

Home range size and overlap in female root voles: effects of season and density

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In small mammals living in highly seasonal environments, observational studies show that female home range size and exclusiveness are smaller in the nonbreeding winter season than in the breeding summer season. This has led to the notion that nonbreeding females are more social and decrease territorial behavior during winter. However, because territoriality decreases with increasing population density, and density normally increases during the breeding season, the effects of density and season on social structure are usually confounded. To find out which of the 2 factors explains space use, we experimentally established 3 high-density and 3 low-density root vole (*Microtus oeconomus*) populations in late spring and monitored the populations into the nonbreeding winter season. Population sizes were controlled throughout the breeding period to minimize seasonal variation in density. Home range sizes were larger in founder females than in field-born females but did not change with season or density. Area exclusively used by individual females was lower in winter than summer, and founder females decreased exclusiveness as density increased. We argue that this seasonal pattern of space use might be caused by variation in benefits of group living, whereas founder females also responded to density-dependent competition by reducing area exclusively used. *Key words:* density, *Microtus oeconomus*, season, space use. [*Behav Ecol* 19:139–145 (2008)]

In highly seasonal environments, small mammals have a distinct summer breeding season, whereas reproduction is low or absent during the winter (Tast 1966; Hansson 1984; Ostfeld et al. 1993). For many vole species, breeding starts as soon as the snow melts and the plants initiate growth (Negus and Berger 1977; Korn and Taitt 1987). Sexual maturation of year-born young then shows a seasonal pattern, where few juveniles born late in the summer reach maturation (Boonstra 1989; Gundersen and Andreassen 1998; Ergon et al. 2001), and dispersal rates are lower later than earlier in the breeding season (Steen 1994, 1995; Aars and Ims 2000; Crespin et al. 2002). Usually, population density of voles is low in the early spring before it increases toward a maximum in late autumn or early winter when reproduction ceases (Ostfeld et al. 1993; Ostfeld and Canham 1995). During the winter, density decreases again due to high mortality and low recruitment (Ostfeld and Canham 1995).

Seasonal changes in population demography are paralleled by changes in social organization. Home range size is typically larger at the beginning of the breeding season when density is low than in the end of the breeding season when density is high (Lambin and Krebs 1991; Sera and Gaines 1994), while home range overlap shows the exact opposite pattern (Lambin and Krebs 1991; Gliwicz 1997). During the nonbreeding season, the home ranges are usually small with large overlap (Erlinge et al. 1990; Priotto and Steinmann 1999; Priotto et al. 2002). For females, these seasonal changes in social organization, home range, and overlap have usually been explained by seasonal differences in reproductive status, climatic condi-

tions, and energetic requirements (reviewed in Ostfeld 1990). Firstly, in female small mammals, territorial behaviors are thought to result from defense of critical food resources needed for gestation and lactation and/or protection of pups against infanticide risks by conspecifics (Ostfeld 1985; Wolff 1993). Hence, when reproduction ceases during the winter season, home ranges of individuals should be less exclusive than in the breeding summer season. Furthermore, if territorial behavior functions mainly to defend pups against infanticidal neighbors rather than to acquire food resources, home ranges should be larger during the nonbreeding season (Wolff 1993). Secondly, the winter season coincides with the time of year when 1) females have much lower energetic requirements because they do not breed (e.g., Liu et al. 2003) and 2) harsh environmental conditions may force individuals to restrict movements in order to further save energy (McDevitt and Speakman 1994; Chappell et al. 2004). Therefore, seasonal changes in energetic requirements and energetic constraints may imply that home range sizes should be smaller during the winter. Thirdly, spatial aggregation of individuals may bring advantages during the winter, such as increased thermoregulation (Wiegert 1961; Madison 1984; West and Dublin 1984), which also may result in less exclusive home ranges during winter.

