



Female home range size is regulated by resource distribution and intraspecific competition: a long-term field study

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The size of an individual's home range is an important feature, influencing reproduction and survival, but it can vary considerably among both populations and individuals. The factors accounting for such variation are still poorly understood, and comprehensive long-term field studies considering various environmental factors that influence home range size are rare. We investigated the effects of seasonality, availability of food, cover, number of direct neighbours and the relative individual body mass on home range sizes in 125 adult female striped mice, *Rhabdomys pumilio*, in South Africa from 2004 to 2008. We used radiotelemetry to estimate home range sizes, trapping to determine the number of direct neighbours, and plant surveys in every home range to determine availability of food and cover. Home ranges were smaller when food quantity was high, many territorial neighbours were present, females had a relatively small body mass and during the nonbreeding season. We conclude that the availability of food resources and intraspecific competition are the main factors influencing home range size in female striped mice. Females enlarged their home ranges when territorial neighbours were few, and there was a significant positive correlation between home range size and quantity of food plants. This indicates that home range size might not reflect the minimal trade-off between access to resources that allow for a female's survival and lowest cost for defending and foraging in that area. Instead, we propose a hypothesis for future research that female striped mice occupy areas several times larger than needed to improve their fitness by providing resources for future offspring.

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An important factor influencing survival and reproductive success is the size of an individual's home range. A home range is defined as the area that an animal traverses during activities associated with food gathering, resting and social behaviours (Burt 1943). Consequently, a home range contains critical resources that determine an individual's fitness. Theoretically, animals are expected to occupy the smallest possible areas within which they can acquire sufficient food for reproduction and survival, and to minimize time and energy spent for territory defence and foraging

(Maynard Smith 1974). Practically, the factors that regulate home range size are still poorly understood.

Several studies have revealed large variation in home range size between individuals of the same population. Intraspecific variation in home range size may be caused by many different factors, such as sex (e.g. Mikesic & Drickamer 1992; Asher et al. 2004; Begg et al. 2005), age (Mikesic & Drickamer 1992), reproductive effort (Tufto et al. 1996; Saïd et al. 2005), availability of nesting sites and cover (Tufto et al. 1996; Getz et al. 2005; Hayes et al. 2007) and food availability (Taitt & Krebs 1981; Ims 1987; Tufto et al. 1996; Jonsson et al. 2002; Saïd et al. 2005).

Intraspecifically, home range size differs seasonally (Lovallo & Anderson 1996; Bixler & Gittleman 2000; Lurz et al. 2000; Kjellerland et al. 2004; Do Linh San et al. 2007; but see Rodrigues & Monteiro-Filho 2000 for no effect). Explanations for the seasonal variation in home range size include seasonal changes in reproductive activity, population density or food availability. In fact, several correlative studies on different species indicate that home

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range size decreases with increasing food availability (Tufto et al. 1996; Lurz et al. 2000; Saïd et al. 2005; Rödel & Stubbe 2006). Furthermore, experimental provisioning of supplemental food resulted in decreases in home range size (Taitt 1981; Taitt & Krebs 1981; Ims 1987; Boutin 1990; Hubbs & Boonstra 1998; Jonsson et al. 2002; but see Broughton & Dickman 1991). However, in areas with a surplus of food, higher rates of immigration can cause an increase in population density (Taitt 1981; Taitt & Krebs 1981; Perrin & Johnson 1999), leading to an increase in competition for limited resources (Hixon 1980). Thus, it is important to consider both food availability and population density and to control statistically how these two factors influence each other and home range size.

Population density influences competition for food resources (Ostfeld & Canham 1995) and is thus inversely correlated with home range size (Ostfeld 1986; Erlinge et al. 1990; Priotto et al. 2002). On an individual level, such density effects might be predominantly caused by interactions with neighbouring conspecifics. For example, animals have been observed to expand their home ranges when neighbours were experimentally removed (Norman & Jones 1984; Boutin & Schweiger 1988) or disappeared (Fitzgerald et al. 1981; Lovallo & Anderson 1995; Baker et al. 2000). The influence of territorial interactions with neighbours often depends on the sex (Baker & Dietz 1996; Lazaro-Perea 2001; Gray et al. 2002; Schradin 2004) and the relative body mass of the neighbours (Schradin 2004). Therefore, it seems important to consider not only the effect of population density, but especially the number and body mass of neighbours.

In sum, various factors are likely to contribute in determining home range sizes. However, in most studies, only a single or a few factors have been studied to explain intraspecific variation in home range sizes (see references above), but single factors alone cannot explain the high variability in home range sizes. Thus, field studies simultaneously investigating different biotic and abiotic factors are needed, which require a large sample size for high statistical power. In the present study, we investigated the influence of a variety of factors on the home range size of 125 female striped mice, *Rhabdomys pumilio*, collected over 5 years and during different seasons, and under varying ecological conditions. We focused on females since territoriality in female mammals is related to the distribution, abundance and renewal rate of critical resources, whereas territoriality in male mammals is influenced by the distribution of females (Ostfeld 1990). The overall aim of our study was to document the extent to which the five most often cited variables influence home range size in female striped mice. We tested the following predictions.

(1) Season: female home ranges are smaller in the hot, dry nonbreeding season than in the breeding season. Even though food is less abundant during the nonbreeding season (Schradin & Pillay 2006), individuals might show reduced activity to save energy, compared with greater energy requirements during the breeding season (Bozinovic et al. 2004).

(2) Cover: females with a home range offering little cover have larger home ranges. Small mammals need cover as protection against predators, and striped mice might not be able to forage regularly in open parts of the home range (Getz et al. 2005; Hayes et al. 2007; Keller & Schradin 2008).

(3) Food: we differentiated between the quantity and quality of food in home ranges (total number of food plants versus food plants/ha). We predicted that female home ranges of low quality (with a low percentage of food plants) are larger than home ranges of high quality. According to Harestad & Bunnell (1979), the main function of a home range is to provide sufficient food to meet an individual's energy requirements. If this is true, we expect the quantity of resources (absolute number of resource items) to be similar over all home ranges.

(4) Number of direct neighbours: we expected home range size to decrease with increasing number of neighbours, since the number of neighbours should be an accurate measure of the spatial constraints of territoriality (Schradin 2004).

