakes, currants, sea salt, and salad oil. A total of 235 mice (114 males and 121 females) was trapped in 2001, 149 mice (84 males and 65 females) in April 2002, and 234 mice (124 males and 110 females) from September 2002 to November 2002. Traps were placed in the shade under bushes where mice had been observed previously. Trapping was done only in the morning and afternoon, but not during the hottest times of the day. Traps were checked continuously. Trapped mice were sexed, weighed, and individually marked with hair dye. Each mouse received a number written on its side with black hair dye (Rapido, Pietermaritzburg, South Africa; see Figure 1B). Mice were retrapped about every 5–6 weeks to refresh the markings and to mark juveniles and emigrants onto the grid. We decided to mark mice permanently in 2002 by toe clipping, the standard method for studies in small mammals (e.g., Jackson, 1999; McGuire, Getz, & Oli, 2002). Toe wounds were disinfected with alcohol, and no recaptures had infected wounds. The decision to use toe clipping was not made lightly. However, we decided not to mark animals with transponders because the large number of mice that needed to be marked over subsequent years (more than 200 a year) would have led to contamination of the study site with electronic waste, a concern raised by the authorities of the nature reserve where we conducted our studies. Also, there is no difference in survival probability between toe clipping and marking with transponders (Braude & Ciszek, 1998). We did not consider ear tags as these are known to lead to increased parasite load (Ostfeld, Miller, & Schnurr, 1993) and to be unreliable, as they are often lost (Harper & Batzli, 1996; Wood & Slade, 1990). Instead, we first tried permanent marking by ear punching, but this method turned out to be unreliable, as the punch marks either split or closed again. Thus, we decided to use toe clipping, which does not appear to have deleterious effects on survival or body weight in other species (Braude & Ciszek, 1998; Korn, 1987; Wood & Slade, 1990).

Nest Sites

We recorded the location of all nest sites. Five nest sites were investigated and the structure recorded. We presented white tissue in front of nests, which resident mice used for nest construction, thus enabling us to identify active nests.

Group Composition

Mice inhabiting one nest site were regarded as one group, and groups were numbered from G1 to G9. Group composition was determined through observations in front of nests during early morning and late afternoon, when mice emerged from or withdrew into nests. At each nest, we recorded the identity of individual subjects and how many mice were present at the nest. During the short field trip in April 2002, we did not mark mice with hair dye and determined only group size, but not sex ratio. Groups were located one at a time. As mice were not toe clipped in 2001, subjects observed in 2001 were not recognized in 2002. However, groups inhabiting the same home range and/or nesting site in 2002 as in 2001 were regarded as the same group.

Scrotal males that were present since the beginning of the breeding season or that weighed over 60 g in October–December were regarded as the breeding males of the groups. At the beginning of the breeding season, females weighing over 60 g were regarded as being pregnant and thus breeding. We also recorded the number of same-aged juveniles in each group. The maximum litter size observed in 12 wild-caught pregnant



Figure 1. A: Field study site in the succulent karoo in December. B: Group of striped mice basking together in the morning sun in front of their nests. Note that the numbers written with black hair dye on their sides are to enable individual recognition.

Rhabdomys was 9, with a mean of 5.3 (Schradin & Pillay, 2003a). Using these data and the number of same-aged juveniles in a nest, we calculated the minimum number of breeding females per group as the number of same-aged juveniles divided by 9 (maximum litter size) as well as the approximate number of breeding females as the number of same-aged juveniles divided by 5.3 (mean litter size).

Behavioral Observations

During 2001 (but not 2002), mice were observed directly using 10×42 binoculars during the day. Focal-animal sampling was performed during the morning (6:00 a.m. to 11:00 a.m.) and afternoon (4:00 p.m. to 7:30 p.m.), the main activity periods of *Rhabdomys* (Schradin, 2003). Every time a marked mouse was located, it was observed and carefully followed for a distance of 3–10 m until it disappeared from view. Observation time totaled 210.0 hr, during which focal observations were performed for 52.1 hr (21.0 hr for males and 31.1 hr for females). For the remaining time, no focal animal was present, and we searched for the next focal animal. A total of 477 focal observations were performed, ranging from 1.0 min to 45.0 min in duration, with a mean of 6.5 min. In total, 19 adult males resident at the start of the breeding season (male breeders), 33 males born during the breeding season, 23 adult females resident at the start of the breeding season (female breeders), and 37 females born during the breeding season were observed as focal animals. All social interactions between focal and other mice and the identity of the actor and receiver were recorded. All behaviors were recorded as events, as the complex and rapid movements of mice made recording of behavioral states impractical. The following behavior patterns were recorded: aggressive interactions (chasing) and sociopositive interactions (sniffing at each other, sitting in body contact, and grooming one another).

In addition to focal-animal observations, observations of mice were performed during mornings and afternoons in front of nests (see above). These observations were done in front of all known group nests at the end of the breeding season (48 observations from November 2001 to January 2002 and 30 observations in December 2002). Observations started when the first mouse left the nest and continued for 30 min thereafter, when normally most group members had already left the nest. All social interactions among group members were recorded.

Home Ranges

During focal-animal sampling, the locations of focal mice were recorded. For this, a map of the study area had been drawn and divided into 2×2 -m grids. Bushes ($N = 95$), which were individually marked, were used as landmarks. We recorded when a focal animal changed its position into another square of the grid.

To determine home-range size, we applied the minimum polygon method (Kenward, 1987). The number of grids (representing 2×2 m) and half grids within this convex polygon was summed to calculate home-range size in square meters. Home ranges were determined only for mice that had been used as focal animals on at least five occasions and that were observed for at least 30 min in total. Obvious excursions by mice were not taken into account for home-range analyses (three cases of 3 different mice). Excursions were noted when the focal mouse had been observed only once in a location that was more than 10 m from other locations where the same mouse had been observed during another time. Data were obtained from 18 mice (8 males and 10 females). Group home ranges were determined by using all data available of all known group members, independent of how often each individual had been observed. The center of group home ranges was determined as the center of gravity of the polygon.

