

Happily together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent

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Abstract The availability of resources, their effect on population density and territoriality, and the ways in which these factors are interwoven with mating systems are important determinants of small mammal space use. It is often difficult to study these patterns in an integrated way, however, especially because long-term data are needed but not readily available. In this paper, we investigate effects of population density, season and breeding status on home range patterns of the promiscuous rodent *Mastomys natalensis* using monthly capture-mark-recapture data collected over 17 years in a 3-ha grid. Home ranges were estimated using minimum convex polygons bounded by trap locations, and home range overlap and visitation rates were calculated as a measure of territoriality. As higher population densities coincide with increased resource availability, we predicted that home range sizes would

correlate negatively with density. Furthermore, as *M. natalensis* is promiscuous and population densities are generally high, we predicted that territoriality would be low, and home range overlap would therefore be high. Contrary to expectations the home ranges of female adults increased with population density, although those of male adults and subadults followed the expected decrease. Home range overlap and visitation rates were generally high, and increased significantly with population density. More importantly, they were never lower than those of simulated datasets consisting of randomly moved home ranges. These results therefore suggest that *M. natalensis* displays a complete lack of territoriality that is rarely seen in small mammals but still meets predictions based on knowledge of density and mating system.

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Keywords Absence of territoriality · Capture-mark-recapture · Density-dependent · Home range · *Mastomys natalensis*

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Introduction

In small mammal societies, space use of individuals is thought to be a function of resource availability, population density, territoriality and mating system (Wolff 1985; Ostfeld 1990; Waterman 2007; Adler 2011). The availability of resources (food, shelter) in time and space will influence animal numbers, and often also the presence and level of territorial behaviour (Ostfeld 1985). Territoriality will also be determined by population density, as territorial defence of resources and/or mates becomes less economical with higher numbers of competitors (Warner and Hoffman 1980; Wolff 1985). Mating systems are strongly interwoven with density and territoriality, as a decreased

mate availability at low population densities is likely to make monogamy and mate guarding more successful (Kleiman 1977), whereas high abundances may facilitate polygyny and/or polyandry, which are often assumed to provide greater fitness benefits than monogamy (Gerlach et al. 2012).

Examples of the role of resource availability can be found in several small mammal groups. In Echimyid rodents, for example, some species experience a patchy distribution of resources, occur at low population densities, exhibit territorial spacing and have a monogamous mating system as predicted (Silva et al. 2008), while others that occur in resource-rich environments experience higher population densities, show little territoriality and have a polygynous mating system (Guichón et al. 2003). Even within species, changes in resource availability have the potential to change spacing behaviour and mating system (Fleming 1971; Lott 1991; Adler et al. 1997; Endries and Adler 2005). Prairie voles (*Microtus ochrogaster*), for instance, are more likely to form monogamous pair bonds and exhibit low levels of inter-pair territory overlap when population densities are low, as opposed to when densities are higher (Getz and Hofmann 1986). The role of food in shaping territoriality has also been shown experimentally: territorial behaviour of the California vole (*Microtus californicus*) has been shown to decline with decreased food availability (Ostfeld 1986; Ims 1987; Ostfeld et al. 1988). These effects of resource availability are not necessarily the same for the two sexes however. It is often thought that, while female distribution is strongly linked to resource availability, the space use of males is strongly influenced by that of females (the “Females in Space” hypothesis, see Ostfeld 1990; Waterman 2007).

Population density is also intricately linked to territoriality. Because only a certain number of animal territories fit into a given area, higher densities may result in larger home range overlap when territoriality decreases (Warner and Hoffman 1980; Dobson 1984; Wolff 1985). Alternatively, territorial behaviour may be rigid and limit density increases beyond certain points through density-dependent dispersal or breeding suppression (Wolff 1997). When species maintain strict territoriality, home range overlap and inter-individual contacts are not expected to increase with density, limiting possible fluctuations in population size. In situations where territoriality is absent however, large density fluctuations may be possible, and home range overlap and individual contacts will increase with population density.

