



Original investigation

Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo

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Abstract

The striped mouse (*Rhabdomys pumilio*) is widely distributed in southern Africa, inhabiting a wide range of habitats. We describe the demography of the striped mouse in the arid succulent karoo of South Africa, and compare our findings with those of published results for the same species from the moist grasslands of South Africa. In both habitats, breeding starts in spring, but the breeding season in the succulent karoo is only half as long as in the grasslands, which can be explained by different patterns and levels of rainfall; the succulent karoo receives mainly winter rain and rainfall is much less (about 160 mm year⁻¹) than in the grasslands (> 1000 mm year⁻¹) which experience summer rain. Population density increased from 37 (start of breeding season) to 171 (end of breeding season) mice per hectare. A high yearly survival rate of 27% during our study from summer to the next breeding season resulted in a population density that was 10 times higher in the succulent karoo than in grasslands. The comparatively high population density may result in habitat saturation and thus forced philopatry, promoting group living in the succulent karoo, which contrasts with the solitary life-style exhibited by populations in moist grasslands.

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Introduction

When one species occupies different habitats, we can expect population differences in demography and reproductive behaviour, which might influence the social structure of populations (Lott 1991). The striped mouse *Rhabdomys pumilio* offers an ideal opportunity for studying ecological plasticity and the influence of different habitats on demography. The striped mouse is a diurnal murid rodent (adult mass 30–40 g) with a wide distribution in southern Africa that includes

habitats such as grassland, marsh, forests, semi-deserts and deserts (Kingdon 1974). Most field studies on striped mice have been conducted in moist grasslands, where the species is reported to be solitary and territorial. In grasslands in Zimbabwe, females and their most recent litters share a nest, whereas males occupy separate areas (Choate 1972). The same pattern apparently exists in the grasslands of KwaZulu-Natal Province, South Africa, where female striped mice have

exclusive territories and male territories overlap with several female territories (Willan 1982; Willan and Meester 1989; Perrin et al. 2001; Schradin and Pillay 2005). Field studies at several other South African localities, such as grasslands near Pretoria (Brooks 1974) and in KwaZulu-Natal midlands (Wirminghaus and Perrin 1993), as well as in semi-succulent thorny scrub in the Eastern Cape Province (Perrin 1980b) report that the striped mouse is solitary. In contrast, the striped mouse is reported to have a more communal social system in arid habitats, such as the Kalahari (Nel 1975), and the Namib (Krug 2002).

The succulent karoo in the north-western part of South Africa is of particular interest in studies of striped mice since this region is arid, with an average rainfall of 160 mm p.a., occurring mainly during winter (Acocks 1988). This biome has been identified as one of 25 global biodiversity hotspots (Myers et al. 2000), since it contains several endemic plant species, mainly succulents and ephemerals (Cowling et al. 1999). Plants are patchily distributed and do not provide homogenous cover. The succulent karoo differs from the moist grasslands in the level of rain per year (160 mm vs. > 1000 mm), the period of rainfall (winter vs. summer), as well as the diversity of plant species and temporal changes in plant cover. We expected these ecological differences to be mirrored in differences of population demography. The aim of this study was to describe the demography of the striped mouse in the succulent karoo of South Africa.

Material and methods

Study site and period

The study was conducted in Goegap Nature Reserve near Springbok in the Northern Cape Province of South Africa. Vegetation at the field site was dominated by *Zygophyllum retrofractum* shrubs, succulents and different species of ephemerals in spring. The study was performed from September 2001 to January 2002 (spring to middle of summer), 2 weeks in April 2002 (autumn), and from September 2002 to December 2002 (spring to middle of summer). The study area was

80 m × 60 m from September 2001 to November 2001. Trapping data obtained from this area were used to describe the demography of the population. To obtain additional information about group compositions, we enlarged the study area by an additional 60 m × 40 m in December 2001 and further to an area of 200 m × 150 m in September 2002 to include more striped mouse groups. Data obtained in these additional areas are not included in comparisons between trapping sessions.

Trapping and observations

Striped mice were trapped using metal live-traps (26 × 9 × 9 cm³) baited with a mixture of bran flakes, currants, sea salt and salad oil. Two-hundred and thirty five mice (114 males, 121 females) were trapped in 2001, 149 mice (84 males and 65 females) in April 2002, and 234 mice (124 males, 110 females) in September to November 2002.