Statistical Analyses

Data are described as means plus or minus standard errors of the means. We applied nonparametric tests (Siegel & Castellan, 1988) throughout

using InStat (GraphPad Software, San Diego, CA); all tests were two-tailed. The Wilcoxon matched-pairs signed-ranks test is abbreviated as Wilcoxon test, and the Fisher's exact test as Fisher test. All correlations were performed using the Spearman rank correlation (r_s).

Results

Nesting Sites and Nests

Nests were typically situated inside dense *Zygodophyllum retrofractum* bushes. Nests in bushes were above ground, had an oval shape with a diameter of about 25 cm, and were lined with soft hay, resembling a bird's nest. Some nests also were underground inside burrows that were originally dug by Littledale's whistling rats (*Parotomys littledalei*).

Observations of nest construction were done ad hoc. An adult breeding male was observed carrying hay inside the nest. Juveniles of approximately 40 days of age as well as breeding females were observed to transport white tissue inside nests, which we provided outside nests (see the Method section).

Group Composition

Group compositions are given in Table 1. There was usually only 1 breeding male per group, although three groups comprised 2 big scrotal males (G3 and G6 in 2001; G3 in 2002). Normally, there was more than 1 breeding female in the group, with a range of 1 to 4. Table 2 shows the number of potentially reproducing females in each group for both years.

Breeding Animals and Their Adult Offspring

From the middle of October onward, groups contained young adult mice in addition to breeding animals (see Table 1). Offspring of both sexes remained in their natal group after reaching adulthood. Of the young adult males, $71.4\% \pm 19.8\%$ that were observed at nests in December 2002 had been observed at the same nest the previous month ($n = 9$ groups, 66 mice). For females, the value was $80.8\% \pm 20.6\%$ ($n = 9$ groups, 60 mice), and there was no difference between the sexes (Wilcoxon test), $T(N = 8) = 9$, $p = .25$. Emigration of juveniles or young adults into other groups was never observed, but 2 old adult males were observed emigrating into a group of breeding females in October 2001 (G1 and G2). Groups were still large in April (see Table 1), consisting of both males and females, which indicates that offspring remain within their group for several months.

Rhabdomys reach sexual maturity at an age of 1–3 months (Brooks, 1982). Because the breeding season lasts 3 months (September–November), it would have been possible for offspring born at the start of a breeding season to reproduce in the season of their birth. However, significantly more breeding males (34 of 34) were scrotal than their sons (2 of 17; Fisher test, $p < .0001$) in October (data from 2001 and 2002 combined), and the same pattern occurred in December 2001 (scrotal males: 14 of 19; sons: 2 of 33; Fisher test, $p < .0001$). In October, 28 of 48 breeding females showed signs of sexual activity (open vagina or being pregnant), but only 1 of 9 daughters did so (Fisher test, $p = .03$). In December, there was no significant difference between female breeders with an open vagina (2 of 22) compared with daughters (1 of 26; Fisher test, $p = .59$).

Table 1
Composition of Focal Groups, Arranged According to Different Age Classes

Group and age class	2001			2002					
	October	November	December	January	April	September	October	November	December
G1	19	32	16	17	15	5	12	17	21
Breeders	1-3	1-3	1-3	1-3	0	1-4	1-4	1-3	1-3
Adult offspring	0	6-4	4-7	4-9	15	0	0	7-6	8-9
Juveniles	10/5	5/13	1	0	0	0	7	0	0
G2		21	11	18	10	3	10	11	12
Breeders		1-2	1-2	1-2	0	1-2	1-2	1-1	1-1
Adult offspring		7	5-3	8-7	10	0	0	4-5	5-5
Juveniles		11	0	0	0	0	7	0	0
G3		23	21	18	17	5	8	19	17
Breeders		3	2-1	2-1	0	2-3	2-3	2-2	2-2
Adult offspring		15	7-9	5-10	17	0	0	4-11	6-7
Juveniles		5	2	0	0	0	3	0	0
G4			15	12	12	2	7	7	12
Breeders			1-1	1-1	0	0-2	0-1	0-1	0-1
Adult offspring			7-4	7-3	12	0	0	4-2	8-3
Juveniles			0-2	0	0	0	6	0	0
G5		15	21	23	21	5	12	27	26
Breeders		1-3	1-3	1-4	0	1-4	1-2	1-2	1-2
Adult offspring		0	10-5	10-8	21	0	0	14-10	13-10
Juveniles		6/5	1-1	0	0	0	9	0	0
G6				7		4	11	25	27
Breeders				2-2		1-3	1-3	1-3	1-3
Adult offspring				1-2		0	0	0	13-10
Juveniles				0		0	7	7-8/6	0
G7				30	11	3	5	8	11
Breeders				1-2	0	1-2	1-1	1-1	1-1
Adult offspring				8-19	11	0	0	2	5-4
Juveniles				0	0	0	3	1/3	0
G8						3	7	7	8
Breeders						1-2	1-2	1-2	1-2
Adult offspring						0	0	2-2	2-3
Juveniles						0	4	0	0
G9								26	22
Breeders								2-3	2-2
Adult offspring								10-11	9-9
Juveniles								0	0

Note. Juveniles had a body mass below 30 g. Total numbers are shown, and if known, sex is indicated as male-female. Juveniles from different litters are separated by a slash. Mice inhabiting the same area in 2001 and 2002 were regarded as the same group.

