Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels

Jalene M. LaMontagne,* Cory T. Williams, Jenna L. Donald, Murray M. Humphries, Andrew G. McAdam, and Stan Boutin

Department of Biological Sciences, DePaul University, 2325 North Clifton Avenue, Chicago, IL 60614, USA (JML)
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada (CTW, JLD, SB)
Department of Natural Resource Sciences, Macdonald Campus, McGill University, Ste-Anne-de-Bellevue,
Quebec H9X 3V9, Canada (MMH)
Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada (AGM)

* Correspondent: jlamont1@depaul.edu

In territorial species, competitive asymmetries can result in the uneven distribution of food resources as high-quality individuals force young or subordinates to occupy smaller or lower-quality sites, or both. However, spatiotemporal variation in the production of resources also can influence an individual's ability to monopolize resources and, consequently, affect survival. We examined how spatial and temporal variation in food supply affects the distribution of resources among territorial food-hoarding red squirrels (*Tamiasciurus hudsonicus*) by mapping cone production over 62.5 ha of white spruce (*Picea glauca*) forest and measuring the interrelationships between territory size, cone supply, and survival during 4 years of low cone abundance in Yukon, Canada. Territory size and cone production within a territory varied 10- and 520-fold, respectively, with juvenile squirrels occupying smaller territories with fewer cones. Because of small-scale heterogeneity in the distribution of cones, territory size explained low to moderate amounts of the variation in territory-wide cone production within ($r_s =$ 0.49–0.69) and across ($r_s = 0.31$) years. Furthermore, spatial heterogeneity in cone production varied across years such that territory location was not useful for predicting relative food availability from one year to the next. Perhaps as a consequence of this heterogeneity, the number of cones within an individual's hoard was only weakly correlated with territory size ($r_s = 0.42$) and not correlated with territory-wide cone production. Hoard size better predicted overwinter survival than did territory size, whereas cone production on a territory was not predictive of survival. We suggest that caution be used in equating territory size with food supply because small-scale spatial heterogeneity can weaken this relationship, particularly in food-hoarders. Spatiotemporal variation in food abundance, in turn, may cause high-quality territories in one year to be low-quality territories in other years, which will limit the ability of individuals to assess the long-term quality of territories at the time of settlement.

Key words: food hoard, red squirrels, resource distribution, seed masting, spatial heterogeneity, survival, territoriality

Spatiotemporal heterogeneity in resource availability shapes the distribution of animals across the landscape. As such, how animals select habitat in variable environments and how habitat heterogeneity affects survival and reproduction are central issues in conservation biology and ecology (e.g., Boyce et al. 2003; Stamps and Swaisgood 2007). Habitat selection is affected not only by the suitability of the habitat, but also by the density of conspecifics within that habitat (Brown 1964; Fretwell and Lucas 1969). Furthermore, population demography and the spatial distribution of individuals are influenced by relationships between resource distribution and the social structure of populations (Altmann et al. 1996; Barton et al. 1996). For example, territoriality, whereby individuals gain exclusive access to resources through the defense of space, is thought to evolve when resources are distributed such that they are economically defendable (Brown 1964). In cases where the primary resource is food, territory size is expected to reflect a trade-off between benefits gained from exclusive access to the

food supply and the costs required for defense. For instance, the preemptive occupation of territories can force young or subordinate individuals to occupy lower-quality sites, a settlement pattern known as the ideal preemptive distribution (Pulliam and Danielson 1991), an extension of Fretwell's (1972) ideal despotic distribution. However, the benefits and costs of maintaining a specific territory size are unlikely to be static throughout an animal's lifetime, due to changes over time in the distribution and abundance of resources and conspecifics (Stamps 1991; Grant 1993).

Territorial behavior reflects competition for space and spatially distributed resources, and influences habitat selection, reproduction, and population dynamics (Clarke 1970; Packer et al. 2005). Individual variation in territory size may result from heterogeneity in the distribution of resources or from competitive disparities among individuals. Under the ideal free distribution originally proposed by Fretwell and Lucas (1969), territorial animals in environments where resources are homogeneously distributed would be expected to be uniformly distributed, whereas heterogeneity in resource distribution would result in unequal territory sizes but an equal distribution of resources across territories. Alternatively, individuals able to occupy the best habitat may force subordinates in a despotic way to occupy lower-quality patches where their fitness should be lower (reviewed in Adams 2001) or if resources are distributed homogeneously, young or subordinates may be forced into smaller territories, with the size of the territory reflecting the abundance of resources available to the territory holder (Steury and Murray 2003). In contrast, when the spatial distribution of resources is heterogeneous, young may establish territories in lower-quality habitat and territory size may not reflect resource availability. Such despotism is likely to be particularly important in populations where individuals maintain territories throughout the year and the recruitment of young following natal dispersal is limited by available space (i.e., when preemptive processes apply—Pulliam and Danielson 1991). This might occur because territorial residents are more likely to escalate confrontations (Alcock and Bailey 1997) or because juveniles are competitively inferior (Adams 2001), or both. The resulting asymmetry in resource distribution is expected to have important ramifications for survival and reproduction (e.g., Grande et al. 2009; Ritschard and Brumm 2011).

Despite the widely held view that the size and quality of the defended territory are major determinants of fitness (Brooker and Rowley 1995; Both and Visser 2000) relatively few studies have actually quantified differences in food availability between territory holders (e.g., Dill et al. 1981; Wauters and Lens 1995). Furthermore, despite the presumed critical importance of food hoards for survival during times of food scarcity (e.g., overwinter) in food-hoarding species (Vander Wall 1990), the relationship between the amount of food available on a territory and the amount of food hoarded is rarely quantified. Here, we investigate the degree to which spatiotemporal variation in resource availability affected the distribution of resources among territorial mast seed-consumers, red squirrels (*Tamiasciurus hudsonicus*), in Yukon,

Canada. Our primary objective was to understand how spatial heterogeneity in the production of white spruce (*Picea glauca*) cones affected the relationship between territory size and cone supply on trees within a territory, and then link these to hoard size and overwinter survival of red squirrels.