(5) Body mass: females that are larger have larger home ranges than smaller females of the same population. Body mass influences home range size interspecifically (McNab 1963; Harestad & Bunnell 1979; Kelt & Van Vuren 1999), and may also influence home range size within species, as larger striped mice are more competitive and win more territorial encounters (Schradin 2004).

METHODS

Study Area and Period

The study was conducted from May 2004 to February 2008 in the Goegap Nature Reserve in South Africa (29°41.56'S, 18°1.60'E). The vegetation type is Succulent Karoo (Cowling et al. 1999). The area is arid, with an average rainfall of 160 mm per annum which occurs mainly during winter (May to August) followed by spring (September to November) and a dry season from December to April (Cowling et al. 1999). The field site of 7.2 ± 3.4 ha was characterized by a dry riverbed and sandy areas with patchily distributed shrubs.

The study was approved by the animal's ethics committee of the University of the Witwatersrand.

Study Species

The striped mouse is a diurnal muroid rodent with an adult body mass of 30–80 g (Schradin & Pillay 2005b). It is widely distributed throughout southern Africa. In the Succulent Karoo, the striped mouse typically lives in groups consisting of one breeding male, up to four breeding females and their philopatric, adult offspring of both sexes (Schradin & Pillay 2004). However, if population density is low, striped mice can also live solitarily at the start of the breeding season (Schradin et al., in press). After the breeding season, striped mice are always group living (Schradin et al., in press), with groups consisting of up to 30 adults (Schradin & Pillay 2004). Females typically breed in their natal group or establish a new territory in adjacent areas in the next breeding season following their birth. Striped mice usually do not survive for a second breeding season. Individuals interact amicably within the group but respond aggressively towards members of other groups (Schradin 2004). Individual home ranges overlap greatly among group members, but less with the home ranges of mice from adjacent groups (Schradin & Pillay 2004, 2005a).

Striped mice feed mainly on plant materials such as stems, leaves, flowers and seeds (Schradin 2006a; Schradin & Pillay 2006). The breeding season (August to November) coincides with the occurrence of highly nutritious ephemerals in spring (Schradin & Pillay 2005b) and is followed by a long hot dry season with reduced food availability, when striped mice lose 12% on average of their body mass (Schradin & Pillay 2005b).

Trapping and Observation of Animals

Striped mice were live-trapped using metal (26 × 9 cm and 9 cm high) or plastic (29.5 × 8 cm and 6.5 cm high) traps baited with a mixture of bran flakes, currants, sea salt and salad oil. Traps were placed in the shade under shrubs which were identified as nesting sites by radiotracking (see below). Trapping was done in the early morning (starting at sunrise) and late afternoon (ending with sunset), but not during the hottest time of the day. Traps were checked 60 min after they were set. Trapped individuals were weighed and their sex

and reproductive status were determined. All mice were permanently marked using ear tags (7 mm long and 0.17 g in mass; National Band and Tag Co., Newport, KY, U.S.A.), and temporarily using hair dye for individual recognition during field observations.

Focal groups (8 in 2004, 9 in 2005, 10 in 2006, 20 in 2007 and 13 in 2008) were observed regularly and at least one female of each group was always equipped with a radiocollar. Additional nonfocal groups lived at the edge of the field site and their exact nesting sites were unknown. However, traps were placed at several different shrubs, which had been used as nesting sites in previous years when these areas were part of the study site. We determined the number of neighbours for each focal group by counting all adult individuals from all neighbouring groups (focal and nonfocal groups).

Striped mice occupying the same nest were regarded as belonging to one group. Focal groups were observed for 30–45 min in front of their nest (distance 5–10 m) during early mornings and late afternoons several times per month to determine group composition (Schradin & Pillay 2004). Each group was observed for 2 days at least every second week.

Determination of Home Range Size

Radiotracking was performed using Holohil transmitters (BD2C, mass 2 g; and PD2C, mass 3.3 g, always below 10% of body mass, normally below 5% of body mass; Carp, Ontario, Canada), as described elsewhere (Schradin & Pillay 2006). Radiotransmitters do not influence stress hormone levels of striped mice (Schradin 2008b) and were removed after 1–3 months. Mice were anaesthetized for 2 min with ether when radiocollars were fitted or removed, and thereafter released at their nest after they had fully recovered from anaesthesia. In a few cases (approximately 2%) the radiocollar irritated the skin of trapped individuals and was then removed.

Females were radiotracked for 9 days, and we took six fixes per day approximately every 2 h. This was sufficient for achieving a saturation curve of a home range size (Schradin & Pillay 2005a) and to allow striped mice to visit their entire territory between fixes (Schradin 2006b). A radiotagged mouse was approached until either the individual could be seen (approximately 25% of fixes) or until the shrub it was hiding in was determined (homing-in method, White & Garrot 1990). The position of the focal female was recorded to within an accuracy of 5 m using a GPS (eTrex Venture, GARMIN International, Olathe, KS, U.S.A.). In addition, females were radiotracked at night to determine their nesting sites.

We determined 143 home ranges for 125 females. For 18 females, home ranges were determined both during the breeding and dry nonbreeding season. A total of 87 females were radiotracked during the breeding season and 56 females were radiotracked during the dry nonbreeding season (Fig. 1). In 2005, home ranges were determined for the dry nonbreeding season, but were not included in the present study owing to unexpectedly high rainfall resulting in rapid plant growth, such that plant surveys (see below) would not have been indicative of the previous field conditions when home range data were collected (Schradin & Pillay 2006).

Home range sizes were calculated as 100% minimum convex polygons (100 MCP) using the software Ranges 6 (Anatrack Ltd, Wareham, U.K.). For plant surveys, 100 MCP was the most practical method to plot home ranges in the field, which would not have been possible using kernel estimates, which we also report for comparison. To exclude potential outliers, we calculated 95% kernel contours in Ranges 6.

Plant Surveys

The 100 MCP home ranges were marked in the field with iron rods and barrier tape. A 2 × 2 m grid was placed over each home

range using a 30 m measuring tape. At each 2 m point, we recorded the presence or absence of vegetation, the plant species (88% of all counts) or plant genus (97% of all counts), whether a plant was green or dead, and whether the point offered cover for striped mice. Cover included many nonfood plants as well as dead plants, while some food plants, especially seedlings and wildflowers, did not offer cover. When a plant species could not be identified (3% of counts), it was defined as 'unknown'. Each plant species was categorized according to its seasonal appearance (annual or perennial) and palatability, which was known from behavioural observations in the field (see Schradin & Pillay 2006).