Whereas it is customary to set traps in a grid formation or line transect during studies in grasslands, this method is inappropriate in the desert habitats, as traps would heat-up quickly. Our study site comprises many regularly spaced bushes, shrubs and other vegetation, which are used by striped mice. These plants were used as trapping stations and traps were placed in the shade under bushes. Trapping was done for 3 h in the morning and 2 h in the afternoon, but not during the hottest times of the day. Traps were checked continuously. Trapping was done until no unmarked individuals were trapped anymore. Trapping sessions lasted 6 days and were performed in the middle of September 2001, end of October 2001, middle of December 2001, end of April 2002, beginning of September 2002, end of October 2002, and November 2002.

Trapped mice were sexed and weighed. Scrotal testes in males and an open vagina and signs of lactation in females were used to establish reproductive activity. Mice were individually marked by writing a number with black hair dye (Inecto Rapid[®]) on the hair of their flanks. Markings faded and were partly unrecognizable between field sessions. As a consequence, we decided to mark mice permanently in 2002 using toe-clipping, the standard method for studies in small mammals (e.g. Wood and Slade 1990; Braude and Ciszek 1998; McGuire et al. 2002). Toe wounds were disinfected with alcohol, and no re-captures had infected wounds. The decision to use toe-clipping was not made lightly. We did not mark animals with transponders because of the high costs of such devices. Also, there is no reported difference in survival probability between toe clipping and

marking with transponders (Braude and Ciszek 1998). We did not consider ear tags since these are known to lead to increased parasite load (Ostfeld et al. 1993) and to be unreliable, as they are often lost (Wood and Slade 1990). We first tried permanent marking by ear punching, but this method proved to be unreliable, as the punch marks either split or had closed. Micro-tattooing (Leclercq and Rozenfeld 2001) did not work because of the dark skin of striped mice, and also ear-tattoos (Lindner and Fuelling 2002) did not lead to reliable identification. Thus, after unsuccessfully trying three less invasive methods, we decided to use toe-clipping.

Previous behavioural observations revealed that striped mice form groups which nest in bushes and defend a home range (Schradin and Pillay 2003, 2004). Home range sizes of seven groups of our study are reported elsewhere (Schradin and Pillay 2004). To calculate population density, we used the number of mice per hectare living in the group territory as the number of mice per hectare. The entire study area comprised group territories (Schradin and Pillay 2004), and no part of the study area was devoid of striped mice. However, as group territories overlap by approximately 13% (Schradin and Pillay 2004), we increased the calculated population density by 13% (because a group home range was used by mice other than only group members). Population density was calculated for September 2001 and December 2001. The number of groups for which data were available was fewer in September ($N = 5$) than in December ($N = 7$), since more groups were identified over time.

To establish survival probability, we counted the number of mice present at nests during different months and used these data to calculate survivorship per group. Nests were previously located by direct observations, and the habit of group members to bask together in front of their nest in the morning and afternoon made it possible to determine group size during different seasons (Schradin and Pillay 2004). By comparing group size shortly after the breeding season (December 2001) with that four months later in the non-breeding season (April) and before the start of the next breeding season (September 2002) we could obtain an approximate measurement of survival.

Statistics and data analyses

Data are presented as mean \pm SE. Non-parametric tests were applied throughout and all comparisons were two-tailed (Siegal and Castellan 1988). The Mann-Whitney U -test is abbreviated as U -test, and the Wilcoxon-matched pairs sign rank test as Wilcoxon test. Analyses were performed using the software Statview and Instat.

Although striped mice can start breeding with a body weight of around 30 g in grasslands (Brooks 1974; David and Jarvis 1985), all breeding individuals in the succulent karoo weighed at least 40 g and individuals below 40 g did not show indications of reproductive activity (Schradin and Pillay 2004). Thus, we regarded individuals as adults when they weighed at least 40 g.