Population density influences many demographic characteristics in small mammals, such as dispersal (e.g., Aars and Ims 2000; Gundersen et al. 2002), survival (e.g., Prevot-Julliard et al. 1999; Lima et al. 2001), reproduction (e.g., Kviljo et al. 1992; Lima et al. 2001), and space use (e.g., Fortier and Tamarin 1998; Priotto et al. 2002; Luna and Baird 2004). Negative density-dependent changes in home range size or overlap have been found in many vole species (e.g., *Clethrionomys gapperi*: Bondrup-Nielsen 1986; *Microtus californicus*: Ostfeld et al. 1985; and *M. agrestis*: Erlinge et al. 1990, Agrell 1995), although some studies did not find effects of density on space use (e.g., *M. ochrogaster*: Sera and Gaines 1994 and

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M. californicus. Ostfeld 1986). The density dependence in space use responses is probably mediated by density-dependent competition. Given that the population structure changes predictably throughout the season (Ostfeld et al. 1993; Ostfeld and Canham 1995; Bjørnstad et al. 1998), seasonal variation in home range size and overlap in natural populations may thus solely be explained by density dependence.

As space use can correlate with both density and breeding season, observational studies based on seasonal patterns can hardly explain if density, breeding season, or an interaction between those 2 factors can cause the observed pattern. Here, we used field experiments to test if breeding status and density may explain seasonal space use patterns in female root voles (*Microtus oeconomus*) in South East Norway. The main breeding season for root voles lasts from May to the end of September (Tast 1966; Lambin et al. 1992). We therefore established 6 populations of root voles in fenced enclosures and monitored the populations from summer (May) to winter (late December) in order to measure changes in female space use (home range size and exclusive use of the range) according to the reproductive status, season, and changes in density of competitors. If space use matches the reproductive condition through territory requirements, we predicted that home range exclusiveness would be smaller in the nonbreeding season (winter) than in the breeding season (summer). If space use depends on energetic needs due to lactation, we predict also smaller home ranges during the nonbreeding season than the breeding season. If energetic constraints due to unfavorable winter conditions are more important than constraints due to lactation, we predict the opposite pattern in home range size. However, if space use is constrained solely by density-dependent competition, we predicted that home range size and exclusiveness would change irrespective of season and be higher in low-density populations than in high-density populations.

METHODS

The experiments were executed at Evenstad Research Station, South East Norway (250 meters above sea level, 61°25'N, 11°04'E) from end of May to mid December 2004. We established 6 source populations on May 28, before onset of reproduction, with different initial densities by introducing 4 females and 2 males in 3 low-density populations (ca., 40 individuals per ha), and 8 females and 4 males in 3 high-density populations (ca., 80 individuals per ha). All founder animals (individuals released into the enclosures) were F1 generation from a laboratory-bred population of F0 individuals. To reduce differences in food availability between populations, we used seminatural habitats with standardized meadow vegetation. The habitat patch available for each source population was 46 × 27 m large (Figure 1). To allow normal population size development during the summer, we connected these source populations with sink populations (sensu Pulliam 1988; for root voles: Gundersen et al. 2001) through a semipermeable chicken-wire fence that was impassable by breeding individuals (with body mass larger than 30 g, Le Galliard JF, unpublished data). This separation allowed us to compare resident individuals within populations across the season. Most of the breeding activity of root voles occurs from the end of May to September (Tast 1966; Lambin et al. 1992), whereas breeding often last until October in our enclosure system (Gundersen G, personal observation). Therefore, our census from May to December was appropriate to observe seasonal changes in social behaviors in this species.