Within the boreal forests of North America, red squirrels defend individual, nonoverlapping, food-based territories throughout the year (Smith, C. C. 1968; Gurnell 1984; Price et al. 1990). Red squirrels clip and store conifer cones in autumn that are then husked during winter and spring to provide seed that forms the bulk of the squirrel's diet, and maintaining a territory with a central hoard of cones (a midden) is considered essential for overwinter survival (Smith, C. C. 1968). Juvenile squirrels acquire middens at independence through bequeathal (Berteaux and Boutin 2000) or by competing for access to vacant middens during which they tend to be subordinate to adults (Boutin et al. 1993). With the exception of territorial bequeathal by breeding females, individuals tend to occupy the same midden throughout their lives (Larsen and Boutin 1995).

The dominant conifer species in our study area, white spruce, produces variable cone crops over time (LaMontagne and Boutin 2007) that affect many life-history parameters of red squirrels (Boutin et al. 2006). In addition to temporal variation, there is considerable spatial variation in white spruce cone production by individual trees (LaMontagne and Boutin 2007). Variation in cone production among trees occurs due to variation in tree size, energy reserves, and microsite conditions including moisture and sunlight availability (Greene et al. 2002). We hypothesized that cone availability should be of critical importance to red squirrel survival, and that juvenile settlement would be affected by preemptive or despotic interactions, or both. From these hypotheses, we predicted that the production of cones within a territory would be an important determinant of overwinter survival, territory size would only be a good predictor of survival if it reflected the number of cones produced on the territory (i.e., if bigger territories indicated access to more cones), and juveniles would occupy smaller territories with fewer cones. Given the critical importance of cones as a food source in this system (Boutin et al. 2006; Fletcher et al. 2010) and the potential for squirrels to use hoarded cones over multiple years (Donald and Boutin 2011), it is possible that cone production within a territory in any given year might not reflect cone abundance within the hoard. Thus, in a low-cone year we also explored the relationship between hoard size, territory size, and territory cone production. In this scenario, we predicted that the number of cones within the hoard would predict overwinter survival, whereas cone production within the territory and territory size would only be useful if they were highly correlated with the size of the hoard. We also predicted that juveniles would occupy smaller territories with lower cone production and fewer hoarded cones.

MATERIALS AND METHODS

Study system.—We used the North American red squirrel and its primary food item in our study area, white spruce cones

containing seeds, for our model system. With the exception of the mating period when males temporarily vacate their territories to locate spatially dispersed receptive females, the territories of red squirrels encompass their entire home range (Gurnell 1984; Lane et al. 2009). Although squirrels will pilfer from the middens of others, such pilferage is rare in our study population, with stolen cones representing only 0.3% of the total cones that are larder hoarded (Donald and Boutin 2011). We examined the relationship between territory size and annual variation in territory-wide food supply (cone abundance on trees within a territory) across 3 low-food (nonmast) years (2002–2004). In a 4th year (2008), we also obtained data on hoarded food supply (cone abundance in middens). This research conformed to the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the University of Alberta Animal Care and Use Committee.

Study area.—Our study took place in the boreal forest region of southwestern Yukon, Canada (61°N, 138°W), in a 62.5-ha area composed of 2 study plots separated by 150 m and a major road. Grid stakes were established throughout each plot at 30-m intervals to aid mapping of territories and the distribution of cone production (see below). In 2008, territory mapping, cone production, and squirrel survival data were collected from only 1 of the 2 study plots (the more easterly plot). The study area ranges from 900 to 950 m elevation and experiences low precipitation (annual $\bar{X} = 230$ mm) falling primarily as rain during summer; mean snowfall is 100 cm (Krebs et al. 2001). The area is covered by white spruce forest, the dominant tree species and the only coniferous tree species present. The other tree species in the area is trembling aspen (*Populus tremuloides*) and the shrub understory is dominated by gray willow (*Salix glauca*). The structure of the white spruce forest is heterogeneous, ranging from open stands to closed canopy areas, and the trees vary in size (Dale et al. 2001).

Territory mapping.—We mapped red squirrel territories during late July to mid-August each year. Squirrels begin to clip cones in mid-August and cone caching is complete by late September (Fletcher et al. 2010). We assumed territory sizes remained constant during caching such that the cones within an individuals' territory during territory mapping were the resources available for overwinter survival and reproduction the following spring (Boutin et al. 2006; McAdam et al. 2007). All squirrels in each plot were uniquely ear-tagged and marked with colored wires, which facilitated mapping individual territories visually, and the sex and age class (juvenile or adult) of all squirrels were known (McAdam et al. 2007). We delimited the territorial boundary (see "*Statistical analysis*" below) based on the observation of behaviors indicative of territory ownership including territorial calls, caching, chasing another squirrel, scent marking, and eating in a tree. We initiated territory mapping at least 2 weeks after a female's offspring had weaned, when juveniles were expected to have settled on a territory (Berteaux and Boutin 2000). For males and nonbreeding females, the start of territory mapping was based on the weaning date of nearby offspring. Individual

territories were mapped for up to 3 weeks using direct observations until there were sufficient data to delineate a territorial boundary (i.e., territorial locations were recorded for all sides of a territory and if boundaries of adjacent squirrel territories were not contiguous, extra effort was devoted to be certain that unused space existed). Occasionally, red squirrels patrolled their territorial boundary and made multiple territorial calls as they did so; we used all of these behaviors and did not censor locations for time. Territory sizes were estimated using 100% minimum convex polygons using Hawth's Analysis Tools (Beyer 2004) in ArcGIS 9.0 (Environmental Systems Research Institute, Inc. 2004) for each territory based on the locations of at least 17 territorial behaviors following Vlasman and Fryxell (2002) and because there was an asymptote in territory size at this number of points (LaMontagne 2007). We only included territorial behaviors so off-territory forays were not included. Male forays off their territory for mating were not included because mapping was done outside of the mating season. In addition, we examined our raw data points (supplemented with the locations of territorial behaviors of nonfocal squirrels, not shown) and this supported the assertion that red squirrels defend contiguous territories and we therefore used 100% minimum convex polygons following C. C. Smith (1968), Boutin and Schweiger (1988), and Steury and Murray (2003).