Results

Breeding season

Most adults were in breeding condition during September (91% of adults) and October (74% of adults). The number of mice in breeding condition decreased sharply in December (23% of adults) and no animals were in breeding condition in April (Fig. 1). The ratio of reproductively active to non-active adult individuals differed significantly over months with a significant linear trend towards fewer reproductively active animals from September 2001 to April 2002 ($p < 0.0001$, $\chi^2 = 200.64$, $df = 3$). Eighty per cent of females trapped at the start of September 2002 were pregnant, and no juveniles were trapped during this period (Fig. 2e). Small juveniles (14 individuals all weighing below 20 g and about 3 weeks old; Brooks 1982) were trapped during the middle of September 2001 (Fig. 2a). A high proportion of juveniles with a body mass below 30 g were trapped in October 2001 and 2002 (2001: 64 individuals accounting for 45.4% of all trapped individuals; 2002: 53 individuals representing 37.6% of the population; Fig. 2b and f). Only a few relatively large juveniles were trapped in November 2002 and December 2001 (17 individuals accounting for 10.3% of all trapped individuals in this month, none weighing below 20 g; Fig. 2c), and none were trapped in April 2001.

To establish when the last pups were born, we calculated mean body mass for the six smallest juveniles trapped in December 2001 and November 2002 and estimated their approximate age using published information on pup growth (Brooks 1982). Mean body mass in December 2001 was 25.5 and 26.8 g for the six smallest juvenile males and females, respectively, and we estimated their age at

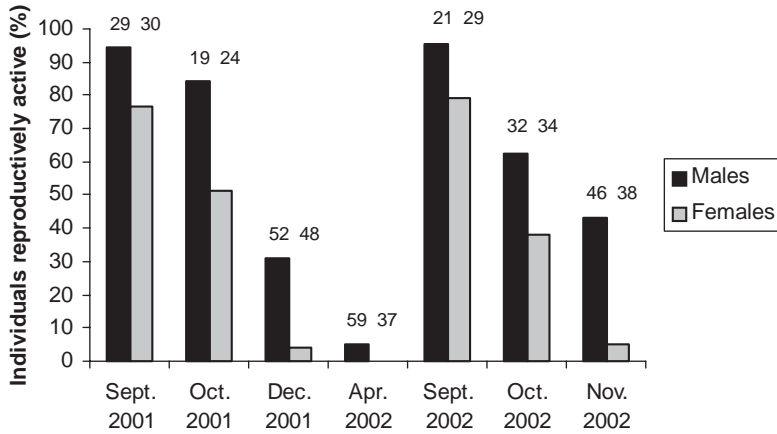


Fig. 1. Percentage adults (mice with a body mass over 40 g) that were potentially reproductively active (i.e. scrotal males and females with an open vagina) during seven different trapping periods. Sample sizes are shown above bars.

