



Manipulation of population density and food availability affects home range sizes of African striped mouse females



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An individual's home range determines its access to resources, significantly influencing its fitness. Food availability and population density are considered to be among the primary factors influencing home range sizes; however, no study has experimentally tested whether these two factors affect home range sizes independently. This is important as these two factors correlate significantly with each other, making it difficult to differentiate the effect of one from the other. First, we supplemented food to 23 female African striped mice, *Rhabdomys pumilio*, belonging to 15 different groups. To avoid an increase in population density by immigration, we also provided food to neighbouring groups. Although population density did not increase, female home range sizes decreased by 43.1%. In a second experiment, we manipulated population density by removing entire social groups of striped mice. We carried out experiments within 7 weeks, a period short enough to control for a change in natural food availability. Experimental decrease of population density caused an increase of female home range sizes of 44.3%. The degree of home range overlap between female striped mice was unaffected by supplemental feeding or by reduction of population density. However, female home range sizes were negatively affected by the total number of female neighbours, especially of heavier individuals. In addition, after removal, females significantly decreased their overlap with neighbouring breeding females indicating that competition with same-sex individuals shapes females' home ranges. This is the first comprehensive experimental field study demonstrating that an increase in food availability and a decrease in population density independently affect home range sizes of individuals.

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A home range is the area inhabited by an individual, which contains the resources necessary to ensure its survival and reproduction (Burt, 1943), significantly influencing its fitness (Bowler & Benton, 2009). Although several factors, such as sex, age and body mass, may be responsible for variation in home range characteristics (Hayes, Chesh, & Ebensperger, 2007; Hoset, Le Galliard, Gundersen, & Steen, 2008; Mikesic & Drickamer, 1992; Ostfeld, 1990; Priotto, Steinmann, & Polop, 2002; Schradin et al., 2010b; Tufto, Andersen, & Linnell, 1996), ultimately, the fitness of an individual is limited by the availability of resources within its home range and by the number of conspecifics with which it competes to

secure access to said resources (Lopez-Sepulcre & Kokko, 2005; Schradin et al., 2010b).

Several studies in mammals (Hubbs & Boonstra, 1998; Ims, 1987; Ostfeld, 1986), birds (Roth & Vetter, 2008) and reptiles (Simon, 1975) have shown that home range sizes decrease when food availability increases (but see also Hayes et al., 2007 for a case in which additional food had no effect), probably because when food is more abundant an individual needs less space to acquire sufficient energy to survive and reproduce (Saïd et al., 2005; Travis & Slobodchikoff, 1993; Tufto et al., 1996). A large home range that includes abundant resources may lead to higher fitness, but it might also attract more competitors. Several correlative (for example Agrell, 1995; Erlinge, Hoogenboom, Agrell, Nelson, & Sandell, 1990; Ostfeld, Lidicker, & Heske, 1985) and a few experimental studies (Baker, Funk, Harris, & White, 2000; Koskela, Mappes, & Ylönen, 1999; Lovallo & Anderson, 1995) have shown that home range sizes decrease when population density increases

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(but see Mares & Lacher, 1987; Ostfeld, 1986; Sera & Gaines, 1994 for some notable exceptions).

An increase in population density is also often associated with an increase in home range overlap between individuals (Ims, 1987; Ostfeld et al., 1985). Sharing parts of the home range with other individuals implies sharing food resources, which can lead to competition. In studies in which neighbours were experimentally removed (pomacentrid reef fish, *Parma victoriae*; Norman & Jones, 1984; red squirrel, *Tamiasciurus hudsonicus*; Boutin & Schweiger, 1988) or had disappeared (bobcat, *Lynx rufus*; Lovallo & Anderson, 1995; willow tit, *Parus montanus*; Hogstad, 1999; red fox, *Vulpes vulpes*; Baker et al., 2000), the remaining individuals enlarged their home ranges, which indicates that territorial interactions with neighbouring individuals prior to removal could have constrained individuals in their space use patterns (Jetz, Carbone, Fulford, & Brown, 2004). Understanding the effects that the availability of resources and the presence of competitors bear on animal space use is critical for explaining the social system of populations (Emlen & Oring, 1977; Hayes et al., 2007; Wang, Liua, Wang, Wana, & Zhong, 2011). Whereas experimental studies have investigated the influence of food resources or the influence of population density on home range sizes, it is difficult to conclude whether the observed decrease in home range sizes was due to changes in food availability, increased population density or a combination of both (Maher & Burger, 2011; Quirici et al., 2010). For example, the provisioning of additional food in experimental studies may have also attracted a greater number of immigrants into the study area, increasing local competition (Hews, 1993; Perrin & Johnson, 1999; Taitt & Krebs, 1981). Careful experimental manipulations of food availability and population density, such as variation of one factor while controlling for the other, could clarify the effects of each variable and demonstrate causation (Maher & Burger, 2011).