The difference in breeding status between breeders and their adult offspring cannot be explained by differences in body weight alone because breeders weighed as much at the start of the breeding season as their adult nonreproductive offspring did at the end of the breeding season. In September, 90% of males with a body weight between 40 and 50 g were scrotal, and 100% of females within the same weight range had an open vagina. This pattern changed dramatically during the following months: When nonbreeding adult offspring attained 40–50 g body weight, the breeders had gained additional weight (all 11 breeders with a body weight below 50 g in September weighed more than 50 g in October; Wilcoxon test), $T(N = 11) = 0$, $p < .0001$. The proportion of reproductively active mice with a body weight of 40–50 g was significantly higher in September than in October and December (Fisher test, $p < .0001$).

Social Interactions Among Group Members

Mice spent the morning and afternoon in front of the nest engaged in sociopositive interaction (see Figure 1B) but spent the

rest of the day foraging alone. No agonistic interactions were observed between group members. Data collected in 2001 revealed that mice were much more often observed to perform sociopositive interactions in front of the nest (120 interactions in total, morning and afternoon combined) than during focal-animal sampling during the day (25 interactions; Fisher test, $p < .0001$).

Data collected in front of nests in December 2002 revealed that breeders, mainly breeding males, initiated more social interactions than adult offspring (see Figure 2). However, the overall difference only approached significance (Friedman test), $Fr(N = 7 \text{ groups}) = 7.172$, $p = .066$.

Home Ranges

For both sexes, the variance in home-range size was high (males: 990 ± 447 m; females: 960 ± 520 m). There was a positive correlation between individual home-range size and group home-range size, $r_s(N = 18) = .568$, $p < .02$. When we controlled for differences in group territory size by comparing males and females of the same groups in a paired design, there was no

Table 2
Number of Potentially Reproducing Females

Group and year	Adult females at the start of the breeding season	Females with visible nipples	Females with open vagina	Pregnant females	Same-aged juveniles	Minimum number of breeding females	Approximate number of breeding females
G1 2001	3	3	3	3	13	2	3
G1 2002	4	4	4	4	12	2	3
G2 2001	2	1	1	0	10	2	2
G2 2002	2	2	2	2	8	1	2
G3 2002	2	2	2	2	4	1	1
G4 2002 ^a	1	1	1	1	5	1	1
G5 2002	4	4	3	2	19	3	4
G6 2002	4	4	4	4	14	2	3
G7 2002	2	2	2	0	11	2	2
G8 2002	2	2	2	2	5	1	1
G9 2002	3	3	3	3	13	2	3
F15 2002 ^b	1	1	1	1	—	—	—
F24 2002 ^b	1	1	1	1	—	—	—

Note. The minimum number of breeding females is the number of juveniles divided by 9 (i.e., the maximum litter size). The approximate number of breeding females is the number of juveniles divided by 5 (i.e., the average litter size). Dashes indicate that no data were available.

^aThis group was located only after the breeding season in 2001; so, no data are available prior to this time. Only a single female was observed in the former territory of this group in 2002. ^b These females (F) nested alone but occupied part of the home range of G6.

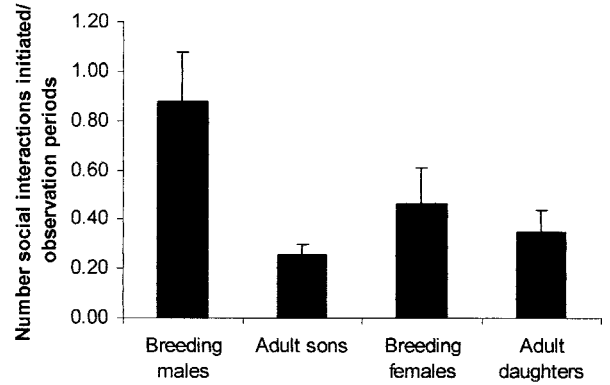


Figure 2. Mean (\pm SEM) number of social interactions initiated by breeding males, adult sons, breeding females, and adult daughters from seven different groups in front of their nests in December 2002. Values are shown for 30-min focal observation periods in front of nest.

difference in home-range size between the sexes (Wilcoxon test), $T(N = 6) = 5, p = .313$. Home ranges of mice of one group overlapped largely with each other (see example in Figure 3) but not with the home ranges of mice from other groups. Overlap with group members was $91.0\% \pm 11.6\%$, whereas overlap with individuals from other groups was $13.0\% \pm 11.8\%$ (Wilcoxon test), $T(N = 16) = 0, p < .0001$. Figure 4 shows the group home ranges

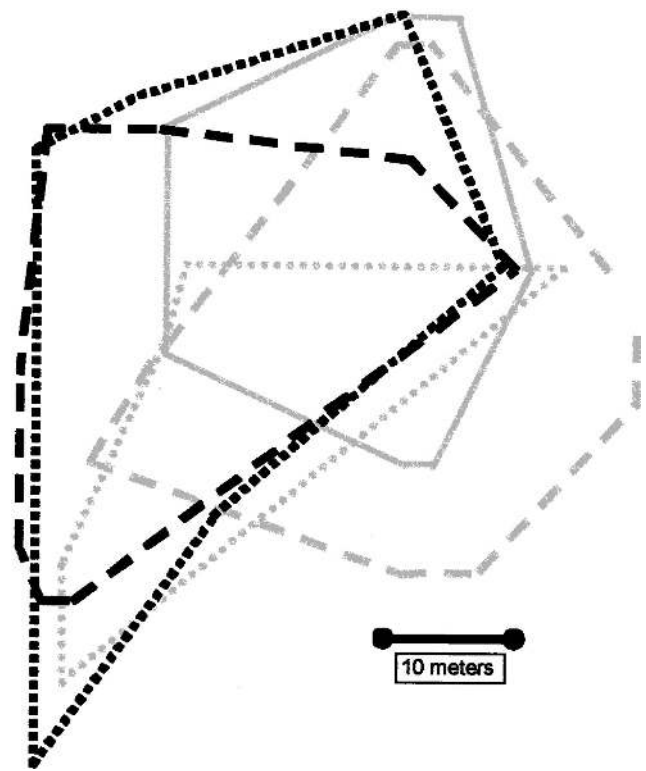


Figure 3. Overlapping home ranges of the mice of one group (3 males' ranges are indicated in gray, and 2 females' ranges are indicated in black). Compare with Figure 4, in which this group's home range is represented with a gray dotted line in the middle of the figure.