Statistical Analysis

Data are presented as mean ± SD. We first tested for the effects of different predictor variables on female home range size (response variable) using linear mixed models (LMM; Pinheiro & Bates 2000). Home range size was log transformed prior to analyses owing to its right-skewed distribution. We verified the normal distribution of the model residuals visually by checking normal probability plots and with the Shapiro–Wilk test, and we verified the homogeneity of variances and goodness of fit by plotting residuals versus fitted values. Statistical analyses were carried out with R version 2.8.0 (R Development Core Team 2008); mixed-effects models were fitted with the package lme4 (0.999375–28; Bates 2005). We calculated *P* values of linear mixed-effects models using likelihood ratio tests based on changes in deviance when each term was dropped from the model (Faraway 2006). We used maximum likelihood estimates for the calculation of likelihood ratio tests and also for Akaike's information criterion (AIC) values.

For the analysis of the factors affecting female home range size, we used an information theory-based approach for model selection. Such an approach is considered to be more appropriate than stepwise model selection approaches based on *P* statistics (see Burnham & Anderson 2002). We constructed a set of candidate models, where we considered combinations of the predictor variables. Model selection was based on AIC (Burnham & Anderson 2002) to identify the most parsimonious model, that is, the model that represents the data adequately with the smallest possible number of parameters. Models were ordered from 'best' (lowest AIC) to 'worst' (highest AIC). We used the second-order AIC, the AICc, which includes a correction term for small sample sizes (Hurvich & Tsai 1989). We report AIC differences ($\Delta\text{AICc} = \text{AICc}_i - \text{minAICc}$) to compare the support generated by the different models for being the best approximation model in the candidate set. Models with $\Delta\text{AICc} \leq 2$ can be considered to have substantial support (Burnham & Anderson 2002). We also calculated normalized Akaike weights (w_i) for each model, which can be regarded as a measure of the evidence in favour of model *i* as being the actual best model of the set (Burnham & Anderson 2002). Since we obtained several models which were all well supported by the data (see Table 1), we used model averaging for calculating the predicted values. For this, we computed parameter estimates averaged over all models of the set and weighed them by the Akaike weights of each model (see details in Burnham & Anderson 2002).

In the models, we entered season (breeding versus dry nonbreeding season) as a factor and the covariates included the number of direct neighbours and the relative body mass of each female, measured as the % deviation to the average body mass of all females in the same year and season. We included the relative abundance (% of all counts done every 2 m) of annual and perennial food plants to test for the influence of resource quality on home range size. Annual plants, which mainly grow in spring, are a high-protein resource for striped mice, determining the length of the breeding season (Perrin 1980; Nel 2003; Schradin & Pillay 2006).

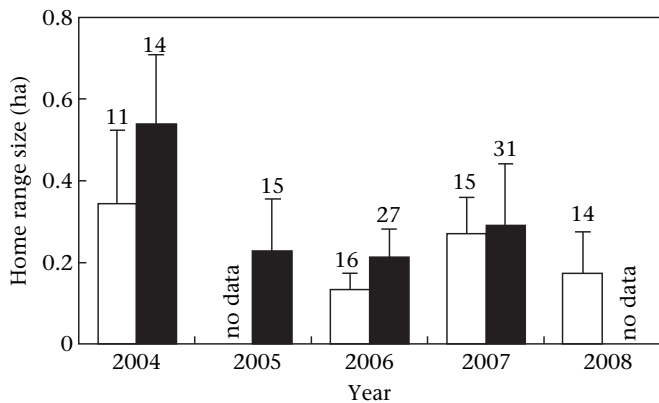


Figure 1. Home range sizes (mean + SD) of female striped mice between 2004 and 2008 during the dry nonbreeding season (white bars) and during the breeding season (black bars). Independent sample sizes are given above bars.

Perennial food plants are available throughout the year. We also included cover as a variable, which correlated significantly but not strongly with the percentage of annual food plants ($r = -0.25$, $P = 0.003$) but not with perennial food plants ($r = 0.19$, $P = 0.02$, $P > 0.05$ after Bonferroni correction). Group identity was included as a random factor, because different females belonged to the same social group. We included female identity as a random factor, because 18 females were radiotracked during both seasons. We considered two-way interactions of body mass with the number of neighbours and with season, because we hypothesized that the effects of body mass (as a measure of body condition) on home range size would vary under different environmental conditions and might differentially influence home range size during the breeding and dry nonbreeding season. To avoid an excessively high number of candidate models, we did not consider other interactions (see Burnham & Anderson 2002). Overall, this resulted in a total number of 104 models included in the set. Note that we also included the 'null model', that is, the model only describing female home range size by a constant value.

For the comparison of the effect sizes of the different explanatory variables, we calculated the ranges in home range size predicted by the parameter estimates obtained by model averaging ($\Delta\hat{H}$) and averaged these data for both seasons. For this, the effects

Table 1
Set of models explaining home range size (H) of female African striped mice

Model term	K	ΔAICc_i	w_i
$H(c+s+pa+pp+n+b)^*$	10	0	0.241
$H(c+s+pa+n+b)$	9	0.52	0.185
$H(c+s+pa+pp+(n \times b))$	11	0.68	0.171
$H(c+s+pa+(n \times b))$	10	1.44	0.117
$H(c+pa+pp+n+(s \times b))$	11	1.81	0.098
$H(c+pa+n+(s \times b))$	10	2.36	0.074
$H(c+pa+pp+(s \times b)+(n \times b))$	12	2.64	0.064
$H(c+pa+(s \times b)+(n \times b))$	11	3.42	0.044

$N = 125$ females with $N = 143$ home ranges. We modelled home range size by season (s , fixed factor with two levels), percentage of cover (c), percentage of annual (pa) and perennial (pp) food plants, number of neighbours (n) and relative female body mass (relative to the average female body mass per group, b). For calculation, we used linear mixed models. The individual identity (because of repeated measurements in different seasons) and group identity were included as random factors in all models. ΔAICc , Akaike weights (w) and the number of estimable parameters (K) are given for each model i . The models are ordered by ΔAICc . Only models with $\Delta\text{AICc} < 4$ are given; the total number of models of the set was 104. Interaction terms indicate that the interactions as well as the main effects of the respective predictor variables were tested.