We experimentally studied the effect of food availability and population density on home range sizes in free-ranging female African striped mice, *Rhabdomys pumilio*. We focused on females because home ranges of female mammals result from the defence of food resources critical for reproduction and survival (Davies & Lundberg, 1984; Ostfeld, 1985; Wolff, 1993). In our study area, the Succulent Karoo, adult breeding female striped mice typically live in family groups, consisting of a breeding male, several breeding females and their philopatric offspring (Schradin & Pillay, 2004). Individuals belonging to the same group share one territory, which they defend aggressively against intruders (Schradin, 2004). Previous studies have shown female home range sizes to be correlated with the availability of food resources, the number of direct neighbours (a correlate of population density), seasonality, cover and relative individual body mass (Schradin et al., 2010b). To experimentally validate these correlative results, we used two separate controlled field experiments to test (1) the influence of food provisioning and (2) the effects of experimentally reduced population density on home range sizes and overlaps.

In the first experiment, we provided food to 15 focal groups using experimental feeders. This experiment was conducted over a short period of 8 weeks. To avoid an increase of population density as observed in previous food supplementation studies, groups at the boundaries and outside of the study area also received experimental food supplementation. We predicted home range sizes of female striped mice would decrease when food was supplemented and increase once food was removed. In the second experiment, we decreased population density by removing some groups within the study area. We limited the entire study period to 7 weeks, a period too short for a substantial decrease in the natural food availability. We predicted home range sizes of female striped mice would increase after their direct neighbours were removed. As the number

of direct neighbours represents a more accurate measure of being spatially constrained than population density (Schradin et al., 2010b), we also estimated the number of direct neighbours for each female.

Owing to benefits associated with group living (e.g. territory defence and vigilance against predation; Krause & Ruxton, 2002), we predicted intragroup overlap in home ranges would remain unchanged in both experiments. We predicted home range overlaps with direct neighbours would (1) decrease when food was supplemented and increase once food was removed and (2) decrease once their direct neighbours were removed and population density decreased. Since female striped mice experience more aggression from neighbouring females than from neighbouring males (Schradin, 2004; Schradin et al., 2010b), we predicted female neighbours would be more influential than the total number of neighbours in determining variation in home range sizes and overlaps.

METHODS

Study Species and Field Techniques

Data for the feeding experiment were collected during the 2007 breeding season (August to November) in the Goegap Nature Reserve in the Northern Cape of South Africa (29°42.30'S–18°02.95'E). Data for the removal experiments were collected during the 2007–2010 breeding seasons at a field site located on the farm Klein Goegap, 3 km away from the first field site.

Striped mice are considered adults at around 4–6 weeks of age when they reach sexual maturity and weigh more than 30 g (Brooks, 1982; Schradin, Schneider, & Yuen, 2009a; Schradin, Scantlebury, Pillay, & König, 2009b). For our study, we considered only females that weighed at least 30 g and were more than 6 weeks of age at the start of the experiment (they were either born during the previous breeding season or early in the breeding season of sampling and showed signs of reproductive activity).

Trapping, direct observations and radiotracking were used to establish group composition and determine the number of neighbouring adult females. Striped mice were trapped using Sherman-like traps (5.1 × 22.9 cm and 6.3 cm high) directly at their nest during early morning and evening (during peak activity times). Traps were placed in the shade facing the entrance of known nests and baited with a mixture of bran flakes, sunflower oil, sea salt and raisins. Trapped mice were sexed, weighed and their reproductive status recorded (for males: immature or mature, testes descended in the scrotal sac; for females: immature, receptive or nursing). For individual recognition, each striped mouse received permanent ear tags (0.8 × 0.2 cm; National Band and Tag Co., Newport, KY, U.S.A.) and was temporarily marked with a nontoxic hair dye (Inecto Rapido, Pinetown, South Africa). Marking of individuals did not influence predation rate (Schradin, n.d.). Behavioural observations were carried out during mornings and afternoons at group nests to determine group composition.

Focal females were equipped with radiocollars (Holohil, Carp, Ontario, Canada) weighing between 2.5 g and 4.5 g. Radiocollars always weighed less than 8% of the total body weight of an individual. Relatively small individuals of approximately 40 g were equipped with the lightest radiocollars (2.5 g) and individuals of more than 60 g received the heaviest radiocollars (4.5 g). All radiocollars were removed after 10 weeks. Carrying a radiocollar does not increase stress hormone levels nor does it increase mortality in striped mice (Schradin, 2008). Determination of home ranges was carried out by radiotracking striped mice six times per day for 9 days, using an AOR 8000 wide range receiver (Tokyo, Japan), an H-

antenna (Africa Wildlife Tracking, Pretoria, South Africa) and a global positioning system (GPS; eTrex Venture, Garmin International, U.S.A.) with an accuracy of ± 3 m. Radiotracking was additionally carried out once at night to establish locations of nesting sites (Schradin & Pillay, 2005a), following the same procedures used previously for striped mice (Schradin & Pillay, 2005b; Schradin et al., 2010b). All radiofixes were obtained from homing. In the Succulent Karoo, striped mice spend most of their time feeding or nesting in shrubs, and rarely stay out in the open. Thus, by homing, we were able to identify the shrub in which an individual was resting or foraging. We did not find telemetry to be disruptive, as evidenced by the fact that we often observed mice interacting in front of their nests during radiotracking.