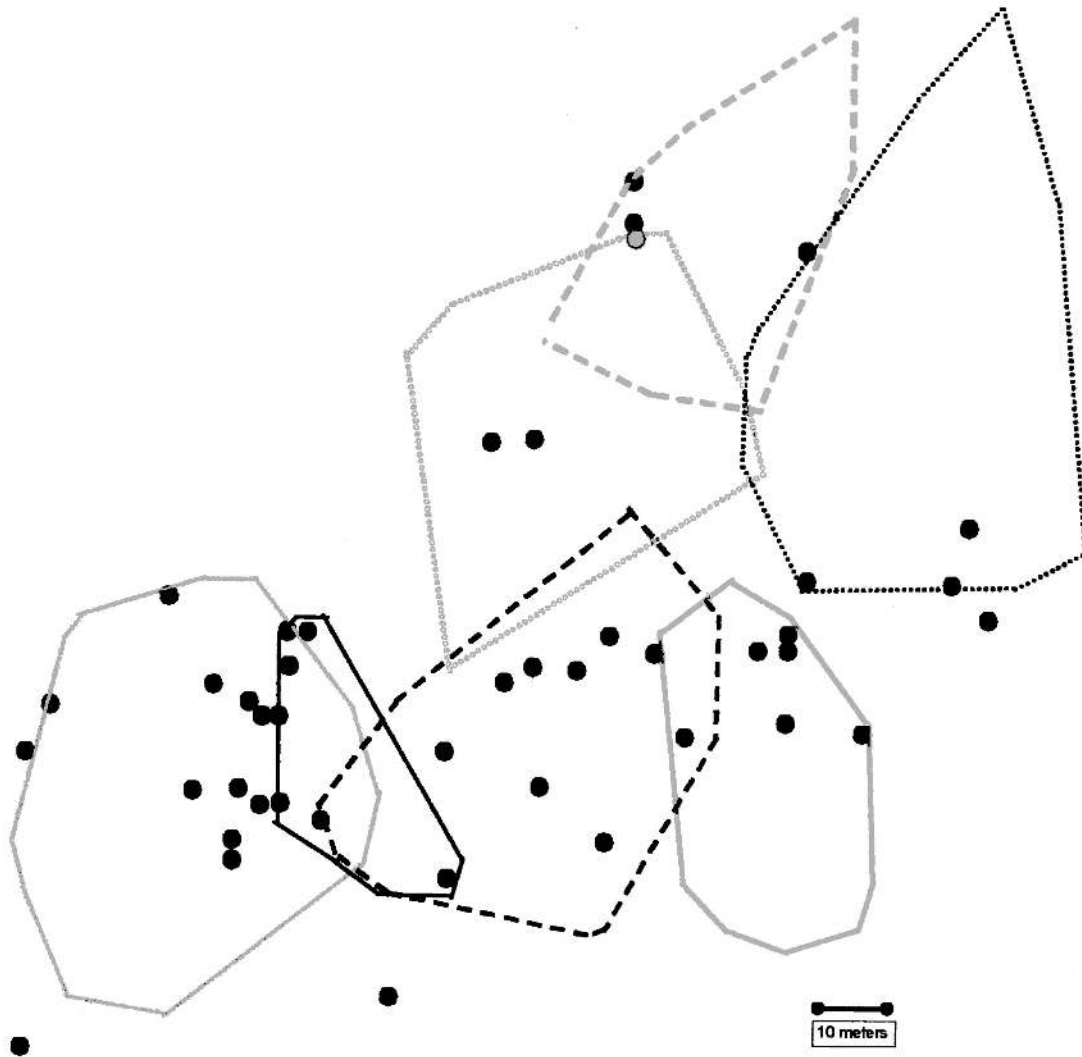


Figure 4. Group home ranges of the seven focal groups. Aggressive interactions (black dots) observed in relation to group territories are included. At one place (indicated by the gray dot in the upper part of the figure), three aggressive interactions were observed during different times.

of the seven focal groups in 2001. There was a significant positive correlation between group home-range size and number of mice in the group at the end of the observation period in 2002, $r_s(N = 7) = .857, p < .04$.

Territoriality

A total of 48 aggressive interactions were observed. Figure 4 shows the locations of aggressive interactions in relation to home-range boundaries. Two interactions at the lower end of the study area were excluded from further analyses, as home-range boundaries of adjacent groups were not known. Aggressive encounters were significantly more likely to occur near home-range boundaries than in home-range centers (binomial test, $p < .001$).

In 12 encounters, both mice were known: In 2 cases, they were from the same group, and in 10 cases, they were from different groups (binomial test, $p < .05$). It was possible to establish the sex

of the mouse initiating the encounter in 26 aggressive encounters: Males initiated encounters on 19 occasions, and females on 7 occasions (binomial test, $p < .05$). It was possible in some cases to determine the sex of the attacked mouse: Males attacked other males on 4 occasions and females on 10 occasions (binomial test, $p > .10$), whereas females attacked a male once and another female on 3 occasions.

Discussion

In a previous study, we reported high levels of paternal care in captive *Rhabdomys* (Schradin & Pillay, 2003d), which did not match the solitary life pattern described for this species in the field. We predicted that *Rhabdomys* would exhibit a social lifestyle in the succulent karoo because of higher food abundance compared with the mesic grasslands. In particular, we expected paternal care to be an alternative male reproductive strategy (Dewsbury, 1985).