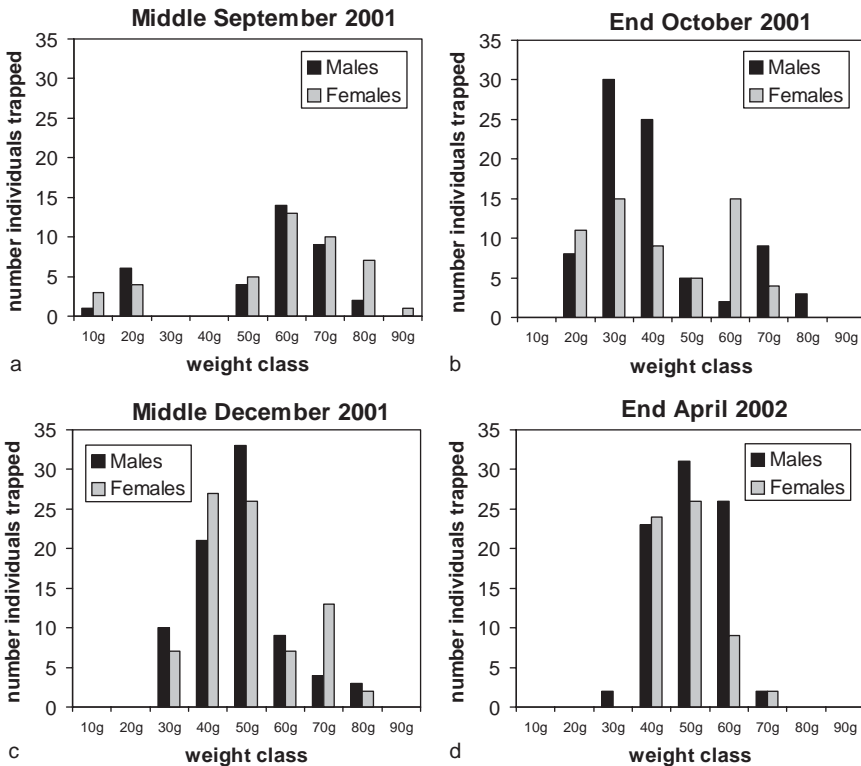


Fig. 2. Striped mice trapped during seven different trapping periods in the original grid of approximately $\frac{1}{2}$ ha. Data are presented in different mass classes of 10 g each (e.g. mass class 40 g includes all animals with a body weight between 30.5 and 40.4 g).

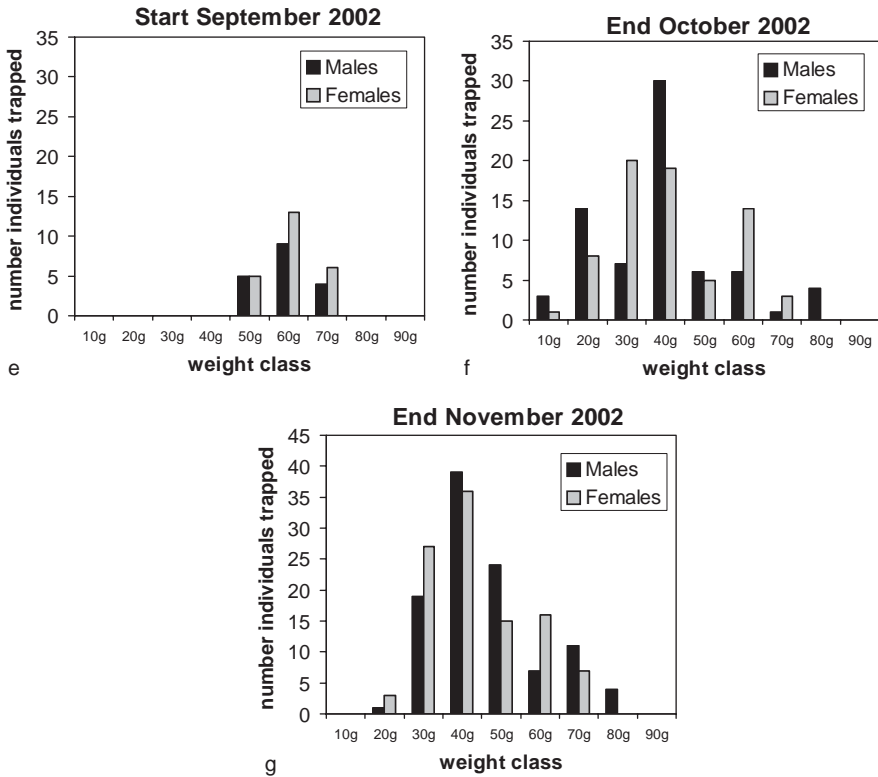


Fig. 2. (Continued)

approximately 4–5 weeks, born in the middle of November. Mean body mass of the six smallest male and female juveniles was 21.45 and 19.4 g, respectively, at the end of November 2002, indicating that they were approximately 4 weeks old and born at the end of October or the beginning of November.

Litter size

Twelve pregnant females were trapped and kept in captivity (these females and their pups were used for other studies in 2001 and 2002; unpubl. data). Litter size was 5.3 ± 2.0 pups (range: 3–9).

Body mass

We compared body mass of adults in different seasons. We controlled for the influence of pregnancy and sexual dimorph-

ism on body mass (see below) by only using males in comparisons. We also controlled for the effect of growth in young males by only considering adult individuals that were already present at the start of the breeding season (September). A paired design (body mass changes of the same individuals) was used to assess changes in body mass. Since striped mice were not marked permanently (toe clipping only in September 2002), comparisons between data collected in April 2002 and September 2002 were made using an unmatched design. Mice did not show significant gains in body mass from September to October 2001 ($p = 0.1$, $T = 11.5$, $N = 11$, Wilcoxon test; Table 1). Of 12 individuals marked in December 2001 and still recognizable in April 2002, 11 lost body weight ($p = 0.001$, $T = 0$, $N = 12$, Wilcoxon test). Individuals lost on average $12.1 \pm 7.6\%$ (range: 0–23.6%) body mass during this

Table 1. Mean \pm SE body mass of adult male striped mice during different months.