* Top model of the set.

of the appropriate other significant predictor variables of the model were set constant at their means. We calculated Nagelkerke's Pseudo R^2 (Nagelkerke 1991) to assess the explained variance of the top model of each set. Partial Nagelkerke's R^2 were also calculated for each explanatory variable of the model by dropping the respective variable out of the model and calculating the changes in R^2 .

We also tested for correlations between individual home range size and the absolute amount of food available in each home range. Again, we used linear mixed models, with individual and group identity as random factors.

RESULTS

Variation in Home Range Size

Home range estimates using MCP correlated significantly with estimates using kernel contours ($r_{142} = 0.93$, $P < 0.001$). As expected, 95% kernel contour estimates were smaller than 100% MCP (0.22 ± 0.17 ha versus 0.26 ± 0.16 ha; paired $t_{142} = 8.76$, $P < 0.001$).

Variation was large (Fig. 1), with the largest home range of 0.86 ha being 14 times larger than the smallest home range of 0.06 ha using MCP. The 10 largest home ranges were 0.69 ± 0.10 ha and the 10 smallest home ranges 0.08 ± 0.10 ha, a nine-fold difference (MCP). For kernel contours the variation was even larger, with the largest home range of 0.92 ha being 46 times larger than the smallest home range of 0.02 ha. The 10 largest home ranges were 0.60 ± 0.10 ha and the 10 smallest home ranges 0.05 ± 0.01 ha, a 14-fold difference.

Factors Affecting Female Home Range Size

Model selection

The most parsimonious model which best explained female home range sizes (called 'top model') included the additive combination of cover, season, the percentage of annual and of perennial food plants, the number of neighbours and the relative body mass of the focal female (Table 1). This model explained $R^2_{\text{Nagelkerke}} = 54.4\%$ of the variance in home range size. There were, however, several competing models which also found good support by the data, as indicated by their low AIC score ($\Delta\text{AICc} < 2$). In particular, the lower parameterized model (with $K = 9$) excluding the predictor variable 'percentage of perennial food plants' might be important to consider.

Home ranges of female striped mice were comparatively smaller during the dry nonbreeding season than during the breeding season (Fig. 1). Owing to the high number of models with good support for the data, we computed parameter values averaged over all models of the set which we weighted by the Akaike weights (w_i , see Table 1). These parameter estimates obtained by model averaging predict that female home range size decreases with increasing percentage of annuals (Fig. 2b), cover (Fig. 2c), the number of neighbours (Fig. 2d), with decreasing body mass of females (Fig. 2e), and with increasing percentage of perennial food plants (Fig. 2a).

Explained variation and effect sizes

The effect of, and the proportion of variance explained by, the percentage of annual plants ($\Delta\hat{H} = 0.20$ ha, $R^2_{\text{partial}} = 0.23$) were comparatively stronger than those of cover ($\Delta\hat{H} = 0.13$ ha, $R^2_{\text{partial}} = 0.08$), female body mass ($\Delta\hat{H} = 0.11$ ha, $R^2_{\text{partial}} = 0.05$), season ($\Delta\hat{H} = 0.09$ ha, $R^2_{\text{partial}} = 0.09$), number of neighbours ($\Delta\hat{H} = 0.09$ ha, $R^2_{\text{partial}} = 0.07$) and percentage of perennial food plants ($\Delta\hat{H} = 0.06$ ha, $R^2_{\text{partial}} = 0.01$).