Our data indicate that *Rhabdomys* is highly social in the semiarid succulent karoo, where it lives in permanent groups that include breeding males that interact highly amicably with other group members.

Communal Breeding, Polygyny, and Paternal Care

Most females were pregnant at the beginning of the breeding season and also showed an open vagina as additional external signs of reproductive activity. In addition, the number of same-aged juveniles counted in front of nests exceeded the mean and maximum litter size of single females, indicating that parturition of group females is synchronized. Communal breeding (or plural breeding) in rodents occurs when several mature group members breed together, whereas communal nesting occurs when reproducing females use the same nest (Hayes, 2000). Thus, both communal breeding and communal nesting occur regularly in *Rhabdomys* in the succulent karoo, although single-breeding females were also observed. To date, however, we do not know whether and to what extent group females cooperate in rearing one another's young. It is notable that 1 heavily pregnant female was observed to nurse juveniles that were approximately 10 days old in front of the group nest (personal observation). These juveniles could not have been her offspring because her own offspring from a previous litter would have been significantly older (at least 20 days old). Thus, there is anecdotal evidence for allonursing by communal breeding females.

Three factors could drive the selection of communal nesting in the succulent karoo. The first is predator avoidance. Unpublished data (Schradin, 2002) of time-lapse videotaping in two natural nests revealed that always at least one of the group members was awake during the night, leading to increased vigilance. Even light disturbance caused the entire group to quickly leave the nest. However, this advantage does not explain why communal nesting occurs in the succulent karoo but not the grasslands. The second is thermoregulatory benefits of nest sharing (Howard, 1950), which is known to be associated with communal breeding in rodents (Carter & Roberts, 1997). As the breeding season starts 1 month earlier (spring) in the succulent karoo than in the mesic grasslands, communal nesting may be more beneficial in the succulent karoo because of lower night temperatures. The third factor is communal breeding, which is known to lead to fitness benefits in house mice (König, 1993, 1994a, 1994b). Communal breeding usually occurs when cooperatively breeding females are close kin and the social system is egalitarian (Gerlach & Bartmann, 2002). For example, communal breeding of sisters leads to increased fitness in the wood mouse (*Apodemus sylvaticus*; Gerlach & Bartmann, 2002). An egalitarian social system is also likely to occur in *Rhabdomys* from the succulent karoo because daughters delay their reproduction until the next breeding season when females of similar body weight form breeding groups. Also, we did not observe any direct indication of a dominance hierarchy among cooperatively breeding females, indicating an egalitarian society. In contrast, reproductive skew exists in mother–daughter pairs of wood mice, in which the dominant mother can exploit maternal care from her daughter, making it advantageous for the daughter to leave instead of breeding communally with her mother (Gerlach & Bartmann, 2002). This pattern is likely to apply for *Rhabdomys* from the mesic grasslands, where the breeding season is more than twice as long

as that in the succulent karoo, and daughters accordingly start breeding at a very young age (i.e., with a body weight below 30 g). As experienced breeding females (i.e., mothers) weigh normally around 40 g (Brooks, 1974; Perrin, 1980a), daughters will be better off leaving the natal nest and breeding on their own than breeding communally with their mother as a subdominant female, thereby experiencing high reproductive skew.

Contradictory to previous assumptions, paternal care not only is associated with monogamy in mammals but also occurs in polygynous species (Komers & Brotherton, 1997). In fact, paternal care in monogamous mammals might have evolved from a group-living ancestor with 1 breeding male and several breeding females, in which the male participated in infant care (Brotherton & Komers, in press). *Rhabdomys* in the succulent karoo is socially polygynous (paternity has not been determined thus far) and displays paternal care. Males living in stable social groups have the potential to increase their fitness by showing paternal care, simply because they are permanently associated with pups and sleep in the same nest. It might not be very costly for males to groom and warm pups (Schradin & Pillay, 2003d), and males may benefit by being associated with receptive females. Nevertheless, paternal care might have a great impact on male fitness. We have data showing that pup development is better under biparental than exclusive maternal care (Schradin & Pillay, 2003c). In contrast, females do not form social groups but defend exclusive territories against other females in mesic grasslands (Perrin et al., 2001; Schradin & Pillay, 2003b; Willan, 1982). Under such circumstances, males might not have time or even the possibility to show paternal care, as they have to adopt an active searching strategy to get access to receptive females (Ostfeld, 1990).

Adult Offspring Staying in the Group

Offspring of both sexes stay in their natal group even after reaching adulthood. Group sizes thus increase up to 30 adults at the end of the breeding season. Offspring remaining in their natal group can be referred to as helpers when their behavior leads to increased reproductive success of the breeders (e.g., Taborsky, 1994). In *Rhabdomys*, there is clear indication that this is likely to be the case because offspring do not simply benefit from occupying their parents territory but participate in territorial defense (see also Schradin, in press). Juveniles also participated in nest construction. In other species, participation in territory defense and nest building by nonbreeders have been acknowledged as important aspects of helping behavior (for a review in cichlids, see Taborsky, 1994; for birds, see Reyer, 1984; for suricates, see Doolan & MacDonald, 1996; for callitrichids, see Hübner, 1985). Additionally, pups of the group are also very likely to derive thermoregulatory benefits by the presence of juveniles, as the night temperatures can fall close to 0 °C. We would therefore expect that the fitness of breeding pairs would increase because of help provided by juveniles during the breeding season.