	September 2001	October 2001	December 2001	April 2002	September 2002	October 2002	November 2002
Body mass	61.3 \pm 8.0	65.8 \pm 7.4	61.3 \pm 17.1	45.7 \pm 7.7	54.8 \pm 7.4	63.7 \pm 6.4	63.1 \pm 6.0
<i>N</i>	11	11	6	84	23	12	15

period. Mice gained weight from April to September 2002 ($p < 0.0001$, $U = 425.0$, $m = 84$, $n = 23$, U -test), and gained more weight from the beginning of September 2002 to end of October 2002 ($p < 0.003$, $T = 1$, $N = 12$, Wilcoxon test). Body mass did not change from October to November 2002 ($p = 0.24$, $T = 33$, $N = 14$, Wilcoxon test).

Sexual dimorphism

We compared the body mass of male and female striped mice during the non-breeding season in April 2001 to avoid the confounding effects of pregnancy. Males were significantly heavier than females ($p < 0.02$, U -test; males: 45.7 ± 7.7 g, $n = 86$, females: 43.0 ± 7.6 g, $n = 61$).

Population density

Population density at the beginning of September 2001 was highly variable between groups (36.6 ± 21.2 mice ha^{-1} , $N = 5$ groups). Population density was much higher in December 2001 (171.1 ± 40.9 mice ha^{-1} , $N = 7$ groups).

The decrease in group size from January to the end of the summer in April was 27% on average ($N = 6$ groups). From April 2002 to September 2002, group size declined on average by 73% (range: 60–83%, $N = 6$ groups).

Discussion

Before interpreting the demographic patterns of the striped mouse in the arid succulent karoo, South Africa, three issues have to be considered. (1) We trapped at only one site

and conditions may be different in other areas within the succulent karoo. (2) Although the climate in the succulent karoo is very predictable from year-to-year, with only a low variation in the seasonality and quantity of rainfall (Cowling et al. 1999), there is variation between years. (3) Different trapping methods had to be used in the drier areas than in the moist grasslands (see methods), which make comparisons between habitats difficult. These issues notwithstanding, it is important to compare our results with those obtained for striped mice in the grasslands.

Striped mice initiate breeding in August in the succulent karoo, as indicated by the first appearance of juveniles during the middle of September. As juveniles emerge from the nest at approximately 12 days of age and gestation time is approximately 23 days (Brooks 1982), mating must have occurred approximately 35 days earlier, during the first half of August. This is the same as for most populations in other parts of South Africa. However, the breeding season in the succulent karoo terminates at the beginning of November, whereas it lasts until March to April in other parts of the distribution range (Brooks 1974; Perrin 1980a). Earlier cessation of breeding is correlated with differences in the timing of the rainy season. The succulent karoo is a winter rainfall region, whereas most other parts of South Africa receive summer rains. In November, annual herbs which are important food plants for striped mice start drying out (Cowling et al. 1999; pers. obs.).

Females can potentially produce three litters during the 3 month long breeding season (interlitter interval: 23–30 days; Pillay 2000). However, from group sizes at the end of the breeding season, we estimated that females

produced only two litters per season. Mean litter size was 5.3, which is comparable with other populations in southern Africa (Brooks 1982; David and Jarvis 1985; Willan and Meester 1989).

Mice gained mass in spring. In December after the breeding season, mice still had a very high body mass, with breeding males typically exceeding 70 g and sometimes 80 g. Such heavy animals have rarely been reported in other studies. It appears that breeding is not primarily restricted by food. Instead, we suggest that the absence of young protein rich leaves in early summer terminates breeding. In addition, mice store fat in spring and early summer, enabling them to survive the forthcoming hot and dry summer months when food supply is low. This would explain the relatively low (27%) reduction of group size after the breeding season at the end of summer (April compared to December), which is a correlated measurement of mortality rate. However, individuals lost approximately 12% body mass from the beginning to the end of summer, indicating food shortage during summer. Group size decreased remarkably during winter, when the temperatures at night frequently dropped below 0 °C and the rainy season started. Cold and wet weather during winter coupled with the preceding low food abundance are possibly the major contributing factors to the reduction in group size by 73%. Predation might also be important, but the main predators are snakes (pers. obs.) which are inactive in winter.