Food Supplementation Experiment

We studied 23 females belonging to 15 groups within a study area of 10 ha. Food availability was experimentally manipulated by supplying striped mice with a protein-rich diet (a mixture of sunflower seeds, corn and peanuts; Brenco, Tswana Feeds and Packaging, South Africa), provided in an artificial 'feeder' (Fig. 1). Each feeder consisted of a plastic bottle with the top cut open and a hole in its side. The bottle was placed upside down in the field and was encased in a plastic container, which was fitted with a short opening tube (of approximately 15 cm), to allow striped mice to access the food and to prevent birds or larger animals from eating the seeds. Feeders were refilled at regular intervals and were never empty. We often observed striped mice entering feeders.

Of the 15 groups, 13 received two feeders while the remaining larger groups received three feeders each. Feeders were positioned at shrubs with their opening facing the bush. Females were radiotracked to establish home range sizes and to determine where to place the feeders in the field. For one female with a very small home range (0.06 ha), the closest feeder was placed next to the nest. For all other females, the closest feeder was 15.5 ± 12.4 m from the nest. To avoid population density from increasing through immigration of striped mice from neighbouring territories, we placed additional feeders, which were also regularly supplemented with food, outside of the experimental study area. The neighbouring area was regularly trapped. During the experiment we did not observe any individuals immigrating from the neighbouring area. Further, the duration of our experiment was too short to allow for population density to increase by reproduction.



Figure 1. An example of a feeder in the field. Note that during the experiment, the entrance into the box pointed towards and not away from the bush as shown in this picture. Photo credit: G. Schmohl.

Frequency of visits to the feeders was estimated by calculating the total number of locations determined by radiotracking individuals within a 5 m radius of the feeder (Map Source Version 6.11.6, Garmin Ltd).

Home ranges of each female were determined three times: (1) before food was supplemented; (2) during food supplementation; and (3) after the supplemental food was removed. Feeders (empty or full) were present throughout the study. A habituation period of 1 week was allowed between experimental phases to give females sufficient time to become accustomed to the presence or the absence of the food in the feeders.

Removal Experiment

The removal experiment was part of a field manipulation experiment that was carried out to test for the effect of population density on sociality (for more details see Schoepf & Schradin, 2012). Altogether, eight replicates of the experiment were performed, two per year in parallel at different places on a 20 ha field site (Schoepf & Schradin, 2012). Each replicate consisted of six groups: two groups were removed, two neighbouring groups were monitored as experimental groups (experiencing a local decline in population density due to removal) and two groups were used as control groups. Control groups were neighbours to experimental, but not removed groups. Declines in local population in control groups were due to dispersal of some experimental striped mice from the neighbouring groups and to natural predation (Schoepf & Schradin, 2012). Before removal, all adult individuals (60 males and 99 females) were fitted with radiocollars. All individuals were radiotracked for an initial period of 9 days to establish home range sizes and composition of groups and to decide which groups to remove (for more details see Schoepf & Schradin, 2012). Removal of groups (including 13 breeding females) took place immediately after determination of home ranges. The remaining individuals were radiotracked for another 4 weeks following a week of removal. Predation pressure at the field site was high (Schoepf & Schradin, 2012), with both control groups and experimental groups declining in size during the experiment. Altogether, 47 breeding females from control groups and 39 breeding females from experimental groups were radiotracked at the beginning of the study. Of these, only 30 females belonging to control groups and 18 females belonging to experimental groups survived through the entire 7 weeks and were considered for the final data analysis. A total of three females that dispersed into the territories of the removed groups and became solitary were excluded (see Schoepf & Schradin, 2012).

Estimation of Natural Food Availability

To quantify changes in natural food availability during both the supplementation and the removal experiments, we sampled eight plots, 2×2 m each, located randomly within the home ranges of eight groups. Plant surveys were conducted before, during and after food supplementation and before and after removal of individuals using standard protocols (Braun–Blanquet Method; Werger, 1974). In these surveys, we recorded the number of food plants in each plot (palatability was known from Schradin & Pillay, 2006). All plant surveys were carried out on the field site in the Goegap Nature Reserve, 3 km from the experimental removal field site.

Calculation of Home Range Size and Overlap

Home range sizes and overlaps were calculated using 90% kernel contours methods (KC; Worton, 1989) with the software Ranges6 (Anatrack Ltd, Wareham, U.K.). Overlaps were calculated as

percentages of area currently occupied minus the area previously occupied by an individual. We used 50% KC peeled around the kernel centre to estimate core area sizes (e.g. Hubbs & Boonstra, 1998; Ostfeld, 1986). Overlap in home range areas was determined (1) on an individual level, to analyse a potential shift in home range area before and after experimental manipulation and (2) between individuals, to measure areas shared between a focal female, its group members (intragroup overlap) and its neighbours (extragroup overlap). Although KC methods are often favoured (Barg, Jones, & Robertson, 2005; Börger et al., 2006; Matthiopoulos, 2003), in the Appendix we also provide results obtained using minimum convex polygon (MCP) methods to facilitate comparisons with previous studies on striped mice (Schradin & Pillay, 2004, 2005b; Schradin et al., 2010b). Results using MCP were in accordance with the results from KC.

Estimation of Population Density and the Number of Neighbours

Local population density over the 4 years was calculated separately for each individual using the following formula:

$$\text{Local population density} = \frac{\text{Total number of adult individuals in the area}}{((\text{Focal mouse group area}) + (\text{Sum of area occupied by neighbouring groups}))}$$

Groups and individuals (all adults in breeding condition) were considered as neighbours when they were located a maximum of 30 m from the focal mouse group area or from the focal female's home range. Population density was calculated both before and after individuals were removed.

Ethical Note

The study was carried out under licence from the Department of Environment, Food and Agriculture of South Africa and ethical clearance from the University of the Witwatersrand (AES: 2007/38/04). Mice for the removal experiments were captured directly at their nests in the field. Each mouse was kept in its own trap and transported to the captive colony at the research station, 3 km away. At the station, individuals were transferred to a Perspex cage (76 × 22 cm and 15 cm high) provided with bedding (straw), water and food (a mixture of sunflower, wheat and corn seeds, compressed grass pellets, fresh apple and lettuce) ad libitum. After an initial settling in period, each mouse was placed together with a captive mouse of the opposite sex in a breeding cage. The breeding cage consisted of two Perspex and aluminium cages (90 – 60 cm and 60 cm high), connected by a plastic tube. Each cage contained bedding, water and food (as above), and was enriched with climbing, hiding and nesting material. The captive colony is provided with large glass windows and doors and is not insulated. Captive individuals are thus exposed to the same ambient light and temperatures as experienced by wild mice in the field. Removed mice were used for breeding in the captive colony or in other studies (see Schoepf & Schradin, 2012).

Data Analysis

Data analysis was performed using the statistical software R version 2.11.0 (The R Foundation for Statistical Computing, Vienna,

Austria, <http://www.r-project.org>). Data were tested for normality using the Shapiro–Wilk normality test and are presented as mean ± SE. The 90% KC home range sizes were log-transformed, whereas the 50% KC core area sizes were square-root transformed prior to analysis. We used linear mixed effect models (LMM) to (1) test for differences in home range sizes and core area sizes before, during and after the food supplementation experiment, (2) determine differences in home range sizes and core area sizes before and after the removal experiment, (3) assess whether population density or the number of neighbours affected home range sizes of focal individuals and (4) analyse the effects of the presence ($N = 37$) or the absence ($N = 11$) of other breeding females within the group on focal females' home range sizes. For the feeding experiment, home range sizes or core areas were used as the response variables, treatment (before, during and after) was the fixed factor and individual ID nested within group ID was the random factor. For the removal experiment, home range sizes or core areas were the response variables, treatment (control and experiment) and removal (before and after) were the fixed factors, and individual ID nested within group ID was the random factor. Population density, the total number of

neighbours, the number of neighbouring females, the number of heavier neighbouring females and the presence or absence of other females within the group were also included as fixed factors in LMMs to assess their influence on home range sizes. We selected the model that fitted our data best by using Akaike's information criterion (AIC; following Crawley, 2007). We verified our model selection by plotting the model residuals versus the fitted values, by checking the normal distribution of the model residuals using normal probability plots and by checking for heteroscedasticity and leverage (Crawley, 2007). We used paired t tests with Benjamini–Hochberg correction (Benjamini & Hochberg, 1995) to assess differences between treatments during the food supplementation experiments. We used generalized linear models (GLM) with a Poisson family error to determine differences in availability of natural food plants (1) before, during and after food supplementation and (2) before and after removal of individuals in each experimental year. In each GLM, the availability of natural food plants was the response variable and treatment (before, during or after) was the fixed factor. We used generalized linear mixed effects models (GLMM) with a binomial family error to detect differences in home range overlaps between focal females and either other group members or neighbouring breeding females before, during and after the food supplementation experiment, as well as before and after the removal experiment. In each GLMM, percentage of overlap was the response variable, treatment (before, during or after) was the fixed factor and individual ID nested in group ID was the random factor. All tests were two tailed. For all tests, a significance level (α) of 0.05 was selected.

RESULTS

Food Availability

Number of food plants did not vary significantly before, during and after food supplementation (GLM: $F_{2,21} = 1.80$, $P = 0.16$).