Adult offspring staying in their natal group seem to be reproductively inhibited. During the middle of the breeding season, many more breeders showed signs of reproductive capability compared with their adult offspring. Adult offspring at this stage weighed less than old breeders (40–50 g vs. 60–80 g). However, this weight difference cannot explain a lower percentage of young adults not being in breeding condition (8%) because about 88% of

breeders at the beginning of the breeding season also weighed 40–50 g. Furthermore, *Rhabdomys* populations in the mesic grasslands can start breeding at below 30 g, and nearly all mice weighing between 30 and 40 g do breed (Brooks, 1982; Schradin & Pillay, 2003b). We conclude that adult offspring staying at their natal nest do not reproduce, although they would be physiologically capable of reproduction. One reason could be incest avoidance because female *Rhabdomys* avoid breeding with the father, and incestuous breeding leads to inbreeding depression (Pillay, 2002). Another important factor might be the short breeding season of *Rhabdomys* in the succulent karoo, which is only 3 months long (Schradin & Pillay, 2003a) compared with 6 months in the grasslands (Perrin et al., 2001). Whereas offspring of the first litter born during the breeding season could theoretically start breeding after the middle of the breeding season when they are 1.5 months old (Brooks, 1982), their offspring might have a low survival probability. During the dry summer following the breeding season, food abundance is low, mice lose about 12% of body weight, and the mortality rate is 70% during the cold winter (Schradin & Pillay, 2003a). Thus, instead of investing immediately in producing young with a low survival potential, mice might benefit more by delaying reproduction and investing in their own survival and somatic development.

Comparison of Social Organization With Other Muroid Rodents

The social organization of *Rhabdomys* in the succulent karoo comprises large groups containing several breeding females, highly amicable relationships between group members but aggressive responses toward strangers, and offspring of both sexes staying at their natal group even after reaching adulthood and participating in nest building and territorial defense. These behavior patterns could be adaptations to the harsh succulent karoo environment. Annual rainfall is only 160 mm, and temperatures regularly fall below 0 °C during winter and spring nights but can be close to 50 °C during summer days. *Rhabdomys* is not the only diurnal small mammal inhabiting the succulent karoo, and the social systems of the other species there are quite different. The whistling rat (*Parotomys brantsii*), although it lives in large colonies with warrens of sometimes hundreds of individuals next to one another, is a solitary species (Jackson, 1999). Another diurnal rodent at our field site is the bush karoo rat (*Otomys unisulcatus*), whose social system so far is unknown, but it might be either solitary or living in small groups (personal observation). Another diurnal small mammal in the same habitat is the round-eared elephant shrew (*Macroscelides proboscideus*), which might be solitary (Sauer, 1973). Round-eared elephant shrews, whistling rats, bush karoo rats, and *Rhabdomys* inhabit exactly the same habitat, are diurnal, and are highly territorial, and the three rodent species additionally feed to a large extent on the same plant material (personal observation). Despite these similarities, their social systems are very different, indicating that the succulent karoo enables them to develop different strategies to cope with its harsh environment, providing different ecological niches.

The house mouse (*Mus musculus*) appears to have the most similar social system to *Rhabdomys* in the succulent karoo. Like *Rhabdomys*, the house mouse is a group-living solitary forager (Gerlach, 1998), is polygynous (Lidicker, 1976; Wilkinson &

Baker, 1988), shows communal breeding (König, 1993, 1994a, 1994b), and is territorial (Hurst, 1987; Lidicker, 1976). When offspring are weaned, they can stay for some time in their natal group in both species. However, whereas it is common for *Rhabdomys* offspring of both sexes to remain in their natal group several months after reaching adulthood, male house mice often disperse when they reach sexual maturity (Gerlach, 1998; Lidicker, 1976).

One main difference between the house mouse and *Rhabdomys* appears to be in the social relationships of the breeding (also called dominant) males. The dominant male house mouse lives a relatively solitary life (Gerlach, 1998). In contrast, breeding male *Rhabdomys* are highly social, greeting other group members at the nest by sniffing them and grooming and sitting in body contact with females and juveniles (see Figure 2). The social nature of *Rhabdomys* males is further demonstrated by four behaviors (Schradin & Pillay, 2003d): (a) Their amicable relationship with juveniles is similar to that between breeding females and juveniles, (b) wild males retrieve pups experimentally presented to them, (c) captive males exhibit high levels of paternal care, and (d) wild males sleep together with group members. Unpublished results (Schradin, 2002) from a study that videotaped two natural nests revealed the breeding male grooming and licking pups in the nest. In contrast, male house mice do not often sleep in the same nest as the rest of the group, particularly during communal breeding (Lidicker, 1976). Whereas male house mice can show paternal care when kept in captivity in a monogamous situation, they seem to invest their time mainly in territorial defense under polygynous conditions, thereby reducing their social interactions with juveniles (Gandelman, Paschke, Zarrow, & Denenberg, 1970; Gerlach, 1998; Lidicker, 1976).

Conclusion

The striped mouse exhibits a social system in the succulent karoo, which is very different from its solitary lifestyle in other parts of South Africa (Brooks, 1974; Perrin, 1980a; Willan, 1982). In the succulent karoo, *Rhabdomys* is clearly group living. Why mice stay together and share the same nest and territory is not yet understood, but we predict that both ecological constraints and benefits of philopatry are important factors (Hayes, 2000). Ecological constraints are imposed by high food availability, which results in high population density and habitat saturation, as demonstrated by a population density of 151 mice/hectare in our field site (Schradin & Pillay, 2003a), which is several times greater than that reported from mesic grasslands (10 to 40 mice/hectare; Perrin et al., 2001). Benefits of philopatry would include benefits of predator avoidance because of increased vigilance during nest sharing as well as thermoregulatory benefits (Howard, 1950), which are important reasons for communal breeding in rodents (Carter & Roberts, 1997). Communal breeding itself offers a great advantage when reproductive skew is low (Gerlach & Bartmann, 2002). Whereas *Rhabdomys* breeds and nests communally in the succulent karoo, these mice forage alone. Their food (leaves, flowers, and seeds) is patchily distributed, and foraging in a group would not assist in food exploitation but rather would increase predation risk. Mice stay in their natal group even after reaching adulthood, participating in nest building and territorial defense but not in reproduction, potentially showing helping behavior. In con-

clusion, *Rhabdomys* in the succulent karoo is best described as a group-living solitary forager with communal breeding and helpers at the nest, one of the most complex social systems found in rodents.