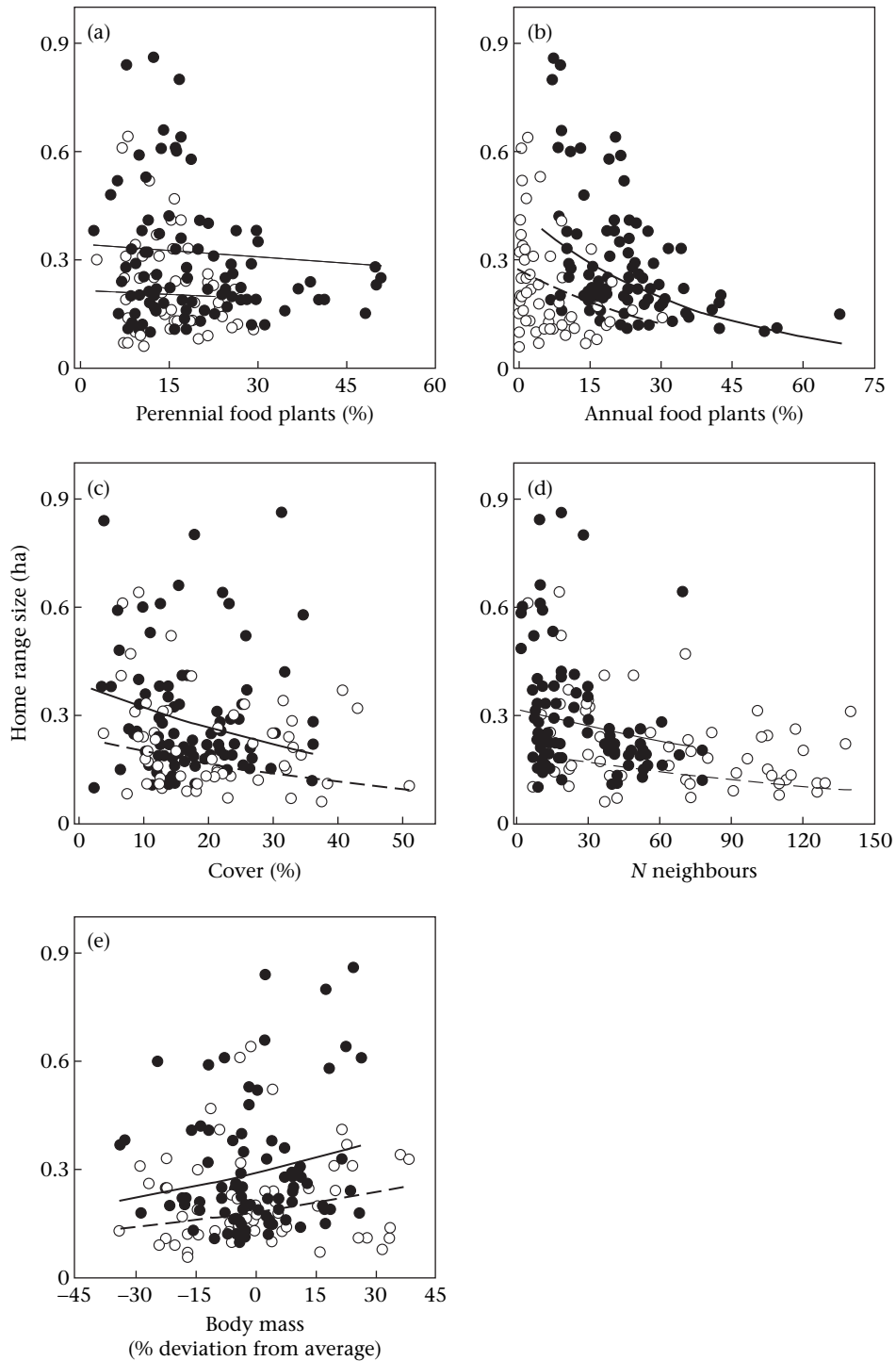


Figure 2. Model graphs for the partial effects of the predictor variables explaining home range size in female African striped mice, according to the average, weighted parameter estimates of the models of the set (see Table 1) as obtained by model averaging (Burnham & Anderson 2002). Data from the breeding season are shown as black circles, model predictions as solid lines; data from the dry nonbreeding season are given as white circles, model predictions are given as dashed lines. For the calculation of the predicted values for each explanatory variable, the appropriate variable was varied within the observed range of the data while the others were set constant at their means. Note that parameters were retransformed for the calculation of the model graph.

Correlations between Home Range Size and Food Availability

Females with larger home ranges had a greater quantity of annual ($\chi^2_1 = 9.48$, $P = 0.002$) and perennial food plants ($\chi^2_1 = 34.55$, $P < 0.001$) in their home ranges. However, their home ranges were of lower quality, because of a lower percentage of

perennial food plants (Fig. 2, statistics provided above). Thus, despite the fact that more food plants (quantity) were growing in larger territories, fewer food plants were available per ha (quality).

During the breeding season, larger home ranges ($N = 87$) tended to have more annuals, although not significantly so ($\chi^2_1 = 3.43$, $P = 0.064$), but a lower percentage of the area was covered with

annuals ($\chi^2_1 = 38.82$, $P < 0.001$). Larger home ranges also contained significantly more perennial food plants ($\chi^2_1 = 7.70$, $P = 0.006$) but had a lower percentage of perennial food plants ($\chi^2_1 = 4.41$, $P = 0.036$).

During the dry nonbreeding season, when annuals were rare, larger home ranges ($N = 56$) did not provide more annuals ($\chi^2_1 = 0.01$, $P = 0.92$), but the percentage of annuals was still lower than in smaller home ranges ($\chi^2_1 = 6.31$, $P = 0.012$). However, females with larger home ranges had significantly more perennial food plants ($\chi^2_1 = 11.50$, $P < 0.001$), and the percentage of perennial food plants in their home range was lower than in smaller home ranges ($\chi^2_1 = 4.44$, $P = 0.035$).

DISCUSSION

Most studies on intraspecific home range size variation have investigated only a single or a few factors. However, as many variables might contribute to shaping the variation of home range size in a rather complex pattern (Fig. 3), a single-factor approach is problematic. The best way to understand the processes underlying behavioural phenomena is by taking several proximate mechanisms into account. In this study, we demonstrated that seasonality, availability of food resources, cover, the number of direct neighbours and the relative individual body mass influenced home range

size of female striped mice, which varied greatly between individuals, with the largest home ranges being 14 times larger than the smallest ones.

In several rodent species, individuals have smaller home ranges at high population densities than at low population densities (Erlinge et al. 1990; Koskela et al. 1999; Priotto et al. 2002). However, mean population density may not always be a good estimate of the number of territorial neighbours an individual encounters. Our results revealed that the habitat was not homogeneous and that the number of neighbours differed for individual females during the same year and season. Neighbours compete with each other, for example for access to food, but can also commit infanticide (Boonstra 1978; Hoogland 1985; Rödel et al. 2008). Infanticide is regarded as one main reason for females of small mammals being territorial (Wolff 1993), and has also been observed in the striped mouse (field: Schradin & Pillay 2003; captivity: Schradin et al. 2009). Our study indicates that home ranges might be compressed below their optimal size by pressure from neighbours (Maynard Smith 1974; Hixon 1980; Patterson 1985). This is supported by our result that heavier females with a better competitive ability (Schradin 2004) had larger home ranges. Thus, low territorial restriction, owing to fewer larger neighbours, might have enabled female striped mice to occupy larger home ranges.