Quantifying cone availability.—We determined the annual spatial distribution of cones produced per live white spruce basal area using 3 steps, thus reflecting the factors that influence white spruce cone availability. Cone availability is influenced by the size and density of trees (Greene et al. 2002), so 1st we determined the annual live spruce basal area density across our study area. We sampled a series of quadrats (100 m² each) at 60-m intervals over each study plot (30-m intervals in 2008 for the easterly plot only), originating at 0°, 120°, and 240° from grid stakes ($n = 558$ sampling locations; 186 stakes $\times$ 3 quadrats, total area sampled = 55,800 m²). Within the quadrats, the number of live white spruce trees and the diameter at breast height (DBH) of each tree > 5 cm DBH (capable of producing cones—LaMontagne and Boutin 2007) was recorded ($n = 5,587$ trees). We calculated the total basal area of live trees within each quadrat assuming trees were round. The basal area densities of trees per 10 m² cells were kriged (ordinary kriging, in ArcGIS 9.0) using an exponential semivariogram with information from the neighboring 8 stakes (to distances of approximately 100 m) over the study area to create a map of annual live spruce basal area density. We used exponential kriging both because we expected that the correlation of tree basal area density would decline with distance and because it provided a better fit to the empirical semivariogram than the spherical semivariogram based on cross-validation (Isaaks and Srivastava 1989—comparative preliminary analysis not shown). Cross-validation of the exponential model showed that a standardized root-mean-squared error for basal area in 2002 was 0.943 (close to 1 represents a good fit) and the standardized mean error was

0.003 (close to 0 represents a good fit—Environmental Systems Research Institute, Inc. 2003).

White spruce cone production varies spatially (Nienstaedt and Zasada 1990) even over relatively short distances (LaMontagne and Boutin 2007) and cone production varies with tree basal area (Greene et al. 2002). Therefore, as a 2nd step, we determined annual cone production per square meter of spruce basal area density each year in July or August, prior to cone caching by red squirrels. Every 60 m, the 3 live trees > 5 cm DBH closest to the grid stake had their cones counted and their diameter at breast height recorded ($n = 513$ trees/year). Estimates of cones per tree were obtained by a stationary observer counting the number of cones visible in the crown. The number of visible cones was scaled up to an estimate of total cones per tree using an equation partially derived from our study site (LaMontagne et al. 2005). Annual spatial distribution of cones per square meter of live spruce basal area was created using inverse distance weighting with a power of 1 (optimized in ArcGIS 9.0) and a distance of ~90 m. We used inverse distance weighting because cone production is expected to be more similar among trees locally (LaMontagne and Boutin 2007). As a final step to create overall annual maps of the distribution of cones within the study area we multiplied the distribution of live white spruce basal area for each year and the annual cone production per unit basal area for the appropriate year using the raster calculator of ArcGIS 9.0. The cone supply for each territory was estimated as the total number of white spruce cones produced within each 100% minimum convex polygon, using the appropriate annual cone production map described above and Zonal Statistics in Hawth's Analysis Tools (Beyer 2004). See Fletcher et al. (2010) and LaMontagne (2007) for more information on mapping cone availability.

In the fall of 2008, we also estimated the number of spruce cones hoarded by red squirrels following the caching season. The hoard size in the primary midden of each individual in the study areas was estimated by separating the midden into 4 quadrants and counting all closed cones to a depth of 20 cm in sixteen 0.6×0.6-m quadrats (4 quadrats per quadrant). Cones from the current year (new) were distinguished from cones from previous years (old) based on coloration; new cones were purple-green whereas old cones were brown. The length and width of the midden were measured and used to estimate the area of the midden (assuming an elliptical midden shape). Our index of the total number of cones within the hoard was calculated by multiplying average cone density within the 16 quadrats by the estimated area of the midden (Donald and Boutin 2011).

Overwinter survival.—A census of the red squirrel population was conducted every August and May, and individuals were considered to have not survived over winter if they did not appear in the census that followed territory mapping (Boutin et al. 2006). This assumption was made because red squirrels rarely change their territory location once becoming established (Larsen and Boutin 1995) and habitat quality outside of the study grids is poor. See Boutin et al. (2006) and McAdam et al. (2007) for further details on red squirrel data collection.

Statistical analysis.—We assessed the relationship between territory size and territory cone supply for each year separately using Spearman rank correlations, because the data were not bivariate normally distributed. To determine if the relative quality (cone supply) of a territory location (independent of territory size) was consistent across years, we estimated cone production on trees in 0.1-ha circular areas centered around each primary midden based on our cone density map and determined the between-year Spearman rank correlation in cone supply.

We examined differences in ln-transformed territory sizes using linear models with year, age class (adults and juveniles), and sex as factors, including all possible interactions. Annual trends in territory cone supply were examined based on comparing the mean and median values for each year, because ln-transformation did not resolve the violation of the assumption of equal variance across groups. We compared ln-cone supply between age classes and sexes using a 2-factor analysis of variance. Some individuals were mapped in multiple years (5 in 3 years and 10 in 2 years); therefore, we adjusted the degrees of freedom to represent the number of independent observations (i.e., individuals). Back-transformed mean territory size and 95% confidence intervals (95% *CI*s) are given in the "Results."

For the 2002–2004 data, we investigated the effects of territory size, cone supply on trees (total cones produced within each territory), age class (juvenile or adult), sex, and year on overwinter survival (survival to the May census following territory mapping) using logistic regression models. We constructed models using all linear combinations of parameters, and conducted a diagnostic test of the full model for lack of fit by checking the delta deviance measures for each data point to ensure they were not much greater than 4 (Hosmer and Lemeshow 2000); our model did not show evidence of lack of fit. Having found little support for an effect of cone production within a territory on overwinter survival with the initial 3 years of data (see "Results"), we subsequently measured an additional parameter in 2008, the number of cones hoarded within an individual's primary midden. We then used logistic regression models to investigate the effects of territory size, cone supply on trees, midden cone abundance, age class, sex, and age (in years). We used all combinations of parameters except that we never included age class and the continuous covariate "age" in the same model.