Patterns of home range overlap are therefore useful for studying territorial behaviour. Yet while there is a reasonably large body of literature on home ranges of territorial monogamous, polygynous and polyandrous species (Blair 1941; Ostfeld 1986; Gaulin and Fitzgerald 1988;

Ostfeld and Heske 1993; Priotto et al. 2002; Schradin 2004; Steinmann et al. 2008), there are few datasets long enough to investigate home range patterns of a species in relation to, separately, population density and season. In this paper, we use a long-term capture-mark-recapture (CMR) study to analyse the spatial patterns in the African multimammate mouse *Mastomys natalensis*, a promiscuous murid that exhibits strong seasonal and interannual fluctuations in population density. This extensive dataset provides the statistical power necessary to test specific hypotheses about the effects of sex, breeding status, season and population density on home range size and territoriality.

Mastomys natalensis is one of the most widespread murid rodents in sub-Saharan Africa (Granjon et al. 2011). Due to its generalist nature (Veenstra 1958; Coetzee 1975; Leirs 1994) it occurs in a wide variety of habitats, but thrives in agricultural fields where it can cause considerable crop damage (Fiedler 1988; Mwanjabe et al. 2002; Sluydts et al. 2009; Leirs et al. 2010). *Mastomys natalensis* has a promiscuous mating system, where multiple paternity seems to be common (Veenstra 1958; Coetzee 1975; Isaacson 1975; Leirs 1994; Duplantier et al. 1996; Kennis et al. 2008). A “scramble competition” strategy (where males roam around to find as many receptive females as possible) has been suggested for this species, based on the highly asynchronous post-partum estrus of females during the breeding season, the positive correlation between male body weight and mating success, and the lack of evidence for a harem structure (Leirs 1994; Jackson 1999; Schradin and Pillay 2004; Kennis et al. 2008). In Tanzania, the location of our study population, densities of multimammate mice fluctuate strongly over years and seasons, ranging from less than 30 animals/ha during the breeding season to more than 300 ha⁻¹ during the non-breeding season in some years (Sluydts et al. 2007). Food availability, strongly linked to rainfall, is very predictable throughout the year (Leirs 1994).

The role of *M. natalensis* as a significant agricultural pest and a reservoir host of important zoonotic infections such as plague and Lassa virus (Frame et al. 1970; Isaacson 1975; Wulff et al. 1977) has stimulated several home range and movement studies on this species. Radiotelemetry studies (Leirs et al. 1996; Hoffmann and Klingel 1998) yielded high resolution data but, as with earlier CMR studies (Christensen 1996; Leirs et al. 1996; Monadjem and Perrin 1998), were limited by small sample sizes and limited time frames, varying from a few weeks for the telemetry studies to approximately 2 years for the CMR studies. It has therefore not previously been possible to use these data to reliably infer home range differences between demographic categories (adult/subadult, male/female), or to quantify effects of interannual fluctuations of population density on spacing behaviour.

Using *M. natalensis* as a model species, the present study tests several hypotheses about small mammal space use. Because of the positive correlation between population densities and availability of resources, we expect a negative correlation between density and home range size for male and female subadults and female adults. The predictable and abundant availability of resources, coinciding with high population densities that would make territory defence less economical (Wolff 1985), would further result in a non-clustered and non-territorial distribution of female adults during the breeding season. A non-clustered distribution of females, combined with the fact that estrus is asynchronous during the breeding season, would suggest an absence of territoriality in male animals if their space use is indeed determined by both resources and female distribution (Ostfeld 1990; Waterman 2007). Additionally, if males indeed use a scramble competition strategy (Kennis et al. 2008), they are expected to have larger home ranges than females during the breeding season. The promiscuous mating system, which may be a strategy to avoid infanticide by males (Wolff and Macdonald 2004), is likely to result in an absence of territorial behaviour of females towards males and vice versa. Because this does not protect against infanticide by other females, this may, contrary to the first prediction above, be a reason for females to be territorial towards each other during the breeding season. Female breeding territoriality may also arise if females try to limit access to food resources near their nest.