Female striped mice quickly discovered and frequently used the feeders provided, and their home range kernel centres were close to the position of the feeders. Number of visits to the feeders varied significantly before, during and after food supplementation (13.30 ± 1.27 versus 9.61 ± 1.33 versus 7.61 ± 1.10 , respectively; LMM: $F_{2,22} = 8.47$, $P = 0.001$). Females spent significantly less time visiting the feeders after, rather than before, the experiment (paired t test: $t_{22} = -4.27$, $P = 0.001$), and before, rather than during, the experiment (paired t test: $t_{22} = 2.98$, $P = 0.04$). Number of visits to the feeders did not differ significantly during and after the experiment (paired t test: $t_{22} = -1.63$, $P = 0.15$).

Supplemental feeding significantly influenced female home range sizes (LMM: $F_{2,22} = 5.85$, $P = 0.006$; Fig. 2). Specifically, female home range sizes decreased significantly when food was provided (before and during: paired t test: $t_{22} = 2.48$, $P = 0.03$) and increased again once food was removed (during and after: paired t test: $t_{22} = 4.64$, $P = 0.03$). Female home ranges at the end of the experiment returned to similar sizes to those recorded at the beginning of the experiment once it was terminated (before and after: paired t test: $t_{22} = -0.03$, $P = 0.97$).

Core area sizes varied significantly before, during and after food was provided (LMM: $F_{2,22} = 8.56$, $P = 0.001$; Fig. 2). Specifically, core areas of home ranges decreased significantly when food was provided (before and during: paired t test: $t_{22} = 3.28$, $P = 0.01$) and increased when food was removed (during and after: paired t test: $t_{22} = 4.86$, $P = 0.01$). Core areas at the end of the experiment returned to similar sizes to those recorded at the start of the experiment (before and after: paired t test: $t_{22} = -0.03$, $P = 0.98$).

Females mostly occupied the same area during the different phases of the experiment (overlap before and during food supplementation: $63.30 \pm 6.91\%$; overlap before and after food supplementation: $56.76 \pm 6.34\%$; overlap during and after food supplementation: $53.53 \pm 5.41\%$; GLMM: $z_{2,22} = 0.48$, $P = 0.63$), indicating that females did not shift their home ranges when food was provided. Experimental manipulation did not result in focal females decreasing overlap with other females of their own group (before and during: $36.69 \pm 7.44\%$; before and after: $19.57 \pm 6.21\%$; during and after: $22.95 \pm 8.12\%$; GLMM: $z_{2,18} = -1.70$, $P = 0.09$), or with neighbouring females (before and during: $2.49 \pm 0.60\%$; before and after: $2.13 \pm 0.57\%$; during and after: $3.29 \pm 0.72\%$; GLMM: $z_{2,21} = -0.96$, $P = 0.34$).

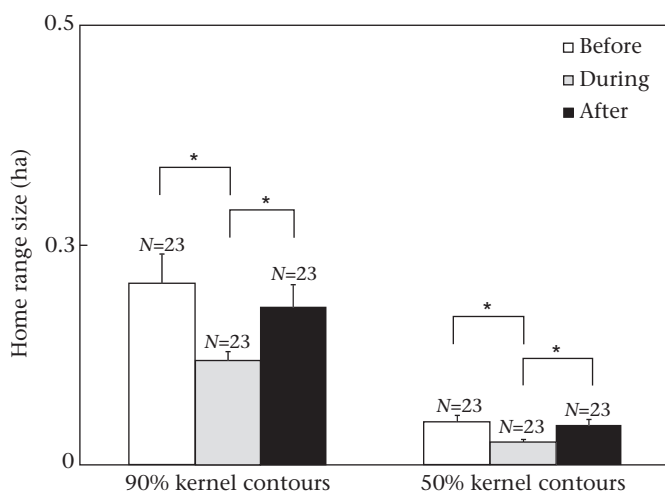


Figure 2. Home range sizes and core area sizes (mean \pm SE) of female striped mice before, during and after food supplementation, generated using 90% and 50% kernel contours methods ($N = 23$). * $P < 0.05$.

Population Density and the Number of Neighbours

Number of food plants did not vary significantly before and after removal of individuals in any of the 4 years (2007: 6.50 ± 0.87 versus 5.13 ± 0.77 ; GLM: $F_{1,14} = 1.30$, $P = 0.25$; 2008: 7.38 ± 0.80 versus 7.50 ± 0.87 ; GLM: $F_{1,14} = 0.01$, $P = 0.93$; 2009: 5.38 ± 0.86 versus 4.38 ± 0.73 ; GLM: $F_{1,14} = 2.19$, $P = 0.14$; 2010: 2.75 ± 0.31 versus 2.88 ± 0.35 ; GLM: $F_{1,14} = 1.91$, $P = 0.17$). Home range sizes of females increased significantly after removal of neighbouring groups (LMM: $F_{1,47} = 16.81$, $P = 0.0002$; Fig. 3). However, home range sizes of experimental females did not differ significantly from those of control females either before or after the removal experiment (LMM: $F_{1,20} = 0.10$, $P = 0.76$). Core area sizes of females tended to increase after the removal of neighbours (LMM: $F_{1,47} = 3.47$, $P = 0.07$). Core area sizes of experimental females did not differ significantly from those of control females either before or after removal (LMM: $F_{1,20} = 0.24$, $P = 0.63$).