To compare the performance of the logistic regression models, we used Akaike weights based on Akaike information criterion corrected for small sample size (AIC$_c$) values (Hurvich and Tsai 1989). Akaike weights provide the strength of evidence for a model over others (Burnham and Anderson 1998) and odds ratios were calculated using model averaging based on the 90% confidence set (Symonds and Mousalli 2011). The relative importance of variables under consideration was compared by summing the Akaike weights of models in the confidence set; those variables tending to be in all of the top

models will have a summed Akaike weight/total confidence set weight closer to 1 (Symonds and Moussalli 2011). We examined the fit of the models using area under the curve estimates from receiver operating characteristic (ROC) curves (Hosmer and Lemeshow 2000). ROC values of 0.5 suggest no discrimination between groups, values between 0.7 and 0.8 represent acceptable model accuracy, and values above 0.8 represent excellent discrimination (Hosmer and Lemeshow 2000).

RESULTS

From 2002 to 2004, we generated a total of 93 territory minimum convex polygons based on 3,374 observed territorial locations ($\bar{X} = 36$ locations per territory $\pm$ 1 *SE*). We mapped 21 individuals in 2002 (14 adult females, 6 adult males, and 1 juvenile), 32 in 2003 (14 adult females, 13 adult males, and 5 juveniles), and 40 in 2004 (17 adult females, 10 adult males, and 13 juveniles). From 2002 to 2004, white spruce cone production was highly variable within years, evidenced by a high coefficient of variation in cones per tree (2.20 in 2002, 2.78 in 2003, and 3.10 in 2004; see Fig. 1), and the mean number of cones per tree was higher in 2002 (105 cones) than in 2003 (23 cones) or 2004 (34 cones; $n = 170$ trees), with median values of 6, 0, and 0 cones per tree, respectively. In 2008, we generated 35 minimum convex polygons based on 827 territorial locations ($\bar{X} = 24 \pm 4$ locations per territory) of 13 adult females, 17 adult males, and 5 juveniles. The within-year variation in white spruce cone production was highest in 2008, as evidenced by the coefficient of variation in cones per tree (6.0 in 2008), whereas the mean number of cones produced per tree (39 cones; median 0) was similar to that in 2004.

Variation in territory size and cone supply.—Between 2002 and 2004, red squirrel territory size varied 10-fold, from 0.09 ha to 0.86 ha, with a 520-fold range in our index of territory cone production, from < 100 to > 52,000 cones per territory (Fig. 2). The overall mean red squirrel territory size was 0.34 ha (back-transformed ln-mean and 95% *CI* of mean: [0.30–0.37 ha]) and contained an average of 8,763 cones (median = 4,913 cones) on trees. The overall ln-territory size model was highly significant ($F_{10,62} = 4.93$, $P < 0.001$). On average, adult red squirrels had territories that were 1.8 times larger than those of juveniles (adults: 0.38 ha, 95% *CI*: [0.34–0.42 ha]; juveniles: 0.21 ha, 95% *CI*: [0.17–0.25 ha]; $F_{1,62} = 19.37$, $P < 0.001$), and there was a significant effect of year on territory size ($F_{2,62} = 3.56$, $P = 0.034$). Mean territory size was significantly smaller in 2002 (0.26 ha, 95% *CI*: [0.21–0.31 ha]) than in 2003 (0.38 ha, 95% *CI*: [0.34–0.44 ha]; Tukey test, $P = 0.008$) and 2004 (0.35 ha, 95% *CI*: [0.29–0.42 ha]; $P = 0.047$); there was no significant difference in mean territory size between 2003 and 2004 ($P = 0.656$). We found that the density of red squirrels in the study area decreased from 2.5 squirrels/ha in the fall of 2002 to 1.8 squirrels/ha in 2003 and further declined to a low of 1.5 squirrels/ha in 2004. There was no significant difference in the ln-territory size between the sexes (females: 0.34 ha, 95% *CI*: [0.29–0.39 ha], males: 0.33 ha,
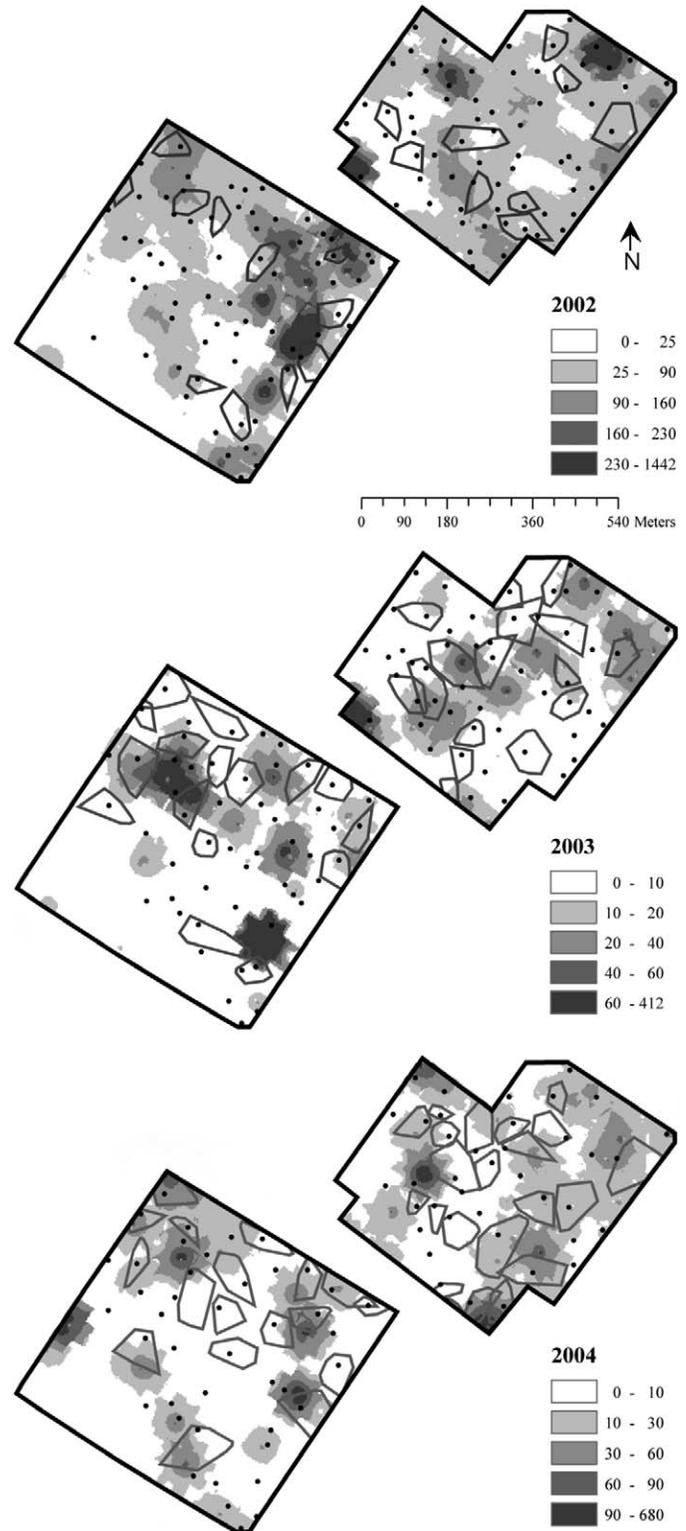