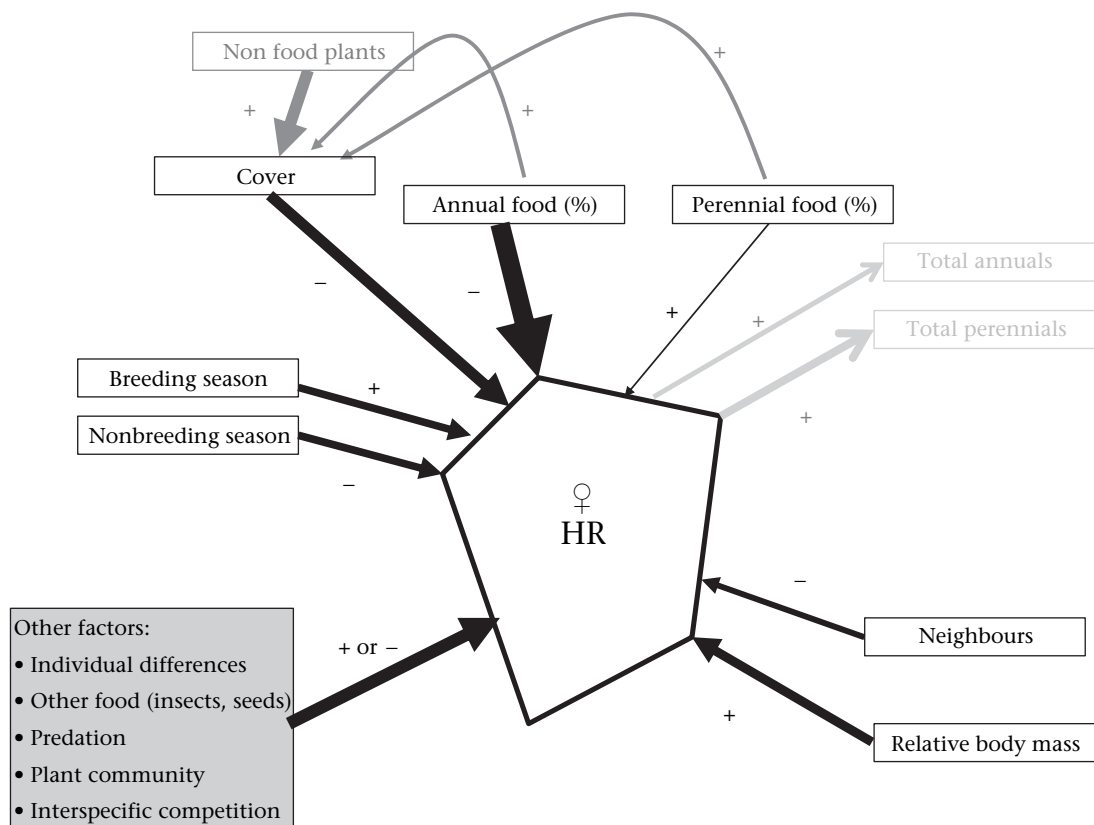


Figure 3. Female striped mice had smaller home ranges ('HR') during the dry nonbreeding season while they increased their home ranges during the breeding season when energetic demands are high. In particular, the access to protein-rich annual food plants was important during the breeding season, and females with better quality territories (with a higher percentage of protein-rich annual and perennial food plants) had smaller home ranges. Higher abundance of annual and perennial food plants led to increased cover availability, which was also influenced by non food plants. Home ranges that offered less cover were larger, probably because noncovered parts of these home ranges could not be used. Females with more neighbours had smaller home ranges, possibly because of territorial encounters. Females that were relatively larger (compared to the population mean) also had larger home ranges, probably because of their greater competitive ability in territorial encounters. Season, cover, abundance of food plants, the total number of neighbours and relative body mass explained 54.4% of the variance, implying that other factors not included in this study must explain the rest of the observed variation (grey box; bottom left). Home range size itself also had important consequences, especially since larger home ranges contained more food resources. Thickness of arrows represents an estimate of the strength of a relationship based on the probability values calculated in this study. Font/arrow colour: black: direct relationship with home range size; dark grey: factors influencing/being influenced by variables explaining home range size; light grey: variables influenced by home range size.

The negative correlation between female home range size and the number of neighbours indicates that female striped mice occupied larger home ranges when undefended areas were available. Females might need larger home ranges in years of low population density, but low population density did not indicate low food abundance. For example, during the 2006 breeding season, population density was high and home ranges were small (22.0 mice/ha and home ranges of 0.2 ha) while in 2007 population density was low and home ranges were larger (7.5 mice/ha and home ranges of 0.3 ha). Nevertheless, food abundance was much greater during the year when home ranges were larger (313 annuals/ha in 2007 compared to 265 annuals/ha in 2006). We propose that future studies consider the hypothesis that females monopolize additional territory to provide additional resources for their offspring. Offspring of both sexes typically remain philopatric in the natal group for several months (Schradin & Pillay 2004). In the dry season following the breeding season, when group sizes are at their maximum (Schradin & Pillay 2005b), food availability reaches its minimum, such that striped mice are food restricted and lose considerable body mass (Schradin & Pillay 2005b). Thus, defending extra resources might improve fitness because of the advantages gained by the offspring during the dry nonbreeding season. This hypothesis could be tested by studying the influence of home range size on female fitness, especially whether females with larger home ranges during the breeding season have more offspring that survive until the subsequent breeding season.

Several previous correlative studies have supported the idea that home ranges function to provide sufficient food resources (Tufto et al. 1996; Lurz et al. 2000; Saïd et al. 2005) and this has been shown experimentally in bank voles, *Clethrionomys glareolus* (Jonsson et al. 2002). In agreement with this, in our study, smaller home ranges contained a greater percentage of food plants and especially a greater relative abundance of annuals. Annuals are short-lived, protein-rich plants, which are thought to be a critical resource for breeding in striped mice (Schradin & Pillay 2006). Spatial distribution of small mammals is often associated with dense cover (Asher et al. 2004; Hayes et al. 2007), probably because predation risk influences foraging activity (Kotler 1984; Anderson 1986; Brown et al. 1988). We found that home ranges with little cover were larger, possibly because striped mice avoided areas without cover for foraging. During the breeding season, striped mice shift their home ranges from the evergreen shrub belt around the dry riverbed into sandy areas with a high abundance of protein-rich annual plants (Schradin & Pillay 2006). During the dry season in summer, however, these sandy areas are of little use to striped mice, as the annuals dry up, resulting in these sandy areas containing barely any food plants and cover.

A reduction of home range sizes in females of small mammals during the dry nonbreeding season, when food is less abundant, is typically explained by reduced reproductive activity and greater population density (Salvioni & Lidicker 1995; Priotto et al. 2002; Endries & Adler 2005) compared to the high costs of pregnancy and lactation during the breeding season (Degen et al. 2002; Kam et al. 2003; Liu et al. 2003). As in degus, *Octodon degus* (Bozinovic et al. 2004), female striped mice might save energy during the hot, dry summer by reducing distances travelled and overall activity levels, leading to smaller home ranges. In support of this, metabolic hormones such as testosterone, glucocorticoids and prolactin are reduced during the dry nonbreeding season, indicating reduced physiological energy expenditure (Schradin 2008a, b).

We stated up-front that high intraspecific variability in home range sizes is poorly understood. This is because most of the previous studies used smaller sample sizes and considered fewer factors, often only one. Using a long-term data set with a large

sample size, we were able to test different hypotheses simultaneously, taking into account how different factors influence and interact with each other to shape female home range size (Fig. 3). Our study explained 54% of the variation in female home range sizes, more than in any previous study we know about. Nevertheless, significant unexplained variation remained. This might be because of individual differences between female striped mice (e.g. in boldness/shyness, or explorative behaviours; Bell 2007; Réale et al. 2007), which are well developed in this species (C.H. Yuen & C. Schradin, unpublished data). Furthermore, predation pressure and the composition of the plant community can differ over a relatively small spatial scale (100 m) in our study area (Keller & Schradin 2008). In addition, variation in interspecific competition, for example by much larger bush Karoo rats, *Otomys unisulcatus* (Schradin 2005) whose population density varies between years, might be another factor accounting for the unexplained variation in our model. Thus, the understanding of how different biotic and abiotic factors may interact in shaping a female's home range remains an important and challenging field of research.

