

INTRASPECIFIC VARIATION IN THE SPATIAL AND SOCIAL ORGANIZATION OF THE AFRICAN STRIPED MOUSE

CARSTEN SCHRADIN* AND NEVILLE PILLAY

Ecophysiological Studies Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, Johannesburg, South Africa

Social flexibility, that is, the expression of different types of social systems within one species, has been reported in several mammalian taxa, including rodents. However, sociality in rodents has been studied mostly in captivity and the results are often regarded as laboratory artifacts. We present field data for 2 populations of the striped mouse (*Rhabdomys pumilio*), a diurnal muroid rodent from southern Africa. The 2 populations inhabit different environments and demonstrate differences in social organization. *R. pumilio* in the arid succulent karoo lives in social groups, comprising multiple adults of both sexes that share 1 nest and the same territory. Striped mice in the moist grasslands of South Africa are solitary. Females inhabit exclusive territories and territories of males overlap those of several females; association between the sexes appears to be restricted to mating. Home ranges of females in the grasslands were 6 times larger and home ranges of males were 10 times larger than their counterparts in the succulent karoo. Onset of reproductive activity occurred earlier and at a significantly lighter body weight in grasslands. In the succulent karoo, sexually mature offspring remain in their natal group without reproducing. We suggest that group living in the succulent karoo is in response to habitat saturation and the benefits of philopatry, whereas living alone in the grasslands may be a response to limiting resources, such as food.

Key words: home-range size, intraspecific variation, paternal care, *Rhabdomys pumilio*, social flexibility, social organization, spatial organization

Social flexibility, that is, intraspecific variation in the expression of the social system, occurs in several vertebrates (Lott 1984), and is thought to be caused by environmental variability (Lott 1991). For example, populations of golden jackals (*Canis aureus*) in habitats with good food abundance form groups of ~20 individuals, whereas populations in areas of low food abundance form monogamous pairs (Macdonald 1979). Prairie voles (*Microtus ochrogaster*) from different populations occur as single females, in pairs, or in groups of many adults of both sexes (Roberts et al. 1998), but such variation can even occur within the same population (McGuire and Getz 1998). Reports of social flexibility in natural rodent populations are rare, despite being observed in captivity regularly. For example, paternal care has been shown in many rodent species in captivity, without any indication that such behavior also occurs under natural conditions (Dewsbury 1985). Paternal care in captivity could be an artifact, but another explanation is that paternal care also occurs in nature

under particular ecological conditions, such as high population density (Dewsbury 1985). One species that may be suitable for studying variation in social systems is the striped mouse (*Rhabdomys pumilio*). In the present study, we present data describing differences in the social structure in 2 striped mouse populations living under different ecological conditions. We previously provided evidence of highly developed paternal care in both populations in captivity and for 1 population in the field (Schradin and Pillay 2003).

Rhabdomys pumilio is a muroid rodent with a wide distribution in southern Africa that includes many different habitats, such as grassland, marsh, forest, succulent karoo (a desert with dwarf succulent shrubs being the dominant plant form), and deserts (Kingdon 1974). Field studies have been conducted mainly on *R. pumilio* occurring in moist grasslands, where it appears to be a solitary. Both sexes maintain territories that overlap the territories of the opposite sex but not the same sex (Brooks 1974; Choate 1972; Willan 1982; Willan and Meester 1989; Wirminghaus and Perrin 1993). Females apparently raise their young alone, and associations between males and females are only for mating (Willan 1982). In the succulent karoo, a desert in the northwest of South Africa, *R. pumilio* lives in groups that comprise 1 breeding male, up to 4 breeding females, and their nonreproducing adult offspring

* Correspondent: schradin@mweb.co.za

of both sexes that remain in their natal territory (Schradin and Pillay 2004). Males are permanently associated with groups of breeding females and display paternal care (Schradin and Pillay 2003; Schradin and Pillay, 2005b). Individuals in a group sleep in the same nest, have the same group territory, and interact amicably with one another, but react aggressively toward individuals from other groups (Schradin 2004). Although striped mice live in groups, they forage alone (Schradin and Pillay 2003, 2004).

Differences in social organization between *R. pumilio* from arid and moist habitats might be either within the norm of reaction of the species (Stamps 2003) or reflect genetic differences. An allozyme study of several striped mouse populations revealed that genetic distance correlated with geographic distance, and suggested the existence of several subspecies (Mahida et al. 1999). A recent mitochondrial DNA study proposed the existence of 2 species, namely *R. pumilio*, representing the social form in the deserts and semideserts, and *R. dilectus*, representing the closely related, solitary, sister species in mesic regions (Rambau and Robinson 2003). These authors admit that use of mtDNA genetic distances to assign taxonomic rank is problematical, and suggest that further studies are needed to validate the recognition of the new species *R. dilectus*. Although there is some indication of reproductive isolation (i.e., reduced interfertility and assortative mate choice) between populations (Pillay 2000a, 2000b), similar levels of interpopulation reproductive failure occurred within and between the species proposed by Rambau and Robinson (2003). Because of these uncertainties about the phylogenetic relationships among populations, we recognize only the species *R. pumilio*, and believe that differences in social organization reflect intraspecific variation in response to prevailing environmental conditions.

Because of their diurnal habits, striped mice are easily observed in the open habitat in the succulent karoo. Direct observations are not possible in the grasslands because of dense vegetation, and mark–recapture techniques have been used in all previous studies. The imprecision of mark–recapture techniques may have failed to reveal that striped mice share nests and form groups in the grassland. Therefore, the aim of this study was to compare the spatial distribution and the social structure of the population of *R. pumilio* in the succulent karoo with that of a population in the grasslands by using radiotelemetry. This use of radiotelemetry to study social systems in rodents is described by Madison et al. (1984) and Tew and Macdonald (1994).

The succulent karoo and grasslands differ in patterns of rainfall, resulting in different vegetation types (Acocks 1988). The succulent karoo is an arid, winter-rainfall area. Spring is dominated by ephemeral plant species that provide important food for striped mice, whereas succulents provide a stable food supply year-round. The grasslands receive good rains, which occur predominantly during summer. Because grass is not palatable for striped mice, they feed instead on grass seeds, berries, and herbs (Curtis and Perrin 1979; Perrin 1980a). Based on these ecological differences and results of previous studies, we made 3 predictions. First, if striped mice in the succulent karoo form permanent social groups and not only sleeping associations for thermoregulatory benefits (Bertreux et al.