Materials and methods

Study area and trapping

Trapping was done in a 3-ha rectangular grid of 30×10 traps spaced 10 m apart on the campus of the Sokoine University of Agriculture (Morogoro, Tanzania). The trapping area is a mosaic environment consisting of patches of woodland, maize field and fallow land. Between 15 Mar 1994 and 6 Jan 2011, rodents were live-trapped monthly for three consecutive nights using Sherman LFA live traps (Sherman Live Trap Co., Tallahassee, FL, USA), baited with a mix of peanut butter and ground maize. All captured rodents were weighed, sexed, and individually marked using toe clipping, as at the time no other method was available for permanently marking large numbers of individuals simultaneously. Reproductive status was determined following a standard protocol (see Leirs 1994 for details). Mice were considered to be subadult until a sign of sexual activity could be observed (scrotal testes in males; perforated vagina, lactating nipples or pregnancy in females), after which they were considered to be adult. This trapping effort resulted in 36,425 separate captures of

15,471 unique individuals, captured during 212,700 trap nights. *Mastomys natalensis* is an opportunistic omnivore, and can rapidly adapt to changes in resource availability, which are positively linked to rainfall (Leirs 1994). The rainy season is bimodal, starting in October and peaking around December (*vuli*-rains) and then again more strongly around March–April (*masika*-rains), followed by a dry season from around June until September–October (Leirs 1994).

Density estimation

The abundance of the rodent population during each 3-night trapping session (during which the population was assumed to be closed) was estimated using the commonly used heterogeneity estimator $M(h)$ in the program CAPTURE (White et al. 1982). The $M(h)$ estimator allows for variability in individual capture probabilities and appears to be quite robust (Parmenter et al. 2003). This estimator has been widely used to evaluate *M. natalensis* densities from field data originating from the same trapping grid (Leirs et al. 1997; Sluydts et al. 2007, 2009) and thus permits straightforward comparison with previous studies. As can be seen in these studies, population densities fluctuate strongly, both seasonally as well as inter-annually, with estimates ranging from less than 10 ha^{-1} to more than 300 ha^{-1} , and are strongly correlated with rainfall (Leirs et al. 1997; Sluydts et al. 2007). During the reproductive season (April–September), numbers of animals increase from minimal to high densities due to the recruitment of juvenile animals (Leirs et al. 1993, 1994). This increase continues into the first months following the reproductive season, after which numbers start to decline until they again reach a minimum in June–July the year after. The sex ratio is approximately equal outside the breeding season, but becomes female-biased during the breeding season (Leirs 1994).

Home range size and overlap

Home range is defined here as the area bounded by the locations at which an individual was trapped, and is assumed to be a proxy for the space used by the animal during its “normal” day-to-day activities like foraging, mating and litter care (Burt 1943). Because of the limited number of locations per individual, and for easy comparison with other studies, home ranges were estimated using the minimum convex polygon (MCP) method with an inclusive boundary strip of 5 m (half the distance between traps; Stickel 1954). Only animals that were trapped in at least 2 different months were used for home range estimations, as we assumed these animals to be resident. Previous studies have shown that applying the MCP

method to CMR trapping data underestimates *M. natalensis* home ranges compared to those based on radio-tracking data (Leirs et al. 1996), however as we are primarily interested in relative differences in home range size and overlap, this is no issue for this study. Because the average dispersal distance for *M. natalensis* (300 m) is larger than the size of the trapping grid, the risk of overestimating home range sizes due to inclusion of dispersal events is negligible (Leirs et al. 1996).

We investigated the effects of breeding status (adult vs. subadult) and season (breeding vs. non-breeding) on home range size and overlap. Because a sufficient number of recaptures is needed to allow polygon estimation, the home ranges need to be estimated over a sufficiently long period within each category. For this reason, it was not possible to investigate the effects of breeding status and season in the same model. Furthermore, as home range estimates were based on data from multiple months, it was not possible to use density estimates from a single month as model inputs. Thus, for each individual in each category, the population density for the model was calculated as the average density across all months that an individual remained in a category.