FIG. 1.—Spatial and temporal variation in precaching white spruce cone density (cones/10 m²) in 2002–2004 across the 2 study plots. White shows areas of low cone production with increasingly darker grays showing the areas of higher cone production. Black circles show the location of all primary middens in the red squirrel (*Tamiasciurus hudsonicus*) populations, and 100% minimum convex polygons of focal squirrel territories are shown. Note that the maximum value of the legend scale differs among years.
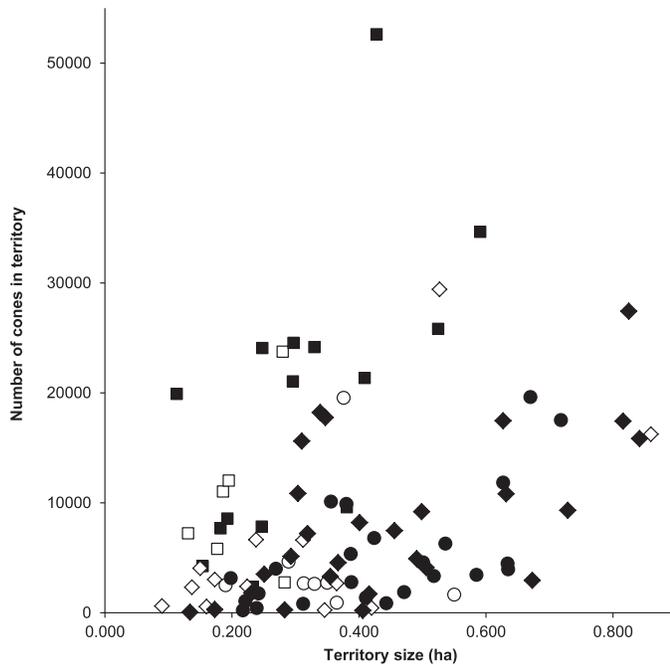
FIG. 2.—Relationship between territory size and the total number of white spruce cones contained within red squirrel (*Tamiasciurus hudsonicus*) territories and whether the territory owner survived over winter (shaded symbols) or did not survive (open symbols), measured as surviving until the May midden census (*n* = 93). All age and sex classes are pooled, with annual data shown as squares (2002, *n* = 21), circles (2003, *n* = 40), and diamonds (2004, *n* = 40).

95% *CI*: [0.28–0.39 ha], $F_{1,62} = 0.06$, $P = 0.807$), and there were no significant interactions between age class, sex, or year (all $P > 0.45$).

The overall ln-cone supply model including age class and sex was significant ($F_{3,69} = 3.86$, $P = 0.013$). There was a significant difference in cone supply between the age classes, with adult territories containing 3.3 times more cones than juvenile territories (adults: 5,635 cones, 95% *CI*: [4,443–7,663 cones]; juveniles: 1,733 cones, 95% *CI*: [820–3,665 cones]; $F_{1,69} = 10.26$, $P = 0.002$). There was no significant effect of sex (females: 5,070 cones, 95% *CI*: [3,514–7,315 cones] versus males: 3,924 cones, 95% *CI*: [2,530–6,085 cones]; $F_{1,69} = 0.002$, $P = 0.969$) or the age class × sex interaction ($F_{1,69} = 0.58$, $P = 0.449$) on cone supply. Territory cone supply was considerably greater in 2002 ($\bar{X} = 16,714$ cones; median = 12,028 cones) than in 2003 ($\bar{X} = 5,097$ cones; median = 2,513 cones) or 2004 ($\bar{X} = 7,521$ cones; median = 4,737 cones), but there was considerable overlap in territory cone supplies across years (Fig. 2).

In 2008, the density of squirrels on the study grid (2.1 squirrels/ha) was lower than in 2002 but higher than in 2003 or 2004. Our annual territory-wide estimate of cone production was lower in 2008 ($\bar{X} = 3,362$ cones; median = 1,757 cones) than in any year from 2002 to 2004. In 2008, territory size was affected by age class (back-transformed mean for adults: 0.19 ha, 95% *CI*: [0.16–0.23 ha]; juveniles: 0.09 ha, 95% *CI*: [0.05–0.12]; $F_{1,32} = 6.51$, $P = 0.016$) but not by sex ($F_{1,32} = 0.19$, $P = $

0.66). Similarly, territory-wide estimates of cone production were affected by age class (adults: 1,992 cones, 95% *CI*: [1,619–2,451 cones]; juveniles: 843, 95% *CI*: [535–1,327]; $F_{1,32} = 10.79$, $P = 0.003$), but not by sex ($F_{1,32} = 0.26$, $P = 0.61$). The index of cones hoarded in middens also was affected by age (adults: 6,056 cones, 95% *CI*: [4,105–8,934 cones]; juveniles: 72 cones, 95% *CI*: [2–2,263 cones]; $F_{1,32} = 19.56$, $P < 0.001$) with 2 of 5 juveniles not having any hoarded cones. Once again, sex did not affect the index of cones hoarded ($F_{1,32} = 6.67$, $P = 0.13$). On average, 57.0% ± 33.6% *SD* of the total cones in the midden were estimated to be from the current year, based on cone coloration.