1996; Canals et al. 1989), striped mice from one nest should also have the same territory, which would not be the case for a solitary population. Thus, we predicted that home ranges of individuals in a group in the succulent karoo would overlap to a much greater extent with each other than with home ranges of individuals from other groups. We expected to find only slight overlap of home ranges if *R. pumilio* exhibits a solitary lifestyle in the grasslands. Second, a solitary social system in muroid rodents often occurs because of competition over limiting resources (e.g., food—Ostfeld 1985, 1990). If food sources are more limited in grasslands than in the succulent karoo (see above), we would expect the home ranges in grassland to be considerably larger than in the succulent karoo. Third, theory predicts that if females are solitary and have large home ranges, males will actively search for receptive females (Ostfeld 1990). Assuming that *R. pumilio* is solitary in the grasslands, we would expect males to have larger home ranges than females, which would overlap the home ranges of several females (Ostfeld 1985, 1990). When females form defendable groups, as in the succulent karoo (Schradin and Pillay 2004), males should associate with these groups, resulting in males having home ranges of a similar size to that of females (Ostfeld 1985, 1990).

MATERIALS AND METHODS

Field Sites

Succulent karoo.—The study was performed during the entire breeding season from September to December 2002 (Schradin and Pillay, 2005a) in Goegap Nature Reserve near Springbok, Northern Cape Province, South Africa (global positioning system [GPS] coordinates, S29 41.712 E18 01.558; altitude, 912 m). Mean annual rainfall is 160 mm. The vegetation consists of succulent karoo (Acocks 1988), and the area has been identified as 1 of 25 biodiversity hotspots globally (Myers et al. 2000). The shrub *Zygophyllum retrofractum* is the dominant plant species. Large sandy patches that contain different species of small succulents and ephemerals also are present.

A 200 × 150-m area was chosen as the study site. A map of the study area was drawn, and included the position of bushes ($n = 95$) as landmarks drawn into a grid, in which squares represented 2 × 2 m. Bushes were marked with plastic flags.

Grasslands.—The study was performed during January and February 2003 in Kamberg Nature Reserve, located in the foothills of the Drakensberg in KwaZulu-Natal Province, South Africa (GPS coordinates, S29 23.258 E29 40.122; altitude, 1,747 m). This location is about 1,130 km from Goegap. The study was performed during the middle of the breeding season, which lasts from October to April (Perrin et al. 2001). Mean annual rainfall is 1,200 mm. The vegetation comprises sourveld grassland (Acocks 1988).

A 300 × 300-m area was used as the study site, which was marked with iron rods that were placed 10 m apart between and within rows. Each iron rod was marked with a uniquely numbered plastic flag. Four weeks later, we established a 2nd site measuring 120 × 100 m and located 10 km from the 1st site. This was done to obtain additional data and to confirm whether the results from the 1st site were representative of the situation in the grasslands. Based on our findings from the 1st site, iron rods were placed 20 m apart.

Trapping

All parts of this study were approved by the animal ethics committee of the University of the Witwatersrand and we followed the American

Society of Mammalogists guidelines for the capture, handling, and care of mammals (<http://www.mammalogy.org/committees/index.asp>).

Rhabdomys pumilio was trapped by using metal live traps (26 × 9 × 9 cm) baited with a mixture of bran flakes, sea salt, and salad oil. Because of differences in habitat structure, trapping was performed differently in the 2 localities. In the grasslands, traps were placed alongside the iron rod markers in a trapping grid. Each site in the grasslands was trapped for 1 month, with 3 trapping sessions, 1 at the beginning, 1 after 2 weeks, and the 3rd after 4 weeks. Each session lasted 3 days, preceded by 3 days of prebaiting. Traps were checked 4 times a day from 0800 to 1700 h. Traps in the succulent karoo were set in the shade of shrubs and bushes, where striped mice had been observed previously; trapping was done only in the morning and afternoon, and not during the hottest times of the day. Trapped animals were sexed and weighed (to the nearest gram) and individually marked using hair dye (photograph in Schradin and Pillay, 2004).

Radiotracking

Radiotracking was performed by using an AOR 8000 wide-range receiver (Tokyo, Japan) and a Telonics RA-14K antenna (Mesa, Arizona). Individuals were equipped with MD-2C radiotransmitters (Holohil, Carp, Ontario, Canada), which weighed 2.5 g including the collar and represented 5.1% of body weight on average (variation, 3.5–9.0%). Individuals were equipped with radiotransmitters for a mean duration of 12.6 days (range, 7–23 days). No indication was found that radiocollars were harmful to tagged individuals. In the succulent karoo, males equipped with radiotransmitters did not change significantly in body weight ($P > 0.6$, $T = 73.5$, $n = 18$, Wilcoxon test), but gained a mean of 1.3 g body weight, which resembled the pattern typical of nontagged males during spring (Schradin and Pillay, 2005a). Of 3 males tagged in the grasslands, 2 lost and 1 gained weight during radiotracking; similar weight changes were observed in nontagged males. Females were not considered in these analyses because their body weight fluctuated due to pregnancy.

The first 9 individuals in the succulent karoo were radiotracked for 9 days. Fixes were taken 6 times a day from 0800 to 1800 h. To ensure independence of data points (Kenward, 1987), intervals between fixes were approximately 2 h. Data obtained from these 9 individuals revealed that home-range size reached a sampling saturation after 6–7 days (Fig. 1A). Thus, all additional individuals were radiotracked for 7 days (42 fixes); for the first 9 animals, data collected only during the first 7 days were used for analysis.

Radiotracking in the succulent karoo.—Fixes were obtained by using the “homing-in” method, that is, an individual striped mouse was approached until we either saw the mouse or identified the bush in which it was located. The location of the mouse was then marked on a map. The position of ~40% ($n = 49$) of individuals was confirmed by visual sightings. Striped mice were very well habituated and did not seem to be disturbed by our presence, as indicated by the high number of visual sightings. By using radiotelemetry, we also established the nest location of all focal striped mice during 36 nights and determined which individuals were sleeping in the same bush.

We radiotracked a total of 56 individuals, including 14 breeding males, 7 adult male offspring, 28 breeding females, and 8 adult female offspring. Adult offspring had been trapped and observed as juveniles at group nests and remained there after reaching adulthood. We radiotracked 6–18 individuals simultaneously for >2 months. Data meeting our criterion of 7 days were available for 49 individuals (18 males and 31 females). Of the remaining 7 individuals, 3 breeding females were preyed upon by jackal buzzards, 1 daughter was killed by an unknown predator, the radiotransmitter of 1 male offspring failed (and was later removed), and 2 individuals disappeared from the study grid.