All founder individuals and newborn individuals caught during trapping sessions were equipped with PIT-tags (passive integrated transponders, Trovan, Eid Aalten BV, Aalten, Holland) administered subcutaneously in the neck. Throughout the

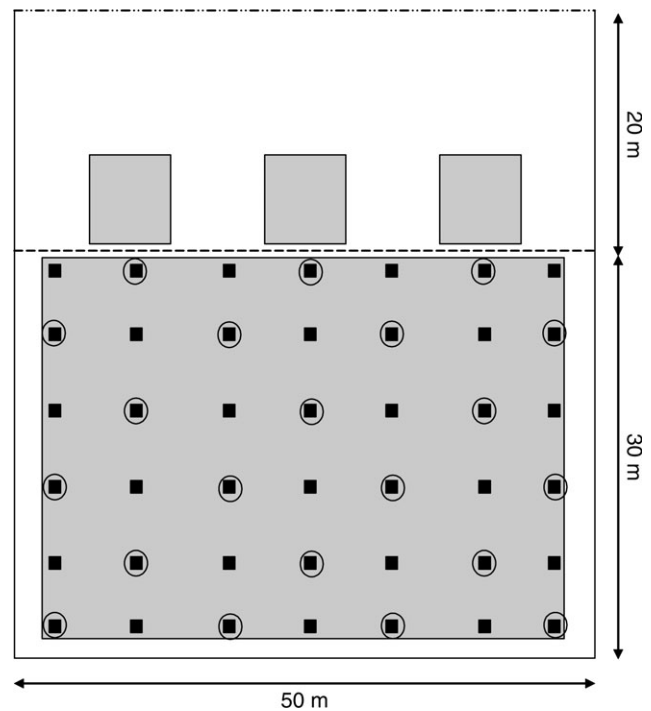


Figure 1
Design of the experimental populations. Each enclosure in our study consisted of a habitat patch (46 × 27 m) connected with sink populations (small gray squares) through a semipermeable chicken-wire fence that allowed juveniles to emigrate from the main populations. Emigrants that settled in the sink populations were removed approximately every 3 weeks. The small black squares show the distribution of live traps, and squares with circles around show the localization of the antennas used in the PIT-tag monitoring system.

study period, we monitored their social behavior by live trapping and observations using an automated PIT-tag system. Forty-two Ugglan live traps (Grahnb, Marieholm, Sweden) were evenly distributed in each source patch, divided in 7 rows with 6 traps in each row (Figure 1). In addition, we put tube-shaped single-coil antennas for PIT-tag monitoring at every second trap (Figure 1) and attached them to Trovan LID665 OEM PIT-tag decoders (EID Aalten BV, Aalten, Holland). The custom-made antenna consisted of a plastic tube (20 × 4 cm) and were placed on the ground along runways to maximize recording rates (Korslund and Steen 2006). Each time a tagged vole passed through the antenna, the decoder recorded PIT-tag ID, date, and time.

One of the high-density populations declined to 3 individuals and one low-density population went extinct before the first trapping. Therefore, we treated the declined population as a low-density population and released new individuals in the extinct low-density population with 4 adult females, 1 adult male, and 20 juveniles, making it a high-density population. This release procedure was followed to mimic the average state (number of adults and juveniles) of the other high-density populations at the time when voles were released into the population. The live trapping and PIT-tag monitoring for this study started on July 16 and lasted until December 14. During summer, we live trapped voles every 18th day for 3 consecutive days with 2 trapping sessions each day. The 2 days after live trapping, we recorded PIT-tag encounters in 3 source populations simultaneously, making 24-h recording in each population. This schedule continued until the middle of October. From the end of October, we trapped individuals every third week and recorded PIT-tags for 3 consecutive days

in each source population after trapping. We used only 24 h from each session of winter recordings for further analyses as we needed to match the amount of data to summer sessions to be able to compare results across seasons. However, because of the ultradian rhythm of root voles (Halle 1995), this duration of our recording session was sufficient to cover an activity cycle. In total, we performed 8 bouts of PIT-tag recordings.

The climatic conditions at our study site are typically seasonal with a cool vegetative growing season with temperatures above 0 °C from April to October and cold winters with temperatures below 0 °C from November to March. In the autumn/winter 2004, the first frost night occurred on October 24 (−0.8 °C), and the first day with mean temperature below 0 °C was October 27 (−2.8 °C). The first “permanent” snow appeared on November 18, with a snow depth of approximately 20 cm.