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References

- Anderson, P. K. 1986. Foraging range in mice and voles: the role of risk. *Canadian Journal of Zoology*, **64**, 2645–2653.
- Asher, M., Oliveira, S. E. & Sachser, N. 2004. Social system and spatial organization of wild guinea pigs (*Cavia aperea*) in a natural low density population. *Journal of Mammalogy*, **85**, 788–796.
- Baker, A. J. & Dietz, J. M. 1996. Immigration in wild groups of golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology*, **38**, 47–56.
- Baker, P. J., Funk, S. M., Harris, S. & White, P. C. L. 2000. Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour*, **59**, 127–146.
- Bates, D. 2005. Fitting linear mixed models in R. *R News*, **5**, 27–30.
- Begg, C. M., Begg, K. S., Du Toit, J. T. & Mills, M. G. L. 2005. Spatial organization of the honey badger *Mellivora capensis* in the southern Kalahari: home-range size and movement patterns. *Journal of Zoology*, **265**, 23–35.
- Bell, A. M. 2007. Animal personalities. *Nature*, **447**, 539–540.
- Bixler, A. & Gittleman, J. L. 2000. Variation in home range and use of habitat in the striped skunk (*Mephitis mephitis*). *Journal of Zoology*, **251**, 525–533.
- Boonstra, R. 1978. Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. *Ecology*, **59**, 242–248.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, **68**, 203–220.
- Boutin, S. & Schweiger, S. 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. *Canadian Journal of Zoology*, **66**, 2270–2274.
- Bozinovic, F. L., Bacigalupe, D., Vásquez, R. A., Visser, G. H., Veloso, C. & Kenagy, G. J. 2004. Cost of living in free-ranging degus (*Octodon degus*): seasonal dynamics of energy expenditure. *Comparative Biochemistry and Physiology A*, **137**, 597–604.
- Broughton, S. K. & Dickman, C. R. 1991. The effect of supplementary food on home range of the southern brown bandicoot, *Isoodon obesulus* (Marsupialia: Peramelidae). *Australian Journal of Ecology*, **16**, 71–78.