To assess if and how home ranges falling partly outside the grid affected estimates of home range size and overlap, we sequentially removed those animals whose polygon centroid fell within bands of increasing width from the edge of the trapping grid; the mean home range of each demographic group was recalculated after each removal. The first band was 0 m (no removal), and the following distances were increments of 2 m up to 48 m. For example, a 6 m band removal meant that all animals whose polygon centroid fell within 6 m of the edge were removed, and the mean polygon size of the remaining animals was re-calculated. For each group, the average polygon sizes were plotted against the distance from the edge. There was a positive correlation between band size and polygon size, which started to level off at 12 m and only slightly increased beyond this distance due to an increasing proportion of large home ranges [Fig. S1 in Electronic Supplementary Material (ESM)]. Therefore, only animals whose polygon centroid was located further than 12 m from the edge were chosen for home range estimation. This distance approximates the radius of an average home range (about 500 m²; Leirs et al. 1996), and removing an edge strip equal to the average home range radius is indeed a frequently used and straightforward approach for minimizing edge effects (Dice 1938; Stickel 1954).

The percentage of the home range area that overlapped with other animals was calculated between demographic groups (female/male, subadult/adult and combinations), for all animals whose lifetime overlapped. This home range overlap percentage was calculated for the animals that were retained after controlling for edge effects, but for all these animals the overlap with all resident animals was

calculated, including those that had their polygon centroid within 12 m of the trapping grid edge.

As home ranges are calculated using resident animals only, the effect of transient animals on home range overlap could not be assessed. For this reason a daily visitation rate was calculated by counting the total number of animal visits to a home range during the residing period (the period between the first and last capture) of the animal of interest, divided by the length of the residing period in days. All animals were used when calculating this visitation rate, thereby including transient animals that were trapped during only one trapping session.

To test whether the observed overlap patterns were true biological patterns (i.e., did not arise by chance from the available combination of home range shapes, numbers and sizes), a permutation test was used, where 100 new generated datasets were compared to the original dataset. For each new dataset, polygons were randomly moved to a different location in the 3-ha grid, keeping the same orientation and shape, after which overlaps were again calculated. The statistical difference in overlap between the original dataset and a relocated dataset was tested using a one-sided *t* test, testing the null hypothesis that the mean overlap percentage of the original dataset is not smaller than that of the simulated dataset, which would indicate an absence of territoriality. A one-sided *t* test was chosen because while the randomly relocated home ranges are able to occupy the entire 3-ha grid, in reality the space that is actually used will be smaller due to habitat heterogeneity. As a consequence, the average overlap values of the randomly moved home ranges are expected to be smaller than those of the real home ranges. Although using a one-sided *t* test excludes the possibility of testing whether the actual home range overlap is significantly larger than that of randomly relocated home ranges due to higher levels of social clustering than expected, it was chosen because we explicitly want to test for the existence of territorial behaviour, and because it would be impossible to discern between the effects of social clustering and habitat heterogeneity. The proportion of non-significant differences was used as the probability of the null hypothesis stating that home range overlap in the original dataset is not significantly smaller than the home range overlap in relocated datasets. A similar method was used to assess the likelihood of obtaining the visitation rates observed in the trapping data. This was done by randomly moving each trap location in the dataset to another place in the grid, and recalculating the visitation rates. This procedure was also repeated 100 times.

Home range size and overlap were analysed using likelihood ratio tests of linear models with breeding status, sex and density as fixed effects and year and individual as random effects. There was a positive correlation between the number of recaptures and the home range size. To

account for this correlation, the number of recaptures was included in each model as an independent variable. Home range visitation rate was analysed using likelihood ratio tests of generalized linear models with Poisson link function. Data manipulation, analyses, statistical testing and plotting was done using “R 2.14.1” (R Development Core Team 2012) using packages adehabitatHR (Calenge 2006), gpplib (Peng and Murta 2012), maptools (Lewin-Koh and Bivand 2012), lme4 (Bates et al. 2012), Matrix (Bates and Maechler 2012). Error margins of means always denote standard errors. Statistical significance was assumed for P values below 0.05.

Results

Home range size: effects of breeding status

Females and males had similar mean home range sizes over their entire lifetime (645 ± 16 and 652 ± 16 m², respectively; $\chi^2 = 2.41$, $df = 1$, $P = 0.121$). Mean home range sizes of adults and subadults differed significantly ($\chi^2 = 12.3$, $df = 1$, $P < 0.001$), with sizes of 636 ± 23 and 546 ± 11 m², respectively. Note here that, due to the positive correlation between number of recaptures and

home range size, the home range sizes estimated over the entire lifetime of an individual are on average slightly larger than those estimated over a period defined by a category such as age or season. The home ranges of adult females increased significantly with increasing population density (Fig. 1; $\chi^2 = 7.77$, $df = 1$, $P < 0.001$), whereas those of adult males did not change with density (Fig. 1, $\chi^2 = 0.62$, $df = 1$, $P = 0.432$). In contrast, home range sizes of subadults decreased with increasing population density (Fig. 1; females $\chi^2 = 7.89$, $df = 1$, $P = 0.005$; males $\chi^2 = 8.86$, $df = 1$, $P = 0.003$).

Home range size: effects of season

Overall, *M. natalensis* home ranges were significantly smaller during the breeding season than outside of it (325 ± 13 vs. 501 ± 10 m²; $\chi^2 = 67.48$, $df = 1$, $P < 0.001$). Surprisingly, male and female home ranges differed significantly in the non-breeding season ($\chi^2 = 7.24$, $df = 1$, $P = 0.007$) but not in the breeding season ($\chi^2 = 0.41$, $df = 1$, $P = 0.523$). In the breeding season, home ranges of both sexes became smaller with increasing population densities (Fig. 2; males: $\chi^2 = 332.77$, $df = 1$, $P < 0.001$; females: $\chi^2 = 281.91$, $df = 1$, $P < 0.001$). A similar pattern was also seen for

Fig. 1 Home range size (m²) of *M. natalensis* plotted against average population density (number per hectare) for females (a, c), males (b, d), adults (a, b) and subadults (c, d). The bold line shows the fitted regression, the dotted lines indicate the 95 % confidence interval of the fitted regression