Relationship between individual territory size and cone supply.—Annual white spruce cone counts estimated in 0.1-ha circular areas ($n = 59$) with primary middens at their center were either only weakly correlated or not significantly correlated between one year and a subsequent year. Cone production surrounding primary middens in 2002 was not correlated with production in 2003 ($r_s = 0.067$, $P = 0.612$) and cone production in 2003 was not correlated with 2004 ($r_s = -0.127$, $P = 0.339$), but 2002 was weakly correlated with 2004 ($r_s = 0.393$, $P = 0.002$). From 2002 to 2004, territory size and territory-wide cone production were weakly correlated (r_s) at 0.312, indicating that only ~10% of the overall variation in the ranks of cone supply was explained by territory size (and vice versa, based on the coefficient of determination [r^2]). Within age classes, the r_s-values were lower, 0.193 for adults ($P = 0.099$) and 0.260 for juveniles ($P = 0.297$). Within years, the correlation (r_s) between rank territory size and rank cone supply was highest in 2002 at 0.687 ($P < 0.001$), with moderate correlations in 2003 ($r_s = 0.493$, $P = 0.004$) and 2004 ($r_s = 0.562$, $P < 0.001$; Fig. 2). Thus, the rank of territory size explained 24–47% of the variation in the rank of cone supply within a year and most of the variability in cone supply could not be explained by territory size (Fig. 2).

In 2008, territory size and estimated territory-wide cone production were weakly correlated ($r_s = 0.42$, $P = 0.01$; Fig. 3A). Territory size and the number of cones hoarded also were weakly correlated ($r_s = 0.42$, $P = 0.01$; Fig. 3B), whereas the number of cones in the hoard was not correlated with the estimated production of cones on the territory ($r_s = 0.28$, $P = 0.10$).

Survival.—From 2002 to 2005, 29% (27/93) of the owners of mapped territories did not survive over winter; 10 of 29 adult males, 6 of 45 adult females, and 11 of 19 juveniles did not survive over winter. Individuals that survived tended to have larger territories (Fig. 2), and females had higher survival than males (83% versus 54%), whereas juveniles had lower overwinter survival than adults (42% for juveniles and 78% for adults). The most-parsimonious logistic regression model for overwinter survival included effects of territory size, age class, and sex (AIC$_c$ weight [w_i] = 0.197, ROC = 0.778). However, model uncertainty was high and empirical support for the "best" model was only 1.14 times that of the next best model (which did not include age class) and 1.89 times that of a model that included only age class and sex (Table 1). The
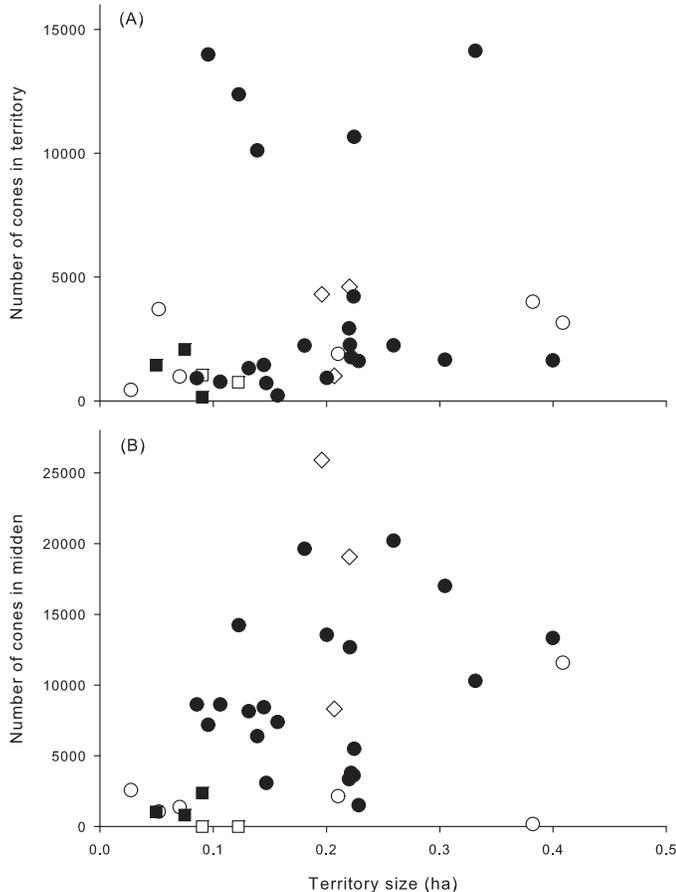
FIG. 3.—Relationship between territory size and the total number of white spruce cones contained within red squirrel (*Tamiasciurus hudsonicus*) A) territories and B) middens in 2008. Shaded symbols indicate squirrels that survived over winter (*n* = 24), whereas open symbols indicate squirrels that did not survive (*n* = 11). Juveniles are indicated by squares, whereas circles indicate 3- to 4-year-olds and diamonds represent 5- to 6-year-olds.

variable "sex" appeared in 100% of the models in the confidence set and the summed AIC_c weights for territory size made up 80% of the total AIC_c weight in the confidence set of models, whereas age class made up 61% of the AIC_c weight of the confidence set (Table 1). Territory cone supply and year appeared in models that made up only 24% and 16% of the weight of the full confidence set of models, respectively. All models in the confidence set showed acceptable model discrimination (ROC > 0.7; Table 1). Model-averaged parameter estimates are shown in Table 2.