Local population density was significantly lower after removal for both experimental and control females (experiment: before 9.49 ± 0.96 versus after 4.88 ± 0.49 ; paired t test: $t_{17} = -9.92$, $P < 0.0001$; control: before 11.23 ± 1.06 versus after 6.60 ± 0.40 ; paired t test: $t_{29} = -8.76$, $P < 0.0001$). The observed increase in home range sizes of both experimental and control females was due to the decrease in the local population density after the removal experiment (experiment: LMM: $F_{1,17} = 8.97$, $P = 0.008$; control: LMM: $F_{1,29} = 18.62$, $P = 0.0002$; Fig. 4a, b). The presence of other females within the group did not affect home range sizes of focal females (presence: 0.34 ± 0.03 ; absence: 0.31 ± 0.06 ; LMM: $F_{1,18} = 0.50$, $P = 0.49$). The total number of direct neighbours negatively affected home range sizes of both experimental (LMM: $F_{2,16} = 5.97$, $P = 0.01$; Fig. 5) and control females (LMM: $F_{2,28} = 4.07$, $P = 0.03$; Fig. 5). The number of female neighbours (experiment: LMM: $F_{2,16} = 4.98$, $P = 0.02$; control: LMM: $F_{2,28} = 4.04$, $P = 0.03$), predominantly of heavier individuals (experiment: LMM: $F_{2,16} = 5.97$, $P = 0.01$; control: LMM: $F_{2,28} = 4.07$, $P = 0.03$), had a particularly negative effect on home range sizes of both experimental (average number of female neighbours before 8.50 ± 1.11 versus after 5.59 ± 0.79 ; heavier females before 2.94 ± 0.57 versus after 3.00 ± 0.71) and control females (average number of female

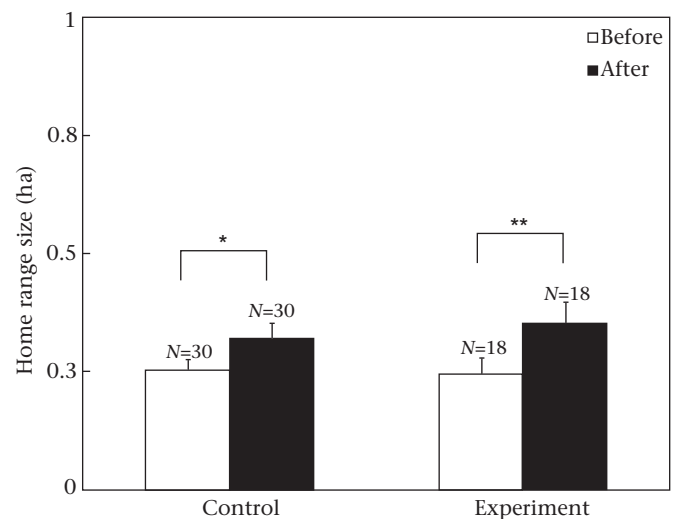


Figure 3. The home range size (mean \pm SE) of experimental females ($N = 18$) and control females ($N = 30$) before and after removal of individuals, generated using 90% kernel contours methods (experimental females before versus after: $t_{17} = 3.42$, $P = 0.003$; control females before versus after: $t_{29} = 2.51$, $P = 0.02$). * $P < 0.05$; ** $P < 0.01$.