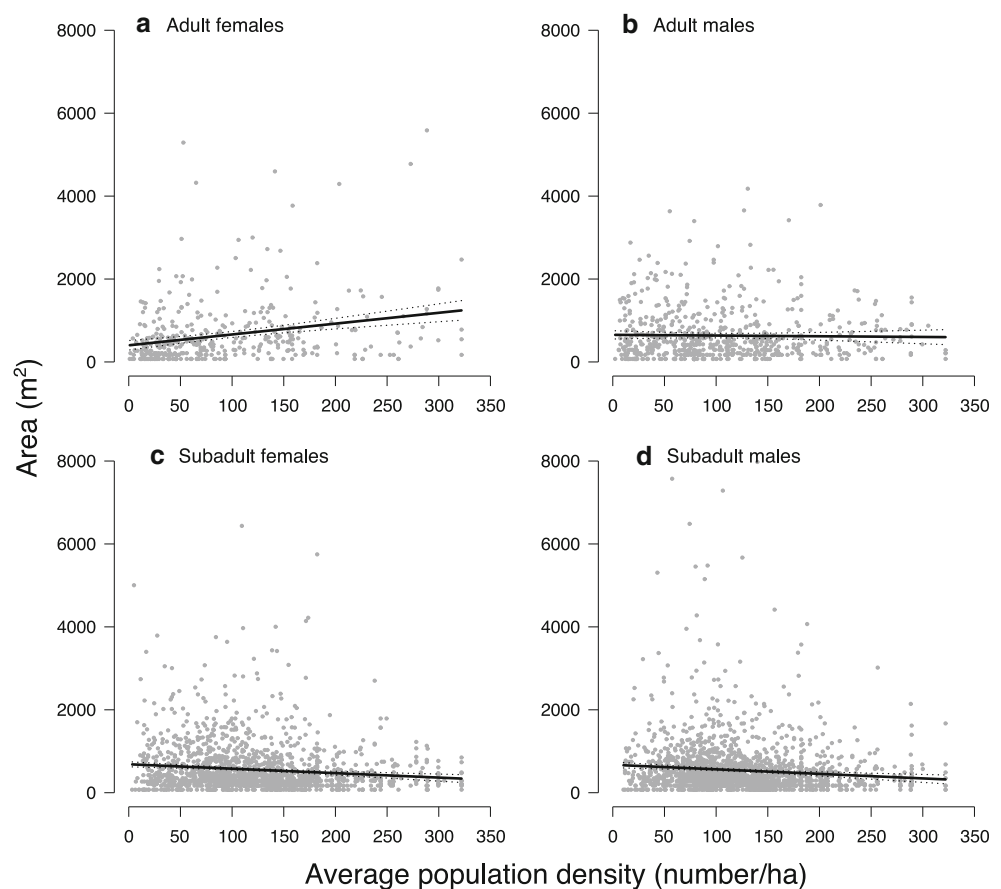


Fig. 2 Home range size (m^2) of *M. natalensis* plotted against average population density (number per hectare) for females (**a, b**) and males (**c, d**) in the breeding (**a, c**) and non-breeding (**b, d**) season. The **bold line** shows the fitted regression, the **dotted lines** indicate the 95 % confidence interval of the fitted regression

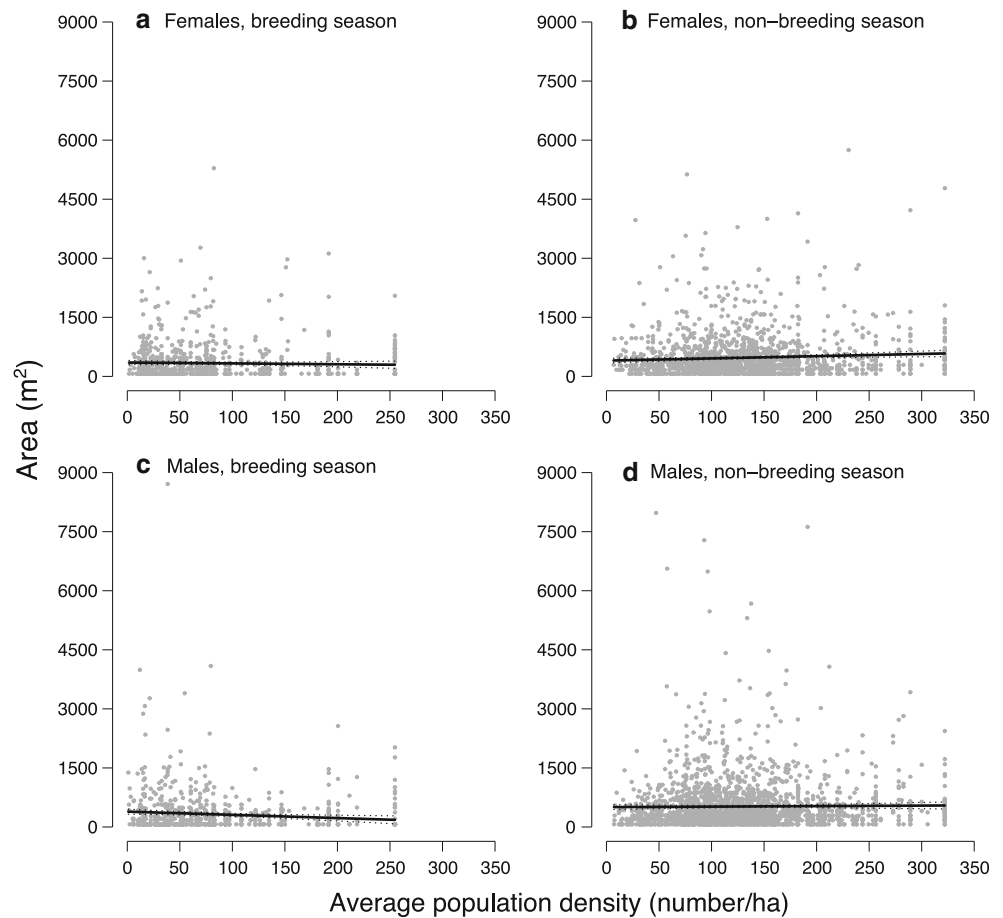


Table 1 Percentage overlap (mean \pm standard error) between categories in different seasons and for different age classes

Category	Sample size	Overlap category	
		Female breeding	Male breeding
Female breeding	835	45 \pm 1 %	39 \pm 1 %
Male breeding	799	47 \pm 1 %	38 \pm 1 %
Category	Sample size	Overlap category	
		Female non-breeding	Male non-breeding
Female non-breeding	1,686	74 \pm 1 %	83 \pm 1 %
Male non-breeding	2,130	77 \pm 1 %	82 \pm 1 %
Category	Sample size	Overlap category	
		Adult	Subadult
Female adult	416	70 \pm 2 %	71 \pm 2 %
Male adult	675	65 \pm 2 %	84 \pm 1 %
Female subadult	1,625	54 \pm 1 %	93 \pm 1 %
Male subadult	1,876	46 \pm 1 %	95 \pm 1 %

The first column is the animal category of which the home ranges are being overlapped by the home ranges of animals in the last two columns. Sample sizes are shown in the second column

males in the non-breeding season (Fig. 2; $\chi^2 = 367.67$, $df = 1$, $P < 0.001$), whereas home ranges of females increased during the non-breeding season (Fig. 2; $\chi^2 = 333.22$, $df = 1$, $P < 0.001$).

Home range overlap: effects of breeding status

For all categories, home range overlap correlated positively with density ($\chi^2 = 833.81$, $df = 1$, $P < 0.001$; Table 1). However, the mean overlap of the home ranges in the original dataset was never smaller than that of the randomly allocated home ranges, for all demographic categories ($P = 1$ for all categories, in all 100 cases; other test statistics not shown due to the high number of permutations; full results are shown in S2 to S5 in ESM), suggesting that the observed overlap patterns were a result of the random combination of home range sizes, shapes and locations in any given period, rather than actual spacing behaviour.

Home range overlap: effects of season

The effects of season on home range overlap were similar to those of breeding status (Table 1). There was a

significant positive correlation between overlap and population density ($\chi^2 = 84.57$, $df = 1$, $P < 0.001$). Again the overlap means of the original dataset were never smaller than those of the relocated simulation dataset ($P = 1$ for all categories, in all 100 cases; full results are shown in S6 and S7 in ESM).

Home range visitation rate

Visitation rate patterns did not seem to differ between different demographic categories (visits to home ranges of adults/subadults/males/females), and therefore seemed to be completely determined by the relative proportion of visitor categories (results are shown in S8 to S10 in ESM). As was the case for home range overlap, there was a significant positive correlation between visitation rate and population density ($\chi^2 = 134.51$, $df = 1$, $P < 0.001$), and between visitation rate and home range size ($\chi^2 = 106.04$, $df = 1$, $P < 0.001$). Visitation rates derived from the original data never differed significantly from simulated data ($P = 1$ for all categories, in all 100 cases), indicating that patterns of home range visitations were largely determined by the relative abundance of different population categories.

Discussion

We hypothesized that the high temporal predictability of abundant resources (Leirs et al. 1989; Leirs 1994), and high population densities throughout a large part of the year (Sluydts et al. 2009) would result in low levels of territoriality in females, as well as a non-clustered distribution of their home ranges. This, in combination with the high levels of promiscuity (Kennis et al. 2008), in turn predicted a low likelihood of territorial behaviour by males towards females or other males. Our data not only supported these predictions, but in fact showed that the overlap and visitation patterns were very similar to those generated by a simulated random positioning of home ranges, which suggests a complete lack of territoriality. We further observed a strong positive correlation between home range overlap and population density, providing additional support for a lack of territoriality. Although similar patterns can be seen in other species (Blair 1941; Fleming 1971; Dewsbury 2006), such a strong absence of territoriality is rare, and is perhaps relevant to the fact that this rodent species is prone to strong population outbreaks that can cause serious agricultural damage (Leirs et al. 2010).

Based on the suggestion that male multimammate mice use a ‘scramble competition’ mating strategy (Kennis et al. 2008), we expected to see a larger home range size of males during the breeding season than during the non-breeding season. Contrary to expectations however, we observed

equivalent male and female home range sizes during the breeding season, and no larger male home range size when compared to those in the non-breeding season. Kennis et al. (2008) found a positive correlation between body weight and the number of offspring, as well as a strong heterogeneity in reproductive success where a large proportion of males have low numbers of offspring. The patterns we observe may therefore indicate that *M. natalensis* males stay within their “normal” home range and use a dominance hierarchy rather than a true scramble competition mating strategy, or a combination of the two. This is not unlikely, as dominance hierarchies are commonly seen in high-density populations for several other species (Davis 1958; Wolff 1989), and this is hypothesized to be more economical when territorial defence becomes too costly (Waterman 2007).

Home range sizes of subadults decreased slightly with increasing population density. It is unlikely that this pattern stems from territorial behaviour, as home range overlap increased with density. One possible explanation for this could be that higher population densities are associated with increased predation pressure, which has been shown by Mohr et al. (2003) to result in reduced activity of *M. natalensis* and therefore smaller home ranges. This explanation is further supported by the observed negative correlation between survival and population density (Leirs et al. 1997). Another possible explanation involves resource availability: if a high availability of resources in the breeding season would result in high population densities, then it is possible that this increased availability results in smaller home ranges, but only if there is a positive correlation between resource availability in the breeding season and the availability later in the year during the high density period. A food supplementation experiment also suggested an inverse correlation between *M. natalensis* home range size and resource availability (Monadjem and Perrin 1998), while Leirs et al. (1990, 1997) showed a clear, positive correlation between rainfall and reproductive rates, presumably through increased resource availability.

Adult females showed no signs of territorial behaviour towards males or other females. Thus, while protection against infanticide may be one of the general drivers of promiscuity (Wolff and Macdonald 2004), our results suggest that infanticide in this species is not strong enough to induce territoriality. Adult females also exhibited a strong increase in mean home range size with density. Although the reason for this is unclear, it is possibly related to the relationship between population density and season. Densities are lower during the breeding season, and it is possible that the smaller than average home ranges of adult females at low densities are related to the need to stay close to their burrow to feed pups or to protect them against

infanticide (Ebensperger and Blumstein 2007). The larger home ranges in higher densities might then be attributed to a compensation period during which adult females need more food to compensate for lost reserves during pup feeding, or perhaps the larger home range estimates are a by-product of the relocation of the burrow nearer the end of the breeding season when densities become higher, a behaviour that has been observed for *M. natalensis* (B. Borremans, personal observation in a breeding colony) and other rodent species in captivity but not yet in field conditions (Brewster and Leon 1980).

Although a large body of support exists for many aspects of the theoretical interactions between resource availability, social spacing, population density and mating system, there are few datasets available through which it is possible to study the effects of density, season, reproductive status and sex on home range size and territoriality. By using a long-term CMR dataset we were able to study these aspects and provide substantial support for the expected influence of population density on home range patterns. Because of the role of *M. natalensis* as a reservoir host and vector for several important infections (Lassa virus, Mopeia virus, *Yersinia pestis*; Frame et al. 1970; Isaacson 1975; Wulff et al. 1977), our study also has implications for the study of the transmission of infections. Both home range overlap and visitation rates suggest that population-scale contact patterns are random and determined by the relative abundance of different demographic categories in the population. This indicates that the “random mixing” assumption that is often used in theoretical models of disease transmission but rarely true in wildlife populations may in fact be applicable to *M. natalensis* (Anderson and May 1979; McCallum et al. 2001), which makes it uniquely suitable as an epidemiological model system, especially for studying the role of density in directly transmitted infections (Lloyd-Smith et al. 2005; Borremans et al. 2011; Goyens et al. 2013).

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