- Brown, J. S., Kotler, B. P., Smith, R. J. & Wirtz, W. O. 1988. The effects of owl predation on the foraging behaviour of heteromyid rodents. *Oecologia*, **76**, 408–415.
- Burnham, K. P. & Anderson, D. R. 2002. *Model Selection and Multimodel Inference. A Practical Information-theoretical Approach*. Berlin: Springer.
- Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346–352.
- Cowling, R. M., Esler, K. J. & Rundel, P. W. 1999. Namaqualand, South Africa: an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*, **142**, 3–21.
- Degen, A. A., Khokhlova, I. S., Kam, M. & Snider, I. 2002. Energy requirements during reproduction in female common spiny mice (*Acomys cahirinus*). *Journal of Mammalogy*, **83**, 645–651.
- Do Linh San, E., Ferrari, N. & Weber, J. M. 2007. Socio-spatial organization of Eurasian badgers (*Meles meles*) in a low-density population of central Europe. *Canadian Journal of Zoology*, **85**, 973–984.
- Endriess, M. J. & Adler, G. H. 2005. Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), Panama. *Journal of Zoology*, **265**, 147–155.
- Erlinge, S., Hoogenboom, I., Agrell, J., Nelson, J. & Sandell, M. 1990. Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. *Journal of Mammalogy*, **71**, 597–603.
- Faraway, J. J. 2006. *Extending the Linear Model With R. Generalized Linear, Mixed Effects and Nonparametric Regression Models*. London: Chapman & Hall.
- Fitzgerald, B. M., Karl, B. J. & Moller, H. 1981. Spatial organization and ecology of a sparse population of house mice (*Mus musculus*) in a New Zealand forest. *Journal of Animal Ecology*, **50**, 489–518.
- Getz, L. L., Oli, M. K., Hofmann, J. E., McGuire, B. & Ozgul, A. 2005. Factors influencing movement distances of two species of sympatric voles. *Journal of Mammalogy*, **86**, 647–654.
- Gray, S. J., Plesner-Jensen, S. & Hurst, J. L. 2002. Effects of resource distribution on activity and territory defence in house mice, *Mus domesticus*. *Animal Behaviour*, **63**, 531–539.
- Harestad, A. S. & Bunnell, F. L. 1979. Home range and body weight: a reevaluation. *Ecology*, **60**, 389–402.
- Hayes, L. D., Chesh, A. S. & Ebersperger, L. A. 2007. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. *Ethology*, **113**, 155–165.
- Hixon, M. A. 1980. Food production and competitor density as the determinants of feeding territory size. *American Naturalist*, **115**, 510–530.
- Hoogland, J. L. 1985. Infanticide in prairie dogs. Lactating females kill offspring in close kin. *Science*, **230**, 1037–1040.
- Hubbs, A. H. & Boonstra, R. 1998. Effects of food and predators on the home-range sizes of Arctic ground squirrels (*Spermophilus parryii*). *Canadian Journal of Zoology*, **76**, 592–596.
- Hurvich, C. M. & Tsai, C. L. 1989. Regression and time-series model selection in small sample sizes. *Biometrika*, **76**, 297–307.
- Ims, R. A. 1987. Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology*, **56**, 585–596.
- Jonsson, P., Hartikainen, T., Koskela, E. & Mappes, T. 2002. Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. *Evolutionary Ecology*, **16**, 455–467.
- Kam, M., Cohen-Gross, S., Khokhlova, I. S., Degen, A. A. & Geffen, E. 2003. Average daily metabolic rate, reproduction and energy allocation during lactation in the Sundevall jird *Meriones crassus*. *Functional Ecology*, **17**, 496–503.
- Keller, C. & Schradin, C. 2008. Plant and small mammal richness correlate positively in a biodiversity hotspot. *Biodiversity and Conservation*, **17**, 911–923.
- Kelt, D. A. & Van Vuren, D. H. 1999. Energetic constraints and the relationship between body size and home range area in mammals. *Ecology*, **80**, 337–340.
- Kjellander, P. A., Hewison, J. M., Liberg, O., Angibault, J. M., Bideau, E. & Cargnelutti, B. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus*): a comparison of two long-term studies. *Oecologia*, **139**, 478–485.
- Koskela, E., Mappes, T. & Ylönen, H. 1999. Experimental manipulation of breeding density and litter size: effects on reproductive success in the bank vole. *Journal of Animal Ecology*, **68**, 513–521.
- Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology*, **65**, 689–701.
- Lazaro-Perea, C. 2001. Intergroup interactions in wild common marmosets, *Callithrix jacchus*: territorial defence and assessment of neighbours. *Animal Behaviour*, **62**, 11–21.
- Liu, H., Wang, D. & Wang, Z. 2003. Energy requirements during reproduction in female Brandt's voles (*Microtus brandtii*). *Journal of Mammalogy*, **84**, 1410–1416.
- Lovallo, M. J. & Anderson, E. M. 1995. Range shift by a female bobcat (*Lynx rufus*) after removal of neighbouring female. *American Midland Naturalist*, **134**, 409–412.
- Lovallo, M. J. & Anderson, E. M. 1996. Bobcat (*Lynx rufus*) home range size and habitat use in Northwest Wisconsin. *American Midland Naturalist*, **135**, 241–252.
- Lurz, P. W. W., Garson, P. J. & Wauters, L. A. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *Journal of Zoology*, **251**, 167–178.
- McNab, B. K. 1963. Bioenergetics and the determination of home range size. *American Naturalist*, **97**, 133–140.
- Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, **47**, 209–221.
- Mikesic, D. G. & Drickamer, L. C. 1992. Factors affecting home-range size in house mice (*Mus musculus domesticus*) living in outdoor enclosures. *American Midland Naturalist*, **127**, 31–40.
- Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Nel, K. N. 2003. The effects of dietary protein on the reproduction and behavioural characteristics of the striped mouse, *Rhabdomys pumilio*. MSc thesis, University of the Witwatersrand.
- Norman, M. D. & Jones, G. P. 1984. Determinants of territory size in the pomacentrid reef fish, *Parma victoriae*. *Oecologia*, **61**, 60–69.
- Ostfeld, R. S. 1986. Territoriality and mating system of California voles. *Journal of Animal Ecology*, **55**, 691–706.
- Ostfeld, R. S. 1990. The ecology of territoriality in small mammals. *Trends in Ecology & Evolution*, **5**, 411–415.
- Ostfeld, R. S. & Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76**, 521–532.
- Patterson, I. J. 1985. Limitation of breeding density through territorial behaviour: experiments with convict cichlids, *Cichlasoma nigrofasciatum*. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 393–405. Oxford: Blackwell.
- Perrin, M. R. 1980. 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. & Johnson, S. J. 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.
- Pinheiro, J. C. & Bates, D. M. 2000. *Mixed-effects Models in S and S-PLUS*. Berlin: Springer.
- Priotto, J., Steinmann, A. & Polop, J. 2002. Factors affecting home range size and overlap in *Calomys venustus* (Muridae: Sigmodontinae) in Argentine agro-ecosystems. *Mammalian Biology*, **67**, 97–104.
- R Development Core Team 2008. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemans, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291–318.
- Rödel, H. G. & Stubbe, M. 2006. Shifts in food availability and associated shifts in space use and diet in stone marten. *Lutra*, **49**, 67–72.
- Rödel, H. G., Starkloff, A., Bautista, A., Friedrich, A. C. & von Holst, D. 2008. Infanticide and maternal offspring defence in European rabbits under natural breeding conditions. *Ethology*, **114**, 22–31.
- Rodrigues, F. H. G. & Monteiro-Filho, E. L. A. 2000. Home range and activity patterns of pampas deer in Emas National Park, Brazil. *Journal of Mammalogy*, **81**, 1136–1142.
- Said, S., Gaillard, J. M., Duncan, P., Guillon, N., Servanty, S., Pellerin, M., Lefevre, K., Martin, C. & Van Laere, G. 2005. Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. *Journal of Zoology*, **267**, 301–308.
- Salvioni, M. & Lidicker, W. Z. 1995. Social organisation and space use in California voles: seasonal, sexual, and age-specific strategies. *Oecologia*, **101**, 426–438.
- Schradin, C. 2004. Territorial defence in a group-living solitary forager: who, where, against whom? *Behavioral Ecology and Sociobiology*, **55**, 439–446.
- Schradin, C. 2005. Nest site competition in two diurnal rodents from the succulent karoo of South Africa. *Journal of Mammalogy*, **86**, 757–765.
- Schradin, C. 2006a. 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*, **135**, 77–82.
- Schradin, C. 2006b. Whole-day follows of striped mice (*Rhabdomys pumilio*), a diurnal murid rodent. *Journal of Ethology*, **24**, 37–43.
- Schradin, C. 2008a. Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*). *Proceedings of the Royal Society B*, **275**, 1047–1052.
- Schradin, C. 2008b. Seasonal changes in testosterone and corticosterone levels in four social categories of a desert dwelling sociable rodent. *Hormones and Behavior*, **53**, 573–579.
- Schradin, C. & Pillay, N. 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. & Pillay, N. 2004. 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. *Journal of Comparative Psychology*, **118**, 37–47.
- Schradin, C. & Pillay, N. 2005a. Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy*, **86**, 99–107.
- Schradin, C. & Pillay, N. 2005b. Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. *Mammalian Biology*, **70**, 84–92.
- Schradin, C. & Pillay, N. 2006. Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behavioral Ecology*, **17**, 452–458.

- Schradin, C., Kinahan, A. A. & Pillay, N.** 2009. Cooperative breeding in groups of synchronously mating females demands large testes to avoid sperm depletion. *Biology of Reproduction*, **81**, 111–117.
- Schradin, C., König, B. & Pillay, N.** In press. Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*.
- Taitt, M. J.** 1981. The effect of extra food on small rodent populations: I. Deermice (*Peromyscus maniculatus*). *Journal of Animal Ecology*, **50**, 111–125.
- Taitt, M. J. & Krebs, C. J.** 1981. The effect of extra food on small rodent populations: II. Voles (*Microtus townsendii*). *Journal of Animal Ecology*, **50**, 125–137.
- Tufto, J., Andersen, R. & Linnell, J.** 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology*, **65**, 715–724.
- White, G. C. & Garrot, R. A.** 1990. *Analysis of Wildlife Radiotracking Data*. London: Academic Press.
- Wolff, J. O.** 1993. Why are female small mammals territorial? *Oikos*, **68**, 364–370.