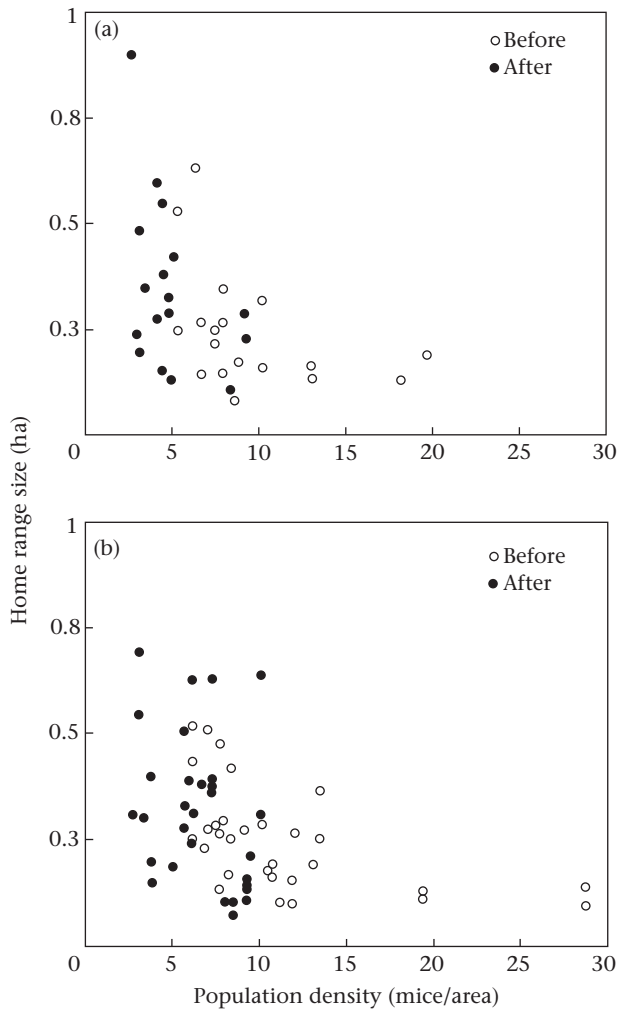


Figure 4. Home range sizes of female striped mice in relation to population density. (a) Control females ($N = 30$); (b) experimental females ($N = 18$).

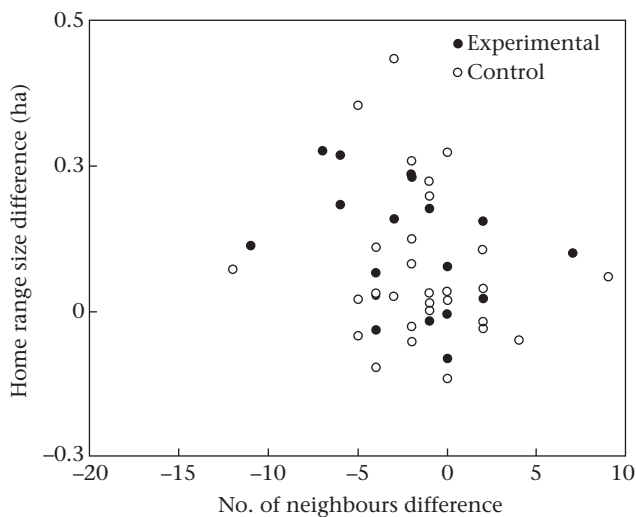


Figure 5. Home range sizes of female striped mice in relation to the number of neighbouring females (after–before values in home range size and number of neighbours are shown). Experimental females: $N = 18$, $r^2 = 0.09$; control females: $N = 30$, $r^2 = 0.02$.

neighbours before 8.37 ± 0.86 versus after 6.47 ± 0.72 ; heavier females before 3.70 ± 0.55 versus after 3.3 ± 0.53).

Control and experimental females did not significantly shift their home ranges during the experiment (experiment: $77.51 \pm 5.95\%$; control: $73.16 \pm 3.26\%$; GLMM: $z_{1,47} = 0.11$, $P = 0.91$), indicating that they used mostly the same area before and after other individuals were removed. Before and after removal of individuals, experimental and control females did not show a significant decrease in their home range overlap with females of their own group (experiment: $61.51 \pm 8.22\%$ versus $43.09 \pm 9.34\%$; GLMM: $z_{1,10} = 1.46$, $P = 0.14$; control: $55.86 \pm 7.23\%$ versus $43.09 \pm 9.34\%$; GLMM: $z_{1,26} = 0.72$, $P = 0.47$). However, experimental females significantly decreased their overlap with neighbouring breeding females ($34.32 \pm 7.39\%$ versus $24.55 \pm 7.03\%$; GLMM: $z_{1,11} = 2.45$, $P = 0.01$). Control females' overlap with neighbouring breeding females remained similar before and after removal ($20.50 \pm 6.27\%$ versus $18.05 \pm 6.04\%$; GLMM: $z_{1,22} = -0.40$, $P = 0.69$).

DISCUSSION

Many studies have reported that home range sizes correlate negatively with food availability and with population density, but the problem is that food availability and population density are positively correlated with each other. Therefore, when experimentally testing for the effects of one factor, it is important to control for the other one. Previous studies failed to do so. Our study experimentally quantified the independent effects of these two factors in the same species. When supplemental high-protein food was provided, female home ranges decreased by 43.1%, and when individuals were removed from neighbouring territories, female home ranges increased by 44.3%.

Food Availability

In female mammals, reproductive success often depends on body condition (Dreiss, Cote, Richard, Federici, & Clobert, 2010; Schradin et al., 2010b) and females therefore compete for access to food resources by defending their home ranges (Wang et al., 2011). Female striped mice significantly reduced the sizes of their home ranges when food was provided, but they did not show any significant change in the overlap with the home ranges of females from their own or from neighbouring groups. This result suggests that the degree of intraspecific competition remained unchanged during our experiment. In contrast, in studies that did not control for immigration and an associated increase in home range overlap (Ims, 1987; Ostfeld, 1986), increased competition could not be ruled out as an explanation for decreased home range sizes.

Home ranges of female striped mice increased when food provisioning was terminated to levels similar to those recorded before the onset of the experiment. Similar effects of food supplementation were found in other species (Enoksson & Nilsson, 1983; Ims, 1987; Roth & Vetter, 2008). However, in previous studies data were collected over longer periods of time and did not control for the correlative effects of increased population density due to increased immigration and recruitment following reproduction (Enoksson & Nilsson, 1983; Roth & Vetter, 2008; Taitt & Krebs, 1981). In contrast, our study was conducted over a much shorter period (food was supplemented for only 2 weeks) and to avoid immigration, we also provisioned groups outside of the study area with feeders. During trapping, we did not observe any neighbouring mice entering our study area, and there was no indication of an increase in population density. We thus conclude that the variation in home range sizes observed during our experiment was caused by food supplementation.

Population Density and the Number of Neighbours

Population density correlates negatively with home range sizes (Fortier & Tamarin, 1998; Luna & Baird, 2004; Priotto et al., 2002), a finding that has been supported by several experimental studies (Baker et al., 2000; Boutin & Schweiger, 1988; Norman & Jones, 1984). In accordance, we found female home range sizes increased significantly after we decreased population density. Interestingly, following the removal of individuals, we observed an increase in home range sizes not only in females whose direct neighbours were removed, but also in females of control groups, whose neighbours remained in the population. This increase can be explained by a reduction in population density owing to some philopatric striped mice belonging to experimental groups moving into the area of the removed groups (Schoepf & Schradin, 2012). Additionally, predator pressure can significantly affect the use of space of a prey species, since increased predation is often associated with larger prey home ranges (Maher & Burger, 2011). At our field site, predator pressure was rather high, with 45% of females disappearing before the end of the study (see Schoepf & Schradin, 2012). Because of predation, even individuals belonging to control groups experienced, although to a lesser degree, a decline in the local population density, which can thus explain why even control females were able to increase their home range sizes.

Female striped mice that shared a nest with other breeding females increased their home ranges more than females that were breeding solitarily. This result indicates important effects in communally breeding females. Kin selection favours space sharing among female relatives (Dobson, 1982; Le Galliard, Gundersen, & Andreassen, 2006; Rosell, Gundersen, & Le Galliard, 2008). Cooperation among females has been shown to be more important than competition in several prairie dog species (Hoogland, 2013) and may explain why overlap with female group members remained unchanged as female striped mice cooperate in territory defence (Schradin, 2004).

A reason why home range overlap remained unchanged between control females and their neighbours might be the significant increase in home range sizes of all females, increasing the likelihood of an increase in overlap with other individuals. While home range sizes of all females increased significantly, increasing the likelihood of an increase in overlap with neighbouring individuals, the encounter rate with neighbours decreased, because there were fewer female neighbours in total (the total number of breeding females in the study site decreased from 119 to 88). Interestingly, females with many female neighbours had smaller home ranges, supporting previous findings that female striped mice restrict each other's space use (Schradin et al., 2010b). Inter-group conflict with other breeding females can be a major cost (Clutton-Brock et al., 2006), resulting in female–female aggression and infanticide, and in striped mice, females are known to be as aggressive as males (Schradin, König, & Pillay, 2010a). This is further supported by the fact that, after removal, experimental females, but not control females, decreased their overlap with potentially competing neighbouring females.

Thus, we conclude that while an increase in home range sizes and thus access to food resources reduced within-group competition over food, within-group cooperation was not affected. Our experiments further suggest that females will reduce direct competition with neighbouring individuals if given the opportunity.

Conclusions

Our experimental results support the hypothesis that variation in home range sizes and overlap is governed both by the availability

of food resources and by population density. The increase in food availability allowed individuals to access food more easily (and thus easily gain energy) while at the same time being able to decrease their home range size substantially. However, when population density decreased, home range sizes increased considerably, which could be interpreted as individuals investing in greater energy expenditure for travelling to potentially gain higher food rewards. We conclude that female striped mice adjust their home ranges dynamically in response to food and presence of conspecifics, but costs and benefits might differ depending on changes in environmental conditions.

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Appendix

Supplemental feeding also significantly influenced female home range sizes when these were calculated using 100% MCP methods (before 0.30 ± 0.03 versus during 0.21 ± 0.02 versus after 0.27 ± 0.03 ; LMM: $F_{2,22} = 5.22$, $P = 0.009$). Specifically, female home range sizes decreased significantly when food was provided (before and during: paired t test: $t_{22} = 2.68$, $P = 0.01$) and increased again once food was removed (during and after: paired t test: $t_{22} = 2.75$, $P = 0.01$). Female home ranges at the end of the experiment returned to similar sizes to those recorded at the beginning of the experiment once it was terminated (before and after: paired t test: $t_{22} = -0.85$, $P = 0.40$).

Home range sizes of females also increased significantly after removal of neighbouring groups when these were calculated using 90% MCP methods (control: 0.27 ± 0.03 versus 0.33 ± 0.03 ; experiment: 0.28 ± 0.05 versus 0.37 ± 0.05 ; LMM: $F_{1,47} = 20.03$, $P < 0.0001$). Home range sizes of experimental females did not differ significantly from those of control females either before or after the removal experiment even when these were calculated using 90% MCP methods (LMM: $F_{1,46} = 0.19$, $P = 0.66$).