References

- Acocks, J. P. H. (1988). *Veld types of South Africa*. (Available from the National Botanical Institute, Private Bag X101, Pretoria 0001, South Africa.)
- Braude, S., & Ciszek, D. (1998). Survival of naked mole-rats marked by implantable transponders and toe-clipping. *Journal of Mammalogy*, *79*, 360–363.
- Brooks, P. M. (1974). *The ecology of the four-striped field mouse, Rhabdomys pumilio (Sparrman, 1784), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria*. Unpublished doctoral dissertation, University of Pretoria, Pretoria, South Africa.
- Brooks, P. M. (1982). Aspects of the reproduction, growth and development of the four-striped mouse, *Rhabdomys pumilio* (Sparrman, 1784). *Mammalia*, *46*, 53–64.
- Brotherton, P. N. M., & Komers, P. E. (in press). Mate guarding and the evolution of monogamy in mammals. In U. Reichard & C. Boesch (Eds.), *Monogamy: Mating strategies and partnership in birds, humans and other mammals*. Cambridge, England: Cambridge University Press.
- Carter, C. S., & Roberts, R. L. (1997). The psychobiological basis of cooperative breeding in rodents. In N. G. Solomon & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 231–266). Cambridge, England: Cambridge University Press.
- Choate, T. S. (1972). Behavioural studies on some Rhodesian rodents. *Zoologica Africana*, *7*, 103–118.
- Crook, J. H. (1964). The evolution of social organisation and visual communication in the weaver birds (Ploceinae). *Behaviour Supplement*, *10*, 1–178.
- Curtis, B. A., & Perrin, M. R. (1979). Food preferences of the vlei rat (*Otomys irroratus*) and the four-striped mouse (*Rhabdomys pumilio*). *South African Journal of Zoology*, *14*, 224–229.
- David, J. H. M., & Jarvis, J. U. M. (1985). Population fluctuations, reproduction and survival in the striped field mouse *Rhabdomys pumilio* on the Cape Flats, South Africa. *Journal of Zoology, London*, *207*, 251–276.
- Dean, W. R. J., & Milton, S. J. (1999). *The karoo*. Cambridge, England: Cambridge University Press.
- Dewsbury, D. A. (1985). Paternal behavior in rodents. *American Zoologist*, *25*, 841–852.
- Dobly, A., & Rozenfeld, F. M. (2000). Burrowing by common voles (*Microtus arvalis*) in various social environments. *Behaviour*, *137*, 1443–1462.
- Doolan, S. P., & MacDonald, D. W. (1996). Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *Journal of Zoology*, *240*, 59–73.
- Gandelman, R., Paschke, R. E., Zarrow, M. X., & Denenberg, V. H. (1970). Care of young under communal conditions in the mouse (*Mus musculus*). *Developmental Psychobiology*, *3*, 245–250.
- Gerlach, G. (1998). Impact of social ties on dispersal, reproduction and dominance in feral house mice (*Mus musculus domesticus*). *Ethology*, *104*, 487–499.
- Gerlach, G., & Bartmann, S. (2002). Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). *Behavioral Ecology*, *13*, 408–418.
- Harper, S. J., & Batzli, G. O. (1996). Monitoring use of runways by voles with passive integrated transponders. *Journal of Mammalogy*, *77*, 364–369.
- Hayes, L. D. (2000). To nest communally or not to nest communally: A review of rodent communal nesting and nursing. *Animal Behaviour*, *59*, 677–688.
- Howard, W. E. (1950). Relation between low temperature and available food to survival of small rodents. *Journal of Mammalogy*, *32*, 300–312.
- Hubrecht, R. C. (1985). Home range size, use and territorial behaviour in the common marmoset *Callithrix jacchus* at the Tapacura field station Recife, Brazil. *International Journal of Primatology*, *6*, 533–550.
- Hurst, J. L. (1987). Behavioural variation in wild house mice *Mus domesticus* Ratty: A quantitative assessment of female social organisation. *Animal Behaviour*, *35*, 1846–1857.
- Jackson, T. P. (1999). The social organisation and breeding system of Brants' whistling rat (*Parotomys brantsii*). *Journal of Zoology, London*, *247*, 323–331.
- Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, *48*, 215–267.
- Kenward, R. (1987). *Wildlife radio tagging*. London: Academic Press.
- Kingdom, J. (1974). *East African mammals*. London: Academic Press.
- Komers, P. E., & Brotherton, P. N. M. (1997). Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London*, *264*, 1251–1270.
- König, B. (1993). Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). *Behavioral Processes*, *30*, 61–74.
- König, B. (1994a). Components of lifetime reproductive success in communally and solitarily nursing house mice—A laboratory study. *Behavioral Ecology and Sociobiology*, *34*, 275–283.
- König, B. (1994b). Fitness effects of communal rearing in house mice: The role of relatedness versus familiarity. *Animal Behaviour*, *48*, 1449–1457.
- Korn, H. (1987). Effects of live-trapping and toe-clipping on body weight of European and African rodent species. *Oecologica*, *71*, 597–600.
- leRoux, A., Schelpe, T., & Wahl, Z. (1997). *South African wildflower guide 1: Namaqualand*. Cape Town, South Africa: Botanical Society of South Africa.
- Lidicker, W. Z. (1976). Social behaviour and density regulation in house mice living in large enclosures. *Journal of Animal Ecology*, *45*, 677–697.
- Lott, D. F. (1991). *Intraspecific variation in the social systems of wild vertebrates*. New York: Cambridge University Press.
- McGuire, B., Getz, L. L., & Oli, M. K. (2002). Fitness consequences of sociality in prairie voles, *Microtus ochrogaster*: Influence of group size and composition. *Animal Behaviour*, *64*, 645–654.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. D., & Kent, J. (2000, February 24). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858.
- Nel, J. A. J. (1975). Aspects of the social ethology of some Kalahari rodents. *Zeitschrift für Tierpsychologie*, *37*, 322–331.
- Ostfeld, R. S. (1990). The ecology of territoriality in small mammals. *Trends in Ecology and Evolution*, *12*, 411–415.
- Ostfeld, R. S., Miller, M. C., & Schnurr, J. (1993). Ear tagging increases tick (*Ixodes dammini*) infestation rate of white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy*, *74*, 651–655.
- Parker, K. J., Phillips, K. M., & Lee, T. M. (2001). Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, *61*, 1217–1226.
- Perrin, M. R. (1980a). The breeding strategies of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827). *Acta Oecologica*, *1*, 383–410.
- Perrin, M. R. (1980b). The feeding habits of two co-existing rodents, *Rhabdomys pumilio* (Sparrman, 1784) and *Otomys irroratus* (Brants, 1827), in relation to rainfall and reproduction. *Acta Oecologica*, *1*, 71–89.
- Perrin, M. R., Ercoli, C., & Dempster, E. R. (2001). The role of agonistic behaviour in the population of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparrman, 1784) and the multi-