Radiotracking in the grasslands.—We radiotracked every mouse that showed signs of reproductive activity, had a body weight above 25 g (i.e., the transmitter weighed <10% of body weight), and was trapped at least twice. All striped mice in site 1 were radiotracked within the same 2 weeks, and all striped mice in site 2 were radiotracked during 2 other weeks. A total of 5 males and 14 females received radiotransmitters (both sites combined). Of these, 2 females were eaten by snakes (*Psammophylax rhombeatus* and *Lamprophis inornatus*), 1 male and 1 female disappeared from the study sites, and 1 male and 2 females died of unknown causes. No relationship was found between body weight and loss or death.

Because of deaths and disappearances, data for 7 days of radiotracking were available for only 3 males and 9 females. We decided also to use data for 2 males studied for 3 and 5 days each and 3 females studied for 3, 3, and 6 days each. We regarded this procedure as more ethical than radiotracking more striped mice, because we did not know whether radiotracking itself had contributed to the losses experienced. In addition, we believed that our assumptions were reasonable because the slope of the curve describing the increase in home-range size for individuals radiotracked for 7 days was the same for the individuals radiotracked for fewer days (Fig. 1B). For these additional individuals, we calculated expected home ranges on day 7 by multiplying home-range size on the last day of radiotracking by the percentage by which home ranges increased from the last day to day 7 in other individuals where such data existed: the increase from day 3 to day 7 was 95.6%, from day 5 to day 7 was 25.5%, and from day 6 to day 7 was 16.6% (Fig. 1B).

A map of the study area was drawn by using the position of the iron rods as landmarks in a grid, in which squares represented 10 × 10 m at site 1, and 20 × 20 m at site 2. A mouse with a radiotransmitter was approached to within 2–5 m from 3 different directions until its position was established (homing-in technique) and marked on the map. Although this method would have disturbed mice, they typically changed their position between 2 fixes (time interval of 2 h), indicating that our chosen time interval was long enough for reliable data collection. Because large ungulates such as wildebeest and blesbok also were present at the field site, striped mice were possibly accustomed to the presence of larger animals.

By using radiotelemetry, we established the nest location of all focal striped mice during 12 nights and determined which individuals were sleeping in the same location. We approached individuals from 3 different directions, as described above. Individuals were regarded as sharing a nest when their radiosignal emanated from exactly the same location, that is, an area of <2 m². Those mice that were regarded as sleeping together were radiotracked simultaneously, that is, their fixes were taken at the same time. To minimize disturbance, we did not search for the actual nests.

Individuals were often outside the grid because their home ranges were larger than expected (see “Results”). Therefore, when striped mice were more than 20 m outside the grid, their location was recorded by using a GPS (eTrex Venture, GARMIN International, Olathe, Kansas). The accuracy of this device at our site was within 4–5 m. All data were collected by using GPS fixes at the 2nd study grid.

Analyses

Home ranges were determined by using the minimum convex polygon method (Kenward 1987). Because this is a widely used method for rodents (e.g., Madison et al. 1984; Tew and Macdonald 1994), comparisons between studies are possible (Sterling et al. 2000). The position of individuals was recorded on maps generated in Microsoft Excel, which were scaled proportionally to the grid size of 2 × 2 m. Home-range sizes were determined by dividing the squares

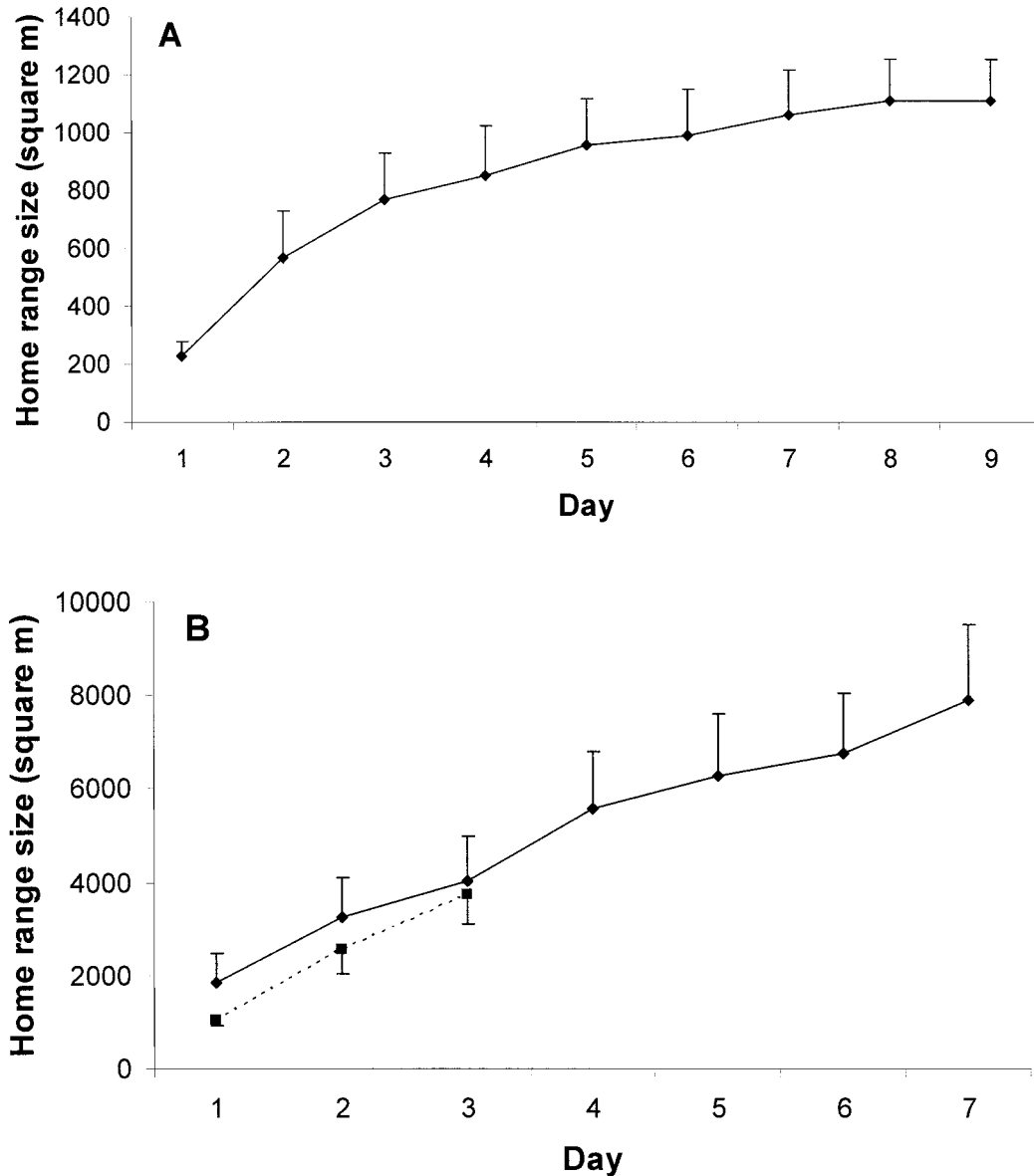


FIG. 1.—Relationship between home-range size (mean \pm SE) and number of days of radiotracking (6 points per day) in the A) succulent karoo and B) grasslands. In the succulent karoo ($n = 9$ individuals), home-range size did not increase significantly after 6 days. In the grasslands ($n = 12$), data for 5 striped mice that were radiotracked for 3 days only are shown with a dashed line. This line has the same slope as the line of mice radiotracked for 7 days.

into triangles and calculating area in square meters. Areas of overlap were subsequently mapped and the size of overlap determined.