Home range estimations

We estimated the 50% kernel home range sizes of all resident individuals based on PIT-tag data using the Animal Movement 2.0 extension for Arc View 3.3 (Hooze and Eichenlaub 2000), and least squares cross validation (LSCV) to choose the correct smoothing (Seaman and Powell 1996; Seaman et al. 1999). To find the home range area exclusively used by each female, we used an overlay procedure provided in the Geoprocessing extension in Arc View 3.3 to extract the part of each home range that did not overlap with neighboring home ranges. We then calculated the proportion of the home range that was exclusive to each female. We decided to use the kernel estimation for several reasons. First, our data were site specific with multiple observations on one location. In this situation, applying a minimum convex polygon (MCP) method would therefore underestimate the overlap between individuals that cooccur in traps at the boundaries of their home ranges. Second, animals move around in a pattern causing spatiotemporal autocorrelation that often has been considered a statistical problem (Schoener 1981; Swihart and Slade 1985). Additionally, removal of such autocorrelation from the data may alter underlying biological patterns (de Solla et al. 1999; Blundell et al. 2001). Kernel estimators are robust to the presence of autocorrelation (de Solla et al. 1999; Barg et al. 2005), thus minimizing the problem of independence of relocations. Third, because our estimates were often based on very few point locations for each individual, MCP would also seriously underestimate home range size (Gautestad and Mysterud 1993). The kernel estimation, however, tends to overestimate home range size at small sample sizes (Seaman and Powell 1996; Seaman et al. 1999). To solve this problem, we chose to estimate a session-specific smoothing parameter, which we found by including all point locations in all enclosures in each trap session and calculated the session-specific smoothing parameter by LSCV (mean number of observations per session is 308.63). By applying this procedure, we restricted the overestimation of home ranges due to few observations, as well as the occasional underestimation we experienced in some instances. As the smoothing parameter may cause high variability between estimates using different smoothing parameters (Seaman et al. 1999; Hemson et al. 2005), the session-specific smoothing parameter ensured similar variability regime of home range estimates within each trapping session. Because we applied different smoothing parameters between sessions, however, we could get home range estimates with seasonal bias due to temporal variation in density. A regression analysis between density and the smoothing factor used for estimates in each session showed that this was not a concern here (adjusted $R^2 = -0.06$, $F_{1,6} = 0.593$, $P = 0.470$). Another potential problem with kernel estimates is that the method does not consider that fences, water, or similar

physical barriers may restrict movement. This is particularly important when spatial scales are small and observations are few. To reduce the effects of this problem, we subtracted any estimated home range area that fell outside the habitat patch.

Statistical analyses

We defined an individual as a disperser if it moved to the sink populations and did not return to the source populations. We focused our analyses on resident females only because there were very few males in each enclosure and excluded dispersers as they often were observed only once in the source population.

To account for the potential nonindependence among observations, plot and individuals within plot were considered as random effects in mixed-effects models with home range size and proportion of exclusive area as response variables. As fixed effects, we used age class (adult founder females vs. females born during the summer), breeding status (reproductively active after the first sign of gravidity and nonactive before starting to reproduce), density of resident females, and the proportion of adult females in the population. We modeled seasonal changes in 3 ways: a continuous change, a stepwise change between trapping session, and a drastic change between summer and winter. For the latter, we defined summer as the period from release to the end of October and winter from the start of November to the last trapping in December. Treatment (high and low initial density) was also included as a fixed factor to control for a possible effect of initial density. To assure that the number of resident females was an appropriate measure of density, we checked that the total number of females or the total number of individuals (males and females) did not explain more variation in home range size and proportion exclusive area. The trapping scheme we followed and the PIT-tag monitoring enable us to capture all individuals present in the populations (Aars et al. 1999). Therefore, we can assume that the observed number of individuals represents the population density in the enclosures, and we do not need to estimate population density. In an increasing population, the fraction of reproducing individuals goes down and reproducing individuals often have larger and more exclusive home ranges than nonbreeding individuals. This change in the fraction of breeding individuals can cause a spurious negative correlation between density and home range utilization despite a possible lack of direct effects of density on home range utilization. To control for this, we paid special attention to the fraction of reproducing individuals in the population during the model selection. To ensure linearity of effects and normality of residuals, home range size was log transformed and proportion exclusive area was arcsine transformed before analyzing the data.

To find the best model describing home range size and proportion of exclusive area, we used the forward selection procedure in R (R Development Core Team 2005) following recommendations of Pinheiro and Bates (2000).

RESULTS

Density

The change in density over season varied between plots. In 3 plots, density was stable or decreased as winter approached, whereas in the 3 other plots density increased, especially late in the season (Figure 2a). All decreasing populations had a high number of dispersing individuals compared with the 3 increasing populations (Figure 2b). In 2 of the decreasing populations, no juvenile females became resident and there was very little reproduction late in the season. In all 3 increasing populations, however, more offspring became resident

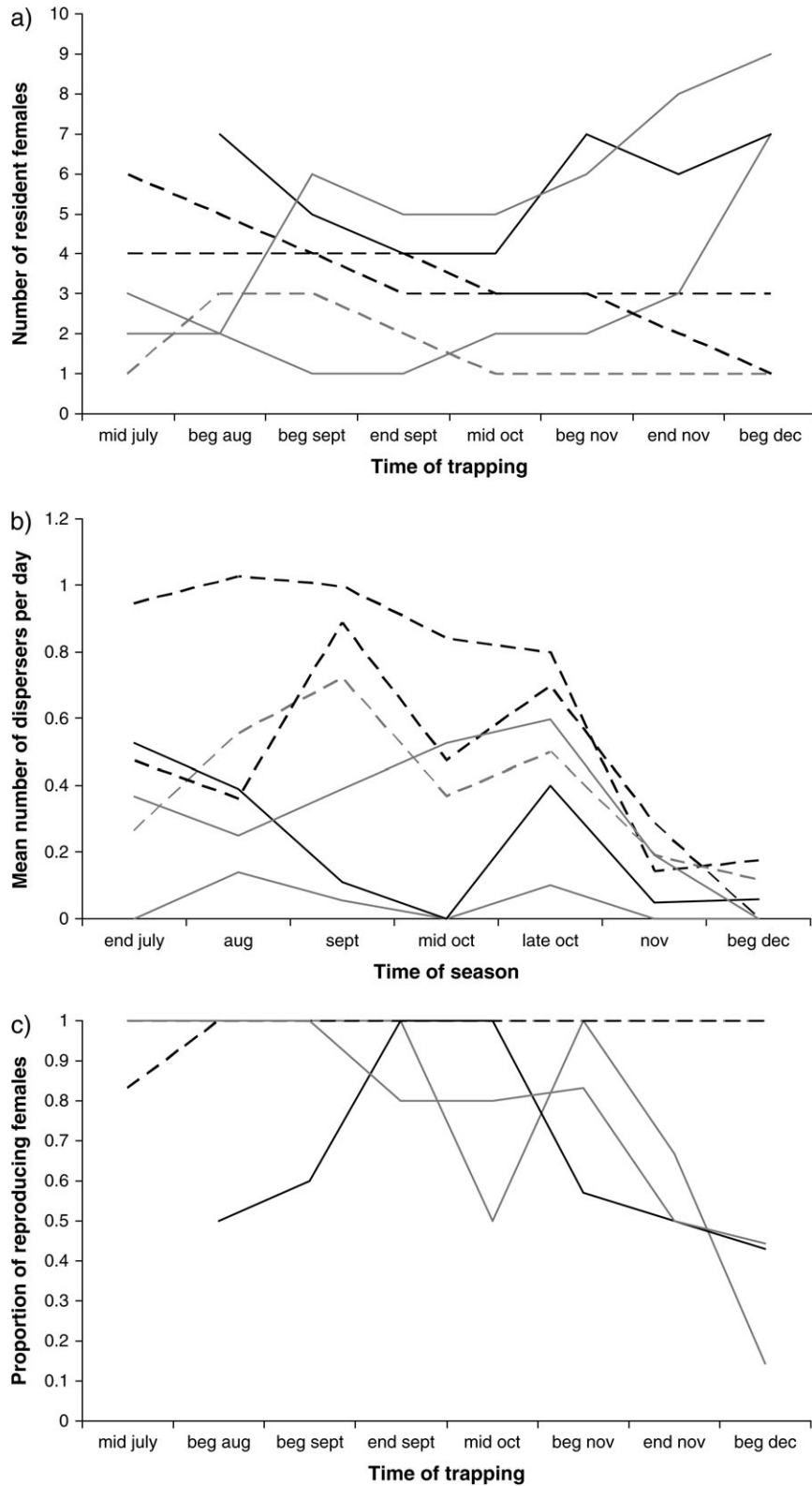


Figure 2 Seasonal changes in the population size (a), daily number of dispersers (b), and proportion of reproducing females (c) in the 6 study populations. High-density populations are shown with black lines and low-density populations with gray lines. Solid lines show the increasing populations, and dotted lines show the decreasing or stable populations.

Table 1
Observed mean home range size and mean proportion of exclusive area \pm standard error in founder and field-born resident females

	Founder females	Field-born females	
		Reprod	Nonreprod
50% Kernel home range	48.96 \pm 2.84	43.69 \pm 5.80	36.45 \pm 3.87
Proportion exclusive area	0.70 \pm 0.03	0.46 \pm 0.08	0.37 \pm 0.07

The values for field-born females are separated into reproducing (reprod) and nonreproducing females (nonreprod).

rather than dispersers. The total mean proportion of juveniles becoming residents was 0.19 ± 0.07 standard error in summer and 0.33 ± 0.15 in winter. Additionally, reproduction in the increasing populations stayed high well into winter, and several juvenile females started to reproduce as well (mean proportion of field-born females reproducing in summer: 0.53 ± 0.23 and in winter: 0.18 ± 0.08). The proportion of adult females in the populations correlated negatively with the number of resident females throughout the seasons (Figure 2c). In the 3 decreasing populations, all females were reproducing. In the increasing populations, however, the fraction of adult females decreased toward the winter because nonreproducing females were added to the populations due to reproduction.

Home range size and exclusiveness

The observed home range sizes and proportion of the ranges used exclusively by females can be found in Table 1. We selected the best model by applying a log-likelihood ratio test at each step of the selection procedure. Breeding status did not enter the best models of home range size and exclusive use of home ranges, and is not reported. However, effects of season and the proportion of reproducing females will be reported because of their importance. The model describing variation in home range size showed that older females had larger home ranges than younger females, and season and the proportion of reproducing females in the population did not affect home range size (Table 2).

The best model explaining area of exclusive use showed lower exclusive use in winter than in summer and a negative effect of female density on exclusive use in adult females, whereas young females did not respond to density (Table 2, Figure 3). The fraction of reproducing females in the populations did not affect proportion of exclusive use of the home range area (Table 2).

DISCUSSION

Home range size of female root voles was larger for founder individuals than for field-born individuals, and there was no effect of season or density on home range size. All females used a lesser proportion of their home range exclusively in winter than in summer. Additionally, founder females decreased exclusiveness with increasing density of resident females, whereas field-born females did not show any response in exclusive use of home range with density. At high density, therefore, the difference in exclusiveness between age classes disappeared irrespectively of season (Figure 3).

A gradual increase in density from spring to fall and early winter is known from most small rodents that fluctuate in numbers throughout the year (Erlinge et al. 1990; Turchin and Ostfeld 1997; Crespin et al. 2002; Priotto et al. 2002; Lima et al. 2003). However, because we minimized the increase in

Table 2
Model estimates with standard error, F values, and probability for home range size and the proportion exclusive use of home ranges (exclusiveness)

Model	Estimate \pm SE	F value	P value
Home range size			
Intercept	3.738 \pm 0.194	$F_{1,123} = 6733.722$	$P < 0.001$
Age class	-0.164 ± 0.105	$F_{1,41} = 5.168$	$P = 0.028$
Prop reprod	0.031 ± 0.198	$F_{1,123} = 0.529$	$P = 0.468$
Season	-0.130 ± 0.103	$F_{1,123} = 1.589$	$P = 0.210$
Exclusiveness			
Intercept	0.118 \pm 0.017	$F_{1,121} = 714.186$	$P < 0.001$
Season	-0.023 ± 0.006	$F_{1,121} = 34.217$	$P < 0.001$
Density	-0.008 ± 0.002	$F_{1,121} = 18.645$	$P < 0.001$
Age class	-0.069 ± 0.016	$F_{1,41} = 5.249$	$P = 0.027$
Prop reprod	-0.001 ± 0.014	$F_{1,121} = 0.008$	$P = 0.930$
Density \times age class	0.010 ± 0.003	$F_{1,121} = 13.604$	$P < 0.001$

The intercept represents estimates for founder females in the summer season, age class represents the difference between founder and field-born females, and season represents the change from summer to winter. Prop reprod, the proportion of females being reproductively active in the population.

density by connecting the source populations with sinks and allowed density to develop freely among our study populations, the population trajectories showed great variation where the densest population consisted of about 70 resident females per hectare and the least dense population had about 7 resident females per hectare (Figure 2a). Thus, we were able to disentangle the effect of season and density.

The seasonal change in the exclusive use of home ranges observed in this study apparently fits with the predictions of the hypothesis that space use is determined by the reproductive condition of females (Erlinge et al. 1990; Pusenius and Viitala 1993; Priotto and Steinmann 1999; Priotto et al. 2002). However, we found no difference in exclusive use between breeding and nonbreeding females, which does not support this hypothesis. We did find a difference in exclusiveness depending on age class, and other studies of reproduction and maturing of females in microtines show that late-born females often do not mature or start breeding the season of

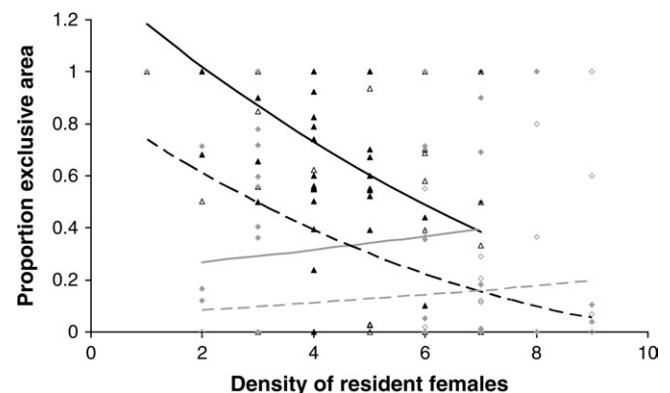


Figure 3
 Density and season-dependent variation in the proportion exclusive use of home ranges. Data shown are model predictions (lines) and observed values (points) in summer (solid lines and triangles) and winter (dotted lines and diamonds). Founder females are represented by black lines and solid points, whereas field-born females are represented by gray lines and open points. Data were analyzed on an arcsinus scale for home range exclusiveness.

their birth (Boonstra 1989; Gundersen and Andreassen 1998; Ergon et al. 2001). All founder females in our populations reproduced during the study, whereas only half of the field-born females reproduced. Thus, most breeding females were founders and not field born, but because breeding in field-born females did not affect exclusive use of home ranges (proportion exclusive home range in reproducing and non-reproducing field-born females is 0.46 and 0.37, respectively), we cannot support the predictions of exclusiveness due to territorial behavior of females in the breeding season.

In addition to the seasonal variation in home range exclusiveness, founder females showed a negative response to density, whereas field-born females kept a low proportion of exclusive area irrespective of density. To our knowledge, no other studies have shown a similar age-dependent density effect on overlap between home ranges, but density effects on exclusive use of home range size seem to be relatively common (Erlinge et al. 1990; Pusenius and Viitala 1993; Priotto et al. 2002; Hayward et al. 2004), although results are equivocal (for density-independent overlap, see Batzli and Henttonen 1993; Sera and Gaines 1994; Priotto and Steinmann 1999; and Luna and Baird 2004). Field-born females may overlap home ranges extensively during the breeding season if they have lower social status than the adult females when they mature in the natal population. The resulting skewed competition may lower the young females' ability to obtain exclusive areas, as it is easier to defend than acquire new area (Hammerstein 1981). Therefore, field-born females may already exist on a minimum required exclusive range and are unable to respond further to increased density. The convergence of the proportion exclusiveness between adult and juvenile females at high densities (Figure 3) supports this pattern.

Territorial behavior governed by energy requirements of females during breeding may also affect the home range size of individuals. The hypothesis that resource demand determines home range size predicts different responses in size over seasons depending on the relative importance of lactation during breeding and harsh environmental conditions during winter. We observed larger home ranges in founder females than in field-born females but found no effect of season. This result suggests that founder females require more energy than field-born females and that resource needs are similar for summer breeding and winter survival. The pattern of equal resource requirements when breeding and surviving during harsh environmental conditions was also found by Fournier et al. (1999) and may explain the mixed support for seasonal changes in home range size (effect of season: Erlinge et al. 1990; Sera and Gaines 1994; Hayward et al. 2004; Schradin and Pillay 2006; no effect of season: Lambin and Krebs 1991; Priotto and Steinmann 1999). Another hypothesis explaining territorial behavior is pup defense (Wolff 1993). The pup-defense hypothesis assumes that home range sizes change according to infanticide risk and predicts that breeding females will have small and exclusive ranges during breeding and larger, overlapping ranges in the nonbreeding season. We observed the opposite pattern in our study, which therefore fits the resource-defense hypothesis of Ostfeld (1985) better than the pup-defense hypothesis.

A third hypothesis concerning seasonal changes in home range size and exclusiveness is that social behavior of females relates to benefits of space sharing. Such benefits may explain both grouping behavior in winter and aggregations of field-born females in summer (e.g., Wiegert 1961; Agrell 1995). During the winter, an advantage of aggregating in groups may come from decreased loss of heat (Wiegert 1961; Madison 1984; West and Dublin 1984). This hypothesis could explain both the lower exclusive use of home ranges observed during the winter and why home range sizes did not change in a sim-

ilar manner. Environmental conditions during winter may force individuals to restrict movements in order to save energy (McDevitt and Speakman 1994; Chappell et al. 2004). However, if individuals live in groups, home range sizes may be maintained either because the increased number of individuals living in the area keeps runways open and free from snow and ice or because the energetic costs of winter climate are compensated for by benefits of aggregation. During summer, Agrell (1995) suggested that field-born females could obtain benefits by aggregating because grouping may increase the probability of future survival and reproduction by preparing females to social constraints before winter. Such benefits may explain why field-born females in our study overlapped extensively despite many being reproductively active in summer.

The traditional view of seasonal changes in space use caused by behavioral adaptations to changes in reproduction, resource availability, or population structure has struggled with a tight link between population density and season. Our experimental study supports the hypothesis that the seasonal pattern in exclusive use of home ranges is a response to benefits of sharing space. This hypothesis can explain the more extensive overlap in winter as well as overlap between field-born females in summer and the lack of seasonal pattern in home range size. The larger home range sizes and more exclusive use of the ranges in founder females than field-born females suggest that the age classes differ in their ability to acquire space. In addition, founder females show a density-dependent exclusive use of home ranges that might imply competition over resources both in summer and winter as exclusive use of home ranges changes with variation in density.

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