- mammate mouse *Mastomys natalensis* (A. Smith 1834) (Mammalia Rodentia). *Tropical Zoology*, 14, 7–29.
- Pillay, N. (2002). Father–daughter recognition and inbreeding avoidance in the striped mouse, *Rhabdomys pumilio*. *Mammalian Biology*, 67, 212–218.
- Rambau, R. V., Stanyon, R., & Robinsom, T. J. (2003). Molecular genetics of *Rhabdomys pumilio* subspecies boundaries: mtDNA phylogeography and karyotypic analysis by fluorescence *in situ* hybridization (FISH). *Molecular Phylogenetics and Evolution*, 28, 564–575.
- Reburn, C. J., & Wynne-Edwards, K. E. (1999). Hormonal changes in males of a naturally biparental and a uniparental mammal. *Hormones and Behavior*, 35, 163–176.
- Reyer, H.-U. (1984). Investment and relatedness: A cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, 32, 1163–1178.
- Roberts, R. L., Williams, J. R., Wang, A. K., & Carter, C. S. (1998). Cooperative breeding and monogamy in prairie voles: Influence of the sire and geographical variation. *Animal Behaviour*, 55, 1131–1140.
- Salvioni, M., & Lidicker, W. Z. (1995). Social organisation and space use in California voles: Seasonal, sexual, and age-specific strategies. *Oecologia*, 101, 426–438.
- Sauer, E. G. F. (1973). Zum Sozialverhalten der Kurzhohrigen Elefantenspitzmaus, *Macroscelides proboscideus* [The social behavior of the round-eared elephant shrew, *Macroscelides proboscideus*]. *Zeitschrift für Säugetierkunde*, 38, 65–97.
- Schradin, C. (2002). [Namaqualand—In the land of mice]. Unpublished video (for demonstrations at conferences).
- Schradin, C. (2003). *Whole day follows of the striped mouse*. Manuscript submitted for publication.
- Schradin, C. (in press). Territorial defense in a group living solitary forager: Who, where against whom? *Behavioral Ecology and Sociobiology*.
- Schradin, C., & Pillay, N. (2003a). *Demography of the striped mouse (Rhabdomys pumilio) in the succulent karoo: A unique population in an extreme environment*. Manuscript submitted for publication.
- Schradin, C., & Pillay, N. (2003b). *Extreme social flexibility in the South African striped mouse: When to live in groups and when to be alone?* Manuscript submitted for publication.
- Schradin, C., & Pillay, N. (2003c). *The influence of striped mouse fathers on pup development under different semi-natural environments*. Manuscript submitted for publication.
- Schradin, C., & Pillay, N. (2003d). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): Laboratory and field evidence. *Journal of Comparative Psychology*, 117, 317–324.
- Schradin, C., Reeder, D., Mendoza, S., & Anzenberger, G. (2003). Pro-lactin and paternal care: Comparison of three species of monogamous New World monkeys (*Callicebus cupreus*, *Callithrix jacchus*, and *Callimico goeldii*). *Journal of Comparative Psychology*, 117, 166–175.
- Siegel, S., & Castellan, M. J. (1988). *Nonparametric statistics for the behavioral sciences*. New York: McGraw-Hill.
- Taborsky, M. (1994). Sneakers, satellites, and helpers: Parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, 23, 1–100.
- Waterman, J. M. (1995). The social organization of the Cape ground squirrel (*Xerus inauris*; Rodentia: Sciuridae). *Ethology*, 101, 130–147.
- Webster, A. B., & Brooks, R. J. (1981). Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, 62, 738–751.
- Wilkinson, G. S., & Baker, A. E. M. (1988). Communal nesting among genetically similar house mice. *Ethology*, 77, 103–114.
- Willan, K. B. R. (1982). *Social ecology of Otomys irroratus, Rhabdomys pumilio and Mastomys natalensis*. Unpublished doctoral dissertation, University of Natal, Pietermaritzburg, South Africa.
- Willan, K., & Meester, J. (1989). Life-history styles of southern African *Mastomys natalensis*, *Otomys irroratus* and *Rhabdomys pumilio* (Mammalia, Rodentia). In M. N. Bruton (Ed.), *Alternative life-history styles of animals* (pp. 421–439). Dordrecht, the Netherlands: Kluwer Academic.
- Wirminghaus, J. O., & Perrin, M. R. (1993). Seasonal-changes in density, demography and body-composition of small mammals in a Southern temperate forest. *Journal of Zoology*, 229, 303–318.
- Wood, M. D., & Slade, N. A. (1990). Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. *Journal of Mammalogy*, 71, 252–255.

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