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, *Tamiascurius 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-