Although an estimated 73% of striped mice died during the cold winter in the succulent karoo, this mortality rate is lower compared to populations in moist grasslands. Few juveniles in the grasslands live beyond two months of age and the annual survival rate is only 2.3% (Brooks 1974). The relatively higher survival rate in the succulent karoo might be explained by a stable basic food supply and benefits of group living (Schradin 2005). Population density was extraordinarily high (~170 mice ha⁻¹) at the end of the breeding season in the succulent karoo, compared with the population density of between 10 (Perrin et al. 2001; Schradin and Pillay 2005) and 40 mice ha⁻¹ (Perrin et al.

2001) in the moist grasslands of KwaZulu–Natal (South Africa). Other studies in South Africa report 35–93 striped mice ha⁻¹ (highveld grasslands; Brooks 1974) and 30 to > 300 mice ha⁻¹ (Cape Flats; David and Jarvis 1985). The Cape Flats is a semi-arid habitat (rainfall of less than 600 mm year⁻¹) with a Mediterranean climate, comprising sandy soil with *Acacia* trees, shrubs and fynbos vegetation. It falls within the winter rainfall range and its vegetation is more similar to that of the succulent karoo than the grasslands. In the absence of appropriate data, we predict that the social system of the striped mouse in the Cape flats will be more similar to that of striped mice in the succulent karoo than in the grasslands.

In other arid areas, the striped mouse is also reported to be group-living, e.g. in the Kalahari (Nel 1975; Nel and Rautenbach 1975; pers. obs.) and in the Namib (Krug 2002). In both deserts the low abundance of suitable shelter is thought to be one main reason for grouping (Nel 1975; Krug 2002). In the Namib, striped mice live in hammocks of nama plants that offer patchily distributed sources of food and cover. Population density in such hammocks can be extraordinarily high, ranging from 30 to more than 2000 mice ha⁻¹ (but as hammocks are smaller than 1 ha, not more than 30 mice occur in one hammock) and annual survival probability of up to 13% is relatively high (Krug 2002). In sum, high population densities together with limited cover availability are two major factors that determine group-living in striped mice in arid habitats (Schradin 2005).

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Zusammenfassung

Demographie der Striemengrasmaus (*Rhabdomys pumilio*) in der Sukkulentenkaroo

Die Striemengrasmaus (*Rhabdomys pumilio*) ist im südlichen Afrika weit verbreitet und kommt in unterschiedlichen Habitaten vor. In dieser Studie beschreiben wir die Demographie der Striemengrasmaus in der ariden Sukkulentenkaroo Südafrikas, und vergleichen unsere Ergebnisse mit den Ergebnissen früherer Studien, welche dieselbe Art in den feuchten Grasländern Südafrikas untersucht haben. Die Fortpflanzungssaison beginnt in beiden Habitaten im Frühling, aber sie ist in der Sukkulentenkaroo nur halb so lange wie in den Grasländern. Der Grund dafür wird im unterschiedlichen Niederschlagsmuster vermutet: In der Sukkulentenkaroo regnet es wenig im Winter (ca. 160 mm), während es in den Grasländern viel im Sommer regnet (>1000 mm). Die Überlebensrate in der Sukkulentenkaroo war vom Sommer zur nächsten Fortpflanzungssaison im Frühjahr mit 27% außerordentlich hoch, während die Populationsdichte zehnmal so groß war wie in den Grasländern. Am Anfang der Fortpflanzungssaison betrug die Populationsdichte 37 Mäuse ha⁻¹, am Ende der Fortpflanzungssaison 171 Mäuse ha⁻¹. Die außergewöhnlich hohe Populationsdichte führt womöglich zu Habitatsättigung und einem Fehlen freier Territorien, was mit erklären könnte, warum die Striemengrasmaus in der Sukkulentenkaroo gruppenlebend ist, in den Grasländern hingegen solitär.

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