All tests performed are nonparametric and 2-tailed (Siegel and Castellan, 1988). The Mann-Whitney U -test is abbreviated as U -test, Wilcoxon matched pairs rank sign test as Wilcoxon test, and the Fisher's exact test as Fisher test. Data are presented as mean \pm SE. For comparison of demography, data of all individuals trapped were used (including all radiotracked individuals) and mean values were used for each individual.

RESULTS

Sleeping in close proximity.—Striped mice in the grasslands never shared nests with same-sex individuals. The 5 tagged males were radiotracked a total of 20 times during nights, and

a male and female from 3 different pairs were located in the same place on 7 (35%) occasions. These were short-term associations, that is, these pairs were located together on 33%, 50%, and 57% of nights sampled. The remaining 2 males and 11 females never associated with other individuals during nights sampled. In the succulent karoo, 42 of the 49 tagged striped mice were permanent members of a group. The remaining 7 individuals displayed loose or no associations with groups. Two males lived alone at the beginning of the breeding season, but were spatially associated with a group later (Fig. 2A); 2 breeding females raised their offspring alone (Fig. 2A); and 2 females and 1 male of 1 group shared the same sleeping site, but sometimes slept alone at the start of the breeding season. Significantly more individuals permanently

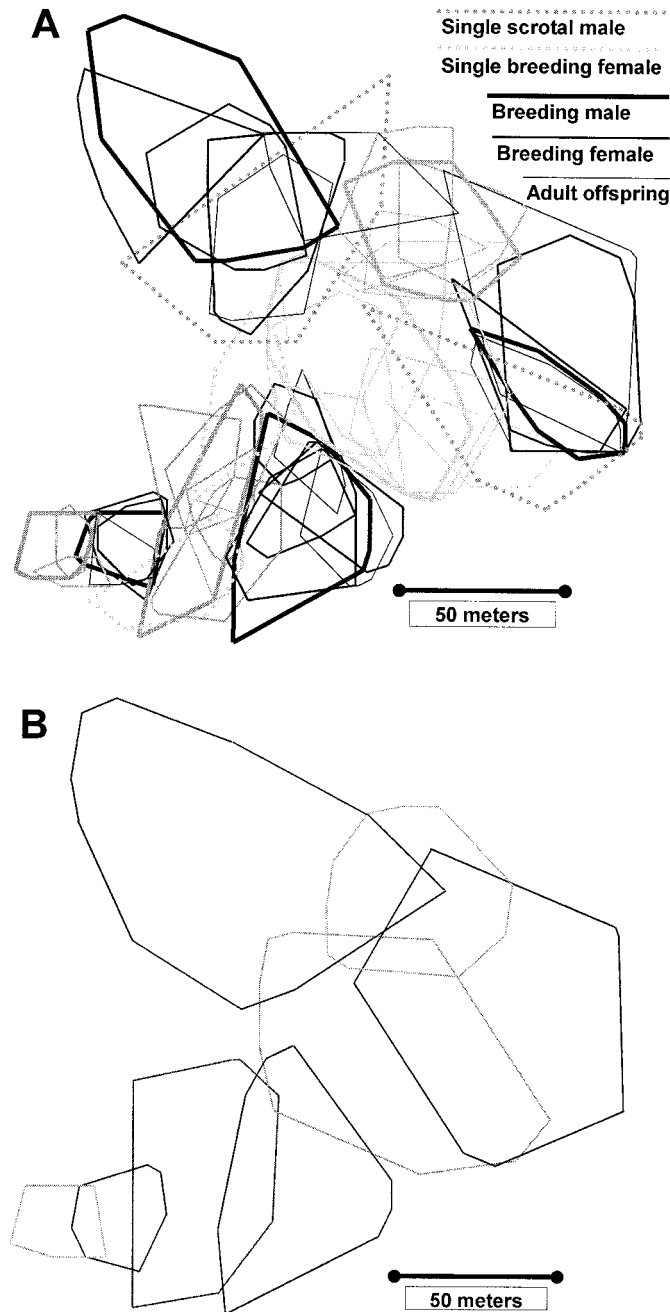


FIG. 2.—Home-range overlap of striped mice in the succulent karoo, Northern Cape Province, South Africa. A) Home ranges of individual animals that shared the same nest site overlap to a significant extent. Group members (breeding male, breeding females, adult son, and adult daughter) are indicated in different line patterns. Members of one group have the same line types, black (4 groups) or gray (4 groups). B) Group home ranges (data of all group members combined per group).

shared sleeping sites (i.e., radiotracked together with other individuals during all nights) in the succulent karoo (42 of 49 individuals) than in grasslands (0 of 20 individuals; Fisher test, $P < 0.0001$).

Home-range overlap.—In the succulent karoo, home ranges of individuals sharing a nest site overlapped to a much greater

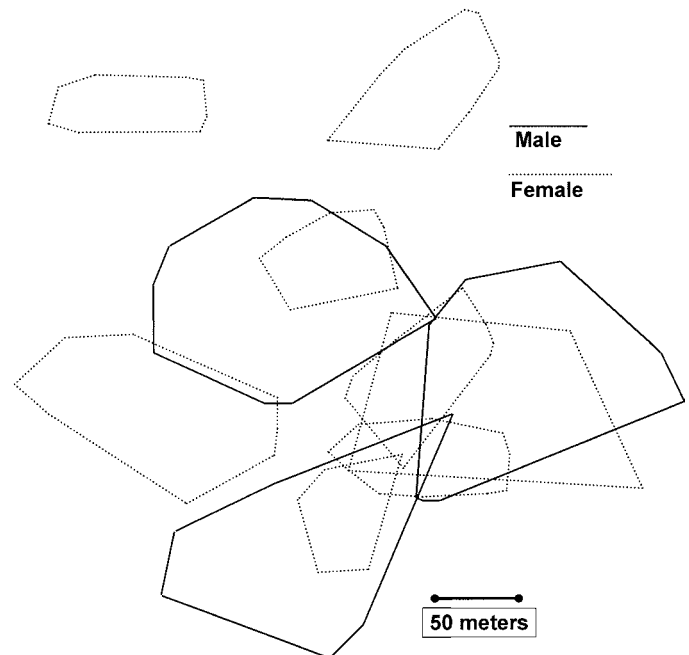


FIG. 3.—Home ranges of male (solid line) and female (stippled) striped mice in grasslands (KwaZulu-Natal Province, South Africa) at field site 1.

extent with one another ($84.0 \pm 2.5\%$) than with home ranges of individuals from other groups ($40.0 \pm 3.9\%$; Wilcoxon test, $T = 27$, $n = 42$, $P < 0.0001$; Fig. 2A). The same trend was evident for adult male offspring (group members, $80.7 \pm 6.8\%$; nongroup members, $48.3 \pm 5.7\%$; $T = 1$, $n = 6$, $P = 0.06$). For adult female offspring, the difference was significant (group members, $97.1 \pm 2.0\%$; non-group members, $12.6 \pm 12.6\%$; $T = 0$, $n = 6$, $P < 0.05$).

In grasslands, no group formation was obvious (Fig. 3). Home ranges of females overlapped more with those of males ($36.7 \pm 12.7\%$) than with those of females ($27.1 \pm 8.3\%$), but this difference was not statistically significant (Wilcoxon test, $T = 20$, $n = 10$, $P > 0.5$; Fig. 3). Home ranges of females overlapped home ranges of a mean of 1.6 other females (range, 0–3) and 0.9 males (range, 0–3). Home ranges of males overlapped by only $1.2 \pm 0.7\%$ with those of other males and by $31.3 \pm 14.4\%$ with those of females ($T = 6$, $n = 3$, $P > 0.2$). Home ranges of 2 males did not overlap with those of other individuals. Home ranges of males overlapped home ranges of a mean of 0.4 other males (range, 0–1) and 2.4 females (range, 0–5) home ranges.

Population comparison.—Home ranges of striped mice in the succulent karoo overlapped to a significantly greater extent than in the grasslands ($P < 0.05$; for statistics see Table 1; compare Fig. 2 with Fig. 3). Total overlap in the grasslands was lower compared with overlap of group members in the succulent karoo. Comparisons were significant for both sexes combined, and for each sex separately (Table 1).

Breeding males in the succulent karoo had 2.9 ± 0.4 breeding females in their group. At field site 1 in the grasslands, males had access to 2.3 ± 0.7 breeding females, which was not

TABLE 1.—Comparison between total home-range overlap of striped mice in the grasslands (KwaZulu-Natal Province, South Africa) and percentage overlap of group members in the succulent karoo (Northern Cape Province, South Africa). Data from individuals with known group affiliations in the succulent karoo are shown. Statistics represent Mann–Whitney *U*-tests.

Sex and habitat	Mean	SE	<i>U</i>	<i>n</i>	<i>P</i>
All			543.5		<0.002
Grasslands	49.0	9.5		17	
Succulent karoo	84.0	2.5		42	
Males			72.0		<0.006
Grasslands	31.3	14.4		5	
Succulent karoo	78.3	4.8		16	
Females			224.5		<0.04
Grasslands	56.3	11.8		12	
Succulent karoo	87.7	2.6		26	

different from the situation in the succulent karoo (*U*-test, $U = 14$, $m = 8$, $n = 3$, $P > 0.7$). Males from field site 2 in the grasslands were not included because they were located on the boundaries of the grid and it is possible that they overlapped with females outside the study site.

Home-range size.—No difference was found between home-range size of females ($912 \pm 93 \text{ m}^2$) and males ($1,305 \pm 225 \text{ m}^2$; *U*-test, $U = 342$, $m = 30$, $n = 18$, $P > 0.1$; Fig. 4) in the succulent karoo. Because home ranges of females in a group were likely to be interdependent, we corrected for statistical independence of data by calculating the mean value for home ranges of all breeding females in a group. Again, breeding males did not have larger home ranges compared with breeding females of their group (males: $1,424 \pm 319 \text{ m}^2$, females: $926 \pm 199 \text{ m}^2$; Wilcoxon test, $T = 4$, $n = 8$ groups, $P > 0.05$). In contrast, males ($12,466 \pm 2,000 \text{ m}^2$) in the grasslands had significantly larger home ranges than females ($5,760 \pm 1,098 \text{ m}^2$; *U*-test, $U = 51$, $m = 5$, $n = 12$, $P < 0.03$; Figs. 3 and 4).

Home ranges of females in the grasslands were >6 times larger than those of females in the succulent karoo (*U*-test, $U = 367$, $m = 12$, $n = 30$, $P < 0.0001$; Fig. 4). Home ranges of males in the grasslands were 10 times larger than those of males in the succulent karoo ($U = 90$, $m = 5$, $n = 18$, $P < 0.0001$; Fig. 4).

Gnawing on transmitters.—Of the 19 transmitters recovered from radiotracked striped mice in the grasslands, none were gnawed. In contrast, all transmitters were gnawed in the succulent karoo, which could not have been done by the mouse with the radiotransmitter itself, but only by another individual. The ratio of gnawed to ungnawed transmitters differed significantly between populations (Fisher test, $P < 0.001$). Furthermore, 9 of 49 transmitters recovered no longer worked because of the gnawing (confirmed by Holohil, manufacturer of the transmitters, who examined the transmitters after the study). The ratio of transmitters that broke down due to gnawing by conspecifics is significantly different between populations (Fisher test, $P = 0.05$).

Demographic data.—Scrotal males in the succulent karoo were significantly heavier than scrotal males in the grasslands (*U*-test, $U = 288$, $m = 22$, $n = 15$, $P = 0.0002$; Fig. 5). The

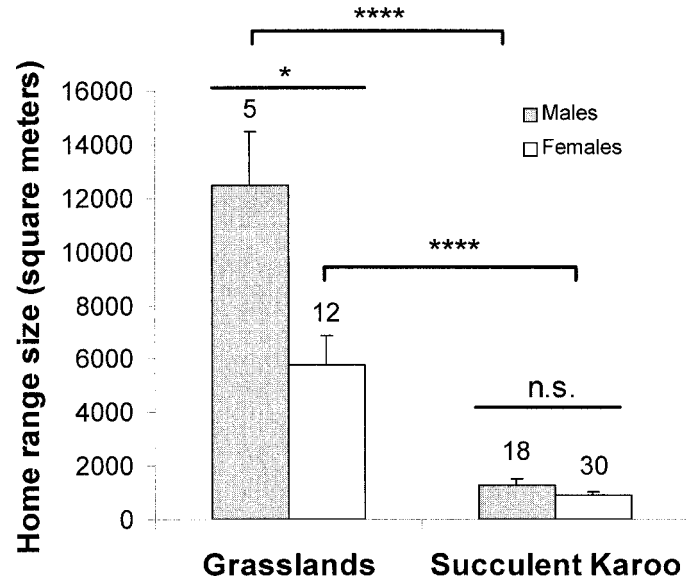


FIG. 4.—Home-range sizes (mean + SE) of males and females in grasslands (KwaZulu-Natal Province, South Africa) and the succulent karoo (Northern Cape Province, South Africa). Sample sizes are shown. n.s.: nonsignificant; asterisks indicate significantly different (*: $P < 0.05$, ****: $P < 0.0001$).

range of body weight of scrotal males was larger in the grasslands (23.6–70.1 g) than in the succulent karoo (41.0–69.7 g). In the grasslands, 3 of 8 males with a body weight between 20 and 30 g were scrotal, whereas none of 4 males weighing in this range were scrotal in the succulent karoo (Fisher test, $P > 0.4$). Seven of 8 males with a body weight between 30 and 40 g were scrotal in the grasslands but none of 15 males in this weight range were scrotal in the succulent karoo (Fisher test, $P < 0.0001$).

Females showing signs of reproductive activity (open vagina, visible nipples indicating lactation, or both) were significantly heavier in the succulent karoo than in the grasslands (*U*-test, $U = 492$, $m = 30$, $n = 19$, $P < 0.0001$; Fig. 5). The range of body weight of reproductive active females was larger in the grasslands (25.3–59.8 g) compared to the succulent karoo (44.2–66.9 g). In the grasslands, 3 of 10 females with a body weight between 20 and 30 g showed signs of breeding, whereas none of 17 females in this weight range were reproductively active in the succulent karoo (Fisher test, $P < 0.05$). For the weight range 30–40 g, all 4 females in the grasslands showed signs of breeding compared to none of the 16 females in the succulent karoo (Fisher test, $P < 0.0002$).

The trapping density during the last trapping session (end of the breeding season) in the succulent karoo was 73.3 striped mice/ha. In the grasslands, 20 mice/ha were trapped in site 1 and 13.3 striped mice/ha in site 2.

DISCUSSION

Population differences in social organization.—Population differences in home-range sizes and overlap suggest differences in social organization. In the succulent karoo, individuals in a group typically spent the night together and used the same

home range, which was distinct from home ranges of other groups. Evidence of social interactions among group members was provided by signs of gnawing of transmitters that must have had been performed by conspecifics in the nest.

No group formation was obvious in the grasslands, where individuals typically slept alone. On a few occasions, a male and female were located in close proximity during the night (3 of 5 males and 3 of 14 females). These associations were not permanent, but were probably for mating (Willan 1982). Home ranges of males overlapped those of several females and to a greater extent than home ranges of other males. Although not statistically significant, these results concur with results from previous mark–recapture studies in grasslands, indicating that females have exclusive territories and males overlap the territories of several females (Brooks 1974; Choate 1972; Willan 1982; Willan and Meester 1989; Wirminghaus and Perrin 1993).

Although examination of our data does not directly reveal the mating system of *R. pumilio*, we can hypothesize about the mating system from the spatial data, assuming that males and females with overlapping home ranges are potential mates. Examination of our spatial data indicates that *R. pumilio* is socially polygynous in the succulent karoo; that is, groups consist of 1 breeding male and 2–4 breeding females (Schradin and Pillay 2004). The social system is therefore similar to that of polygynous house mice (Lidicker 1976). In contrast, home ranges of males were more than twice as large as home ranges of females in grasslands. This pattern is typical for solitary rodents that mate promiscuously (Keesing 1998; Salvioni and Lidicker 1995; Webster and Brooks 1981), and has been suggested to be a mating system in *R. pumilio* from grassland habitats in close proximity to our study site (Willan 1982). Another important consideration is the larger home-range sizes in grasslands compared to the succulent karoo. Because the cumulative curve of home-range estimates was closer to saturation in the succulent karoo (Fig. 1A) than in grasslands (Fig. 1B), home-range sizes in grasslands could have been underestimated and differences between populations may be even more pronounced than demonstrated by examination of our data.

In the succulent karoo, offspring remain in their natal group for several months without reproducing (Schradin and Pillay 2004). However, striped mice in the grasslands leave their natal nest as juveniles (Willan 1982) and start reproducing sooner and at a lighter body mass than their counterparts in the succulent karoo. *R. pumilio* appears to invest in somatic development and survival until the next breeding season in the succulent karoo, but invests in reproduction soon after weaning in the grasslands. This trade-off between reproductive and somatic investment are adaptive because the probability of an individual surviving until the next breeding season is about 20% in the succulent karoo (Schradin and Pillay, 2005a) but only 3% in grasslands (Brooks 1974).

Ecological differences.—We studied 1 population in the succulent karoo and 2 in grasslands and therefore we cannot comment about within-population differences in sociality. Nevertheless, differences between the populations are in-

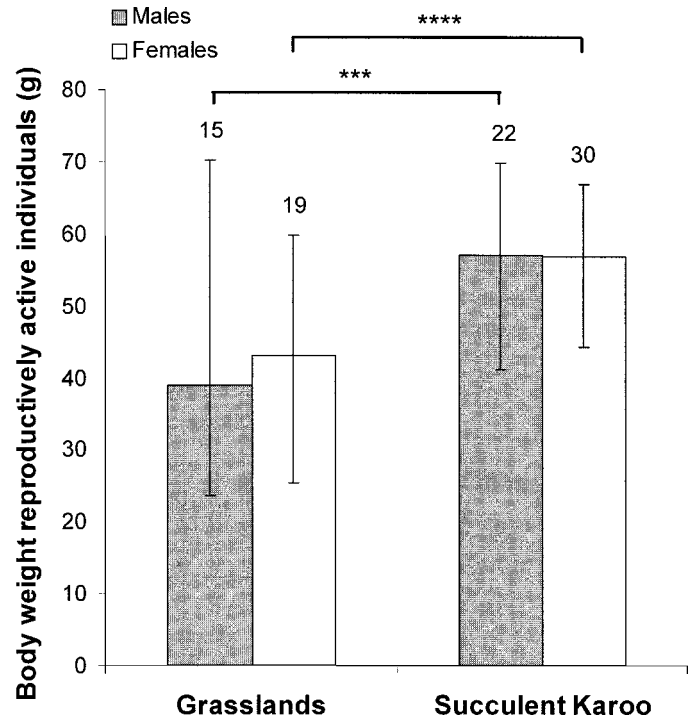


FIG. 5.—Body weight of reproductively active males and females in grasslands (KwaZulu-Natal Province, South Africa) and in the succulent karoo (Northern Cape Province, South Africa). Mean, variation, and sample sizes are shown. Asterisks indicate significant differences (***: $P < 0.001$, ****: $P < 0.0001$).

teresting and can be used to generate testable hypotheses for future research (see also Schradin, in press).

In the succulent karoo, winter rain (160 mm/year) is followed by a dry, hot summer. The vegetation in spring consists of succulents and ephemerals such as wildflowers, which sustain animals through the breeding season, which lasts 3 months (Schradin and Pillay 2005a). Thereafter, striped mice feed mainly on succulents, which are available year round. Comparison of home ranges in grasslands (Fig. 3) and succulent karoo (Fig. 2A) shows differences in habitat packing. Apart from high population density in the succulent karoo, territorial aggression is an important factor regulating space use. Group members (breeders and their offspring) respond aggressively toward individuals of other groups (Schradin 2004). Because territorial aggression mainly occurs at territory boundaries (Schradin and Pillay 2004) and space is a limiting factor in the succulent karoo (Fig. 2), this population can be regarded as being saturated. Habitat saturation might explain why adult offspring stay in their natal territory, as shown in this study and in another study (Schradin and Pillay, 2004). Philopatry could be associated with benefits of group living, such as increased vigilance against predators (Schradin and Pillay 2004), and thermoregulatory benefits by nest sharing (Carter and Roberts 1997; Howard 1950), especially during the cold winter (night temperatures typically $<0^{\circ}\text{C}$), which precedes the breeding season. In contrast, costs of philopatry due to missed breeding opportunities might be low. When the striped mice of the 1st litter of the breeding season reach sexual maturity at 2 months

of age (Brooks 1974), the breeding season is two-thirds complete. Therefore, it might be advantageous to stay in the natal nest, gain weight, and overwinter in the natal group. A combination of ecological constraints and benefits of philopatry (Emlen 1995; Hayes 2000; Solomon 2003) most likely accounts for group living of *R. pumilio* in the succulent karoo.

In the grasslands, rainfall is substantially heavier (>1,000 mm/year) and occurs during summer, which accounts for the long breeding season of about 7 months (Perrin 1980b; Perrin et al. 2001; Willan and Meester 1989). Although grasses are the dominant plants, grass is not palatable for striped mice, which instead feed mainly on grass seeds, berries, and herbs (Curtis and Perrin 1979; Perrin 1980a). The very large home ranges in grasslands indicate that food might be a limiting resource (Ostfeld 1990).

In contrast to the succulent karoo, grassland habitats are not saturated for striped mice and the breeding season is much longer. Individuals born early in the breeding season reach adulthood well before the end of the breeding season, and there is enough space into which they can emigrate. Two potential costs probably act against communal living. Females would be subdominant to their much heavier mother, leading to reproductive skew, as reported for the wood mouse (*Apodemus sylvaticus*—Gerlach and Bartmann 2002), and low food abundance coupled with dispersed food sources means that groups would need even larger territories than single females. This is because home ranges of females are 6 times larger in the grassland compared to the succulent karoo, and individuals in groups would need to cover vast distances to forage to meet per capita energy requirements.

Conclusions.—The reasons for the differences in space use and social organization between the populations of *R. pumilio* are not clearly understood, but differences in ecology and associated demography would provide the conceptual framework for generating testable hypotheses for future studies (see also Schradin, in press). We predict that dispersal is limited because of a high population density in the succulent karoo. Because of predicted thermoregulatory benefits of nest sharing during winter, we predict that there is a direct relationship between survival probability and group size. We expect that a greater number of individuals born at the start of the breeding season will survive to the next breeding season in the succulent karoo, because they have longer time to accumulate resources and invest in somatic development during favorable conditions in spring. We predict that communal breeding will lead to fitness benefits in the succulent karoo, but to reduced fitness in grasslands, at least for subdominant females. Finally, we predict that if a researcher would provide extra food in an experiment in grasslands, population density would increase (as already shown by Perrin and Johnson 1999), and home-range size will decrease, possibly leading to habitat saturation, philopatry, and group living.

Differences in social organization might also reflect genetic differences between the populations. The 2 populations studied occur >1,000 km apart and are likely to be genetically different (Mahida et al. 1999; Rambau and Robinson 2003). However, we showed in a previous study that males from both the

succulent karoo and a grassland locality display paternal care when housed in monogamous pairs in captivity, and there is no statistical difference in paternal behavior between populations (Schradin and Pillay 2003), suggesting that some behaviors are genetically conserved. Nonetheless, it is important in the future to establish the genetic and environmental underpinnings of social behavior in *R. pumilio* from different habitats.

ACKNOWLEDGMENTS

We thank Northern Cape Department of Agriculture, Land Reform, Environment and Conservation, and KwaZulu Natal Wildlife for their assistance, and K. van Zyl, E. Oosthuysen, and their staff at Goegap Nature Reserve and C. Brummer and his staff at Kamberg Nature Reserve for their support during the study. We are thankful to B. Britz and M. Schubert for field assistance. This study was supported by the Swiss National Science Foundation, the Schweizerische Gesellschaft für Naturwissenschaften, the Fonds zur Förderung des akademischen Nachwuchses of the Zürcher Universitätsverein, and the University of the Witwatersrand.

LITERATURE CITED

- ACOCKS, J. P. H. 1988. Veld types of South Africa. Botanical Research Institute, Pretoria, South Africa.
- BERTREAU, D., J. M. BERGERON, D. W. THOMAS, AND H. LAPIERRE. 1996. Solitude versus gregariousness: do physical benefits drive the choice in overwintering meadow voles? *Oikos* 76:330–336.
- BROOKS, P. M. 1974. The ecology of the four-striped field mouse, *Rhabdomys pumilio* (Sparman 1984), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria. Ph.D. dissertation, University of Pretoria, Pretoria, South Africa.
- CANALS, M., M. ROSENMAN, AND F. BOZINOVIC. 1989. Energetics and geometry of huddling in small mammals. *Journal of Theoretical Biology* 141:181–189.
- CARTER, C. S., AND R. L. ROBERTS. 1997. The psychobiological basis of cooperative breeding in rodents. Pp. 231–266 in *Cooperative breeding in mammals* (N. G. Solomon and J. A. French, eds.). Cambridge University Press, Cambridge, United Kingdom.
- CHOATE, T. S. 1972. Behavioural studies on some Rhodesian rodents. *Zoologica Africana* 7:103–118.
- CURTIS, B. A., AND M. R. PERRIN. 1979. Food preferences of the vlei rat (*Otomys irroratus*) and the four-striped mouse (*Rhabdomys pumilio*). *South African Journal of Zoology* 14:224–229.
- DEWSBURY, D. A. 1985. Paternal behavior in rodents. *American Zoologist* 25:841–852.
- EMLEN, S. T. 1995. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences USA* 92:8092–8099.
- GERLACH, G., AND S. BARTMANN. 2002. Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). *Behavioral Ecology* 13:408–418.
- 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.
- KESING, F. 1998. Ecology and behavior of the pouched mouse, *Saccostomus mearnsi*, in central Kenya. *Journal of Mammalogy* 79:919–931.
- KENWARD, R. 1987. *Wildlife radio tagging*. Academic Press, London, United Kingdom.

- KINGDON, J. 1974. East African mammals. Academic Press, London, United Kingdom.
- 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. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266–325.
- LOTT, D. F. 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge University Press, New York.
- MACDONALD, D. W. 1979. The flexible social system of the golden jackal, *Canis aureus*. *Behavioral Ecology and Sociobiology* 5:17–38.
- MADISON, D. M., R. W. FITZGERALD, AND W. J. MCSHEA. 1984. Dynamics of social nesting in overwintering meadow voles (*Microtus pennsylvanicus*): possible consequences for population cycling. *Behavioral Ecology and Sociobiology* 15:9–17.
- MAHIDA, H., G. K. CAMPBELL, AND P. J. TAYLOR. 1999. Genetic variation in *Rhabdomys pumilio* (Sparman 1784): an allozyme study. *South African Journal of Zoology* 34:91–101.
- MCGUIRE, B., AND L. L. GETZ. 1998. The nature and frequency of social interactions among free-living prairie voles (*Microtus ochrogaster*). *Behavioral Ecology and Sociobiology* 43:271–279.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. D. FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
- OSTFELD, R. S. 1985. Limiting resources and territoriality in microtine rodents. *American Naturalist* 126:1–15.
- OSTFELD, R. S. 1990. The ecology of territoriality in small mammals. *Trend in Ecology and Evolution* 5:411–415.
- PERRIN, M. R. 1980a. The feeding habits of two co-existing rodents, *Rhabdomys pumilio* (Sparman, 1784) and *Otomys irroratus* (Brants, 1827), in relation to rainfall and reproduction. *Acta Oecologica* 1:71–89.
- PERRIN, M. R. 1980b. The breeding strategies of two co-existing rodents, *Rhabdomys pumilio* (Sparman, 1784) and *Otomys irroratus* (Brants, 1827). *Acta Oecologica* 1:383–410.
- PERRIN, M. R., C. ERCOLI, AND E. DEMPSTER. 2001. The role of agonistic behaviour in the population of two syntopic African grassland rodents, the striped mouse *Rhabdomys pumilio* (Sparman 1784) and the multimammate mouse *Mastomys natalensis* (A. Smith 1834) (Mammalia Rodentia). *Tropical Zoology* 14:7–29.
- PERRIN, M. R., AND S. J. JOHNSON. 1999. The effect of supplemental food and cover availability on a population of the striped mouse. *South African Journal of Wildlife Research* 29:15–18.
- PILLAY, N. 2000a. Female mate preference and reproductive isolation in populations of the striped mouse *Rhabdomys pumilio*. *Behaviour* 137:1431–1441.
- PILLAY, N. 2000b. Reproductive isolation in three populations of the striped mouse *Rhabdomys pumilio* (Rodentia, Muridae): interpopulation breeding studies. *Mammalia* 64:461–470.
- RAMBAU, R. V., AND T. J. ROBINSON. 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.
- ROBERTS, R. L., J. R. WILLIAMS, A. K. WANG, AND C. S. CARTER. 1998. Cooperative breeding and monogamy in prairie voles: influence of the sire and geographic variation. *Animal Behaviour* 55:1131–1140.
- SALVIONI, M., AND W. Z. LIDICKER, JR. 1995. Social organisation and space use in California voles: seasonal, sexual, and age-specific strategies. *Oecologia* 101:426–438.
- SCHRADIN, C. 2004. Territorial defense in a group living solitary forager: who, where against whom? *Behavioral Ecology and Sociobiology* 55:439–446.
- SCHRADIN, C. In press. When to live alone and when to live in groups: ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparman, 1784). *Belgian Journal of Zoology*.
- SCHRADIN, C., AND N. PILLAY. 2003. Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): laboratory and field evidence. *Journal of Comparative Psychology* 117:317–324.
- SCHRADIN, C., AND N. PILLAY. 2004. The striped mouse (*Rhabdomys pumilio*) from the succulent karoo of South Africa: a territorial group living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* 118:37–47.
- SCHRADIN, C., AND N. PILLAY. 2005a. Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammalian Biology*.
- SCHRADIN, C., AND N. PILLAY. 2005b. The influence of the father on offspring development in the striped mouse. *Behavioral Ecology*.
- SIEGEL, S., AND M. J. CASTELLAN. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- SOLOMON, N. G. 2003. A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* 84:1182–1197.
- STAMPS, J. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. *Animal Behaviour* 66:1–13.
- STERLING, E. J., N. NGUYEN, AND P. J. FASHING. 2000. Spatial patterning in nocturnal prosimians: a review of methods and relevance to studies of sociality. *American Journal of Primatology* 51:3–19.
- TEW, T. E., AND D. W. MACDONALD. 1994. Dynamics of space use and male vigour amongst wood mice, *Apodemus sylvaticus*, in the cereal ecosystem. *Behavioral Ecology and Sociobiology* 34:337–345.
- WEBSTER, A. B., AND R. J. BROOKS. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy* 62:738–751.
- WILLAN, B. R. 1982. Social ecology of *Otomys irroratus*, *Rhabdomys pumilio* and *Mastomys natalensis*. Ph.D. dissertation, University of Natal, Pietermaritzburg, South Africa.
- WILLAN, K., AND J. MEESTER. 1989. Life-history styles of southern African *Mastomys natalensis*, *Otomys irroratus* and *Rhabdomys pumilio* (Mammalia, Rodentia). Pp. 421–439 in *Alternative life-history styles of animals* (M. N. Bruton, ed.). Kluwer Academic Publishers, Dordrecht, Netherlands.
- WIRMINGHAUS, J. O., AND M. R. PERRIN. 1993. Seasonal-changes in density, demography and body-composition of small mammals in a southern temperate forest. *Journal of Zoology* 229:303–318.

Submitted 24 November 2003. Accepted 4 April 2004.

Associate Editor was Nancy G. Solomon.