Overwinter mortality of squirrels that held a territory in fall 2008 was 32% (11/35); 4 of 17 adult males, 5 of 13 adult females, and 2 of 5 juveniles did not survive over winter. Neither of the deceased juveniles had any cones hoarded in their middens in fall 2008. Five of the adult squirrels that died (4 females and 1 male) had fewer than 3,000 cones hoarded; all of these squirrels were 3 or 4 years of age. The remaining deceased adults (1 female and 3 males) had more than 10,000 cones hoarded; these squirrels were 4–6 years of age (Fig. 3B). Table 3 summarizes the AIC_c rankings of the 90% confidence

TABLE 1.—Summary of the 90% confidence set (cumulative weight [w_i] = 0.90), presented in descending order of w_i, of logistic regression models for the influence of territory size (ha), territory cone supply, age class, and sex on overwinter survival of red squirrels (*n* = 93 [74 individuals]) from 2002 to 2005. AIC_c = Akaike information criterion corrected for small sample size; ROC = receiver operating characteristic score.

Model	ΔAIC_c	w_i	ROC
Territory size + sex + age class	0.000	0.237	0.778
Territory size + sex	0.272	0.207	0.769
Sex + age class	1.280	0.125	0.732
Cone supply + territory size + sex	2.163	0.080	0.774
Territory size + sex + year	2.190	0.079	0.768
Cone supply + territory size + sex + age class	2.217	0.078	0.788
Territory size + sex + age class + year	2.364	0.072	0.780
Cone supply + sex + age class	2.494	0.068	0.753

set of logistic regression models for 2008–2009 overwinter survival in red squirrels. The most-parsimonious model included midden cones hoarded and age (as a continuous covariate) and this model was supported 3.41 times the next model that also included sex. All models in the confidence set included age and midden cones. Model-averaged odds ratios showed a positive effect of cone supply within the midden and a negative effect of age, although 95% *CI*s for these parameters were wide (Table 4).

DISCUSSION

We found that small-scale spatiotemporal heterogeneity in the distribution of cones weakened the relationship between territory-wide cone production and territory sizes of red squirrels and resulted in high intraspecific variation in access to food during 4 low-cone years. During our study, mean cone production by individual trees ranged from a low of 23 to a high of 105 cones per tree, which is substantially lower than cone production during mast years in which cone production has ranged from 592 to 1,078 cones per tree (Fletcher et al. 2010). Across 4 low-cone years, we measured a 10-fold variation in territory size, a 520-fold variation in territory-wide

TABLE 2.—Logistic regression odds ratios with 95% confidence intervals in parentheses for the best models, based on Akaike information criterion corrected for small sample size AIC_c weights, influencing red squirrel overwinter survival from 2002 to 2005. The odds ratio relates to increases in territory size in 0.1-ha increments, territory cone supply in 2,000 cone increments, juveniles and males given a value of 0, and adults and females given a value of 1. Year was included as a nominal variable with 2002 as a reference year.

Model	Odds ratio
Territory size	1.378 (0.195–9.739)
Sex	4.557 (0.832–24.953)
Age class	2.089 (0.721–6.051)
Cone supply	1.009 (0.290–3.515)
Year	
2003	1.003 (0.892–1.128)
2004	0.977 (0.822–1.162)

TABLE 3.—Summary of the 90% confidence set (cumulative weight [w_i] = 0.90), presented in descending order of w_i, of logistic regression models for the influence of territory size (ha), territory cone supply, midden cone supply, age, and sex on overwinter survival of red squirrels ($n = 33$) in 2008–2009. AIC$_c$ = Akaike information criterion corrected for small sample size; ROC = receiver operating characteristic score.

Model	ΔAIC$_c$	w_i	ROC
Midden cones + age	0.00	0.478	0.963
Midden cones + age + sex	2.45	0.140	0.963
Midden cones + age + territory size	2.58	0.132	0.963
Midden cones + age + territory cones	2.58	0.132	0.963
Midden cones + age + sex + territory size	5.24	0.035	0.963

TABLE 4.—Model-averaged logistic regression odds ratios with 95% confidence intervals in parentheses for the 90% confidence set, based on Akaike information criterion corrected for small sample size weights, influencing red squirrel overwinter survival in 2008–2009. Males were given a value of 0 and females were given a value of 1. Age is measured in years.

Model	Odds ratio
Midden cones	14.310 (1.159–176.642)
Age	0.016 (< 0.001–0.620)
Sex	0.867 (0.410–1.833)
Territory size	1.034 (0.640–1.672)
Territory cones	1.037 (0.693–1.551)

cone production, and low or moderate correlations between territory size and territory cone production within years. We also found the spatial distribution of cones was not well correlated across years such that relative quality of a site varied from one year to the next. Spatial variability in seed availability can be due to a combination of patchiness in plant density or spatial variation in local site conditions influencing seed production per plant, or both, such that territories of the same size, but in different locations, might produce very different amounts of seed and as such have important implications for the survival of the territory holders (e.g., Waser 1988). Further, when we subsequently measured hoarded food resources, we found that our index of hoarded cone supply was not correlated with cone abundance on trees within the territory and was only weakly correlated with territory size. Although the probability of survival was better explained by variation in territory size than by territory cone supply, neither of these parameters was as predictive of survival as the abundance of cones within an individual's primary midden in 2008. Our results indicate that territory size and territory food abundance may not accurately reflect territory quality when spatiotemporal variation is high and individuals are capable of hoarding resources. Juveniles, however, occupied smaller territories with lower cone production, had fewer cones in their primary middens, and had lower overwinter survival, consistent with predictions of an ideal despotic or preemptive model, or both, of habitat selection.

Cone supply and territory size.—Quantifying intraspecific variation in territory size and food supply is important for determining how the distribution of resources among individuals is linked to fitness (Wiens 1984; Łomnicki 1988; Boutin 1990). In contrast to predictions of the ideal free distribution (Fretwell and Lucas 1969), territory size in red squirrels was not adjusted such that all individuals had equal access to food, because cone production varied widely across territories during all 4 low-cone years. We found that juveniles occupied much smaller territories with lower cone production and smaller cone hoards indicating they were competitively inferior to adults. This competitive asymmetry might be a function of their smaller size relative to adults or it could be because they are competing against established territory holders. In other species, once an individual establishes

territorial residency, they are more likely to escalate confrontations with invaders and win contests, even if they are smaller (Krebs 1982; Alcock and Bailey 1997). This competitive asymmetry can subsequently result in the recruitment of young individuals into subprime habitat (e.g., Wauters et al. 2001; Oro 2008).

Although territory size and cone production were correlated, the correlation was relatively weak, indicating that territory size is not a particularly good indicator of white spruce cone availability on trees within a territory. For example, a 0.4-ha territory could have anywhere from near 0 to 20,000 cones. The weak correlation between territory size and territory-wide cone supply is consistent with previous studies indicating that local cone production by white spruce trees is relatively heterogeneous at a spatial scale that is relevant to territorial red squirrels (Greene et al. 2002; LaMontagne and Boutin 2007). The patchy distribution of cones even during low-food years results in cone escapement (e.g., cones not consumed by squirrels) because squirrels on territories with a high local cone density are unable to clip and hoard all cones within their territory boundary (Fletcher et al. 2010).

We also found that cone density on trees within 0.1-ha circular plots centered on primary middens was either not correlated or only weakly correlated from one year to the next, which suggests that relative habitat quality may not be consistent over time, at least across low-cone years. However, the location of our study area was designed to encompass a relatively contiguous area of high-quality squirrel habitat and we expect that the correlation would be higher if we included low-quality sites located off the study area. That is to say, we expect squirrels are capable of selecting potentially high-quality habitat (e.g., Andrén and Delin 1994), although the realized quality of selected habitat may vary widely during low-cone years. The high level of spatial heterogeneity in cone production within our study area combined with variation in territory size resulted in cone production on a territory varying by over 2 orders of magnitude within 2 of the 3 years during this study (2003 and 2004), and almost 3 orders of magnitude overall during this study. Spatial variation in cone production among trees also occurs during mast years (LaMontagne and Boutin 2007), but because cones tend to be generally abundant during mast-seeding events, and most squirrels hoard < 10% of cones on their territories under mast conditions, it is likely

that even squirrels on small territories may be saturated by cone production (Fletcher et al. 2010).

Although squirrels could relocate to higher-quality habitat during nonmast years, this rarely occurs (Smith, M. C. 1968; Larsen and Boutin 1995), possibly with the exception of females that bequeath their territories to one of their offspring (Price and Boutin 1993; Berteaux and Boutin 2000). Individuals of other species occupying year-round territories rarely change the location of their territory, including kangaroo rats (*Dipodomys spectabilis*—Waser 1988), Ural owl (*Strix uralensis*) pairs (Lundberg 1981), and numerous tropical passerines (Rowan 1966). Familiarity with a territory and its neighbors may increase survivorship or foraging efficiency, and reduce the energy needed for territorial defense (Ydenberg et al. 1988; Price et al. 1990). For red squirrels, movement to habitat with more cones on trees may not be beneficial because cone production within the territory is not correlated with the abundance of cones hoarded in the midden, at least during low-cone years.

Survival.—In our initial study period (2002–2005), we found that overwinter survival was influenced by the sex of the territory owner, as well as territory size and age class of the territory owner. Consistent with previous studies of red squirrels at Kluane (McAdam et al. 2007) and at other locales (Steury and Murray 2003), juveniles had lower survival compared to adults and adult females had higher overwinter survival than did adult males. Steury and Murray (2003) found that red squirrels with smaller territories had higher mortality and suggested that individuals with smaller territories likely had reduced access to food (i.e., fewer cones) and were consequently nutritionally limited or at greater risk of predation due to increased time spent foraging. We anticipated that the abundance of conifer cones would be a better predictor of survival than territory size because conifer seed is regarded as the primary food source of red squirrels in the boreal forest (Smith, C. C. 1968). Thus, we were surprised to find initially that that territory size better explained survival of adult females than did territory-wide cone production. However, squirrels may switch to mushroom hoarding, if available, during low-cone years (Fletcher et al. 2010) and an increase in territory size may have led to more access to alternative food sources, including mushrooms. We did not measure mushrooms available to individual squirrels, nor do we know if the distribution of mushrooms at our study site is more homogeneous than the distribution of cones. It is also unclear if red squirrels can maintain themselves on a low-quality mushroom diet alone (Smith, M. C. 1968) and therefore mushrooms are likely to supplement, rather than replace, a cone diet. Our subsequent measurement of hoarded resources (in 2008) revealed that the number of cones hoarded in middens was an important determinant of overwinter survival; territory size was not a useful predictor of survival when hoarded cone abundance was included in the model. We found that territory size was correlated with our midden cone supply, similar to Steury and Murray (2003), but this relationship was relatively weak, indicating that territory size was a relatively poor predictor of the hoarded cone supply. Surprisingly, cone production on the territory was not correlated with the midden cone supply. This lack of correlation may be partly due to time lags between cone production and consumption (Gurnell 1984). In support of this hypothesis, we found that the proportion of cones within the midden that was from the current year was highly variable. Because cone production at a particular territory was only weakly correlated from one year to the next, current cone production would not be expected to be reflective of cones hoarded in previous years. This effect is likely to be particularly pronounced in our 2008 data set because of the high spatial variation in cone production in that year.

Consistent with an earlier red squirrel study (e.g., Steury and Murray 2003), we found that the survival of adult males was lower than that of females, at least during our initial period of study (2002–2005). Although the mechanisms responsible for sex-specific mortality rates in red squirrels are unknown, it may relate to the period during which males temporarily abandon their territories during the breeding season (Smith, C. C. 1968; Lane et al. 2008). Although reproductive costs are often thought of in terms of risk of energy or nutrient exhaustion, survival costs associated with increased susceptibility to predation or pathogens also can be important (reviewed in Magnhagen 1991). Male red squirrels may be particularly vulnerable to predators when they leave familiar habitat to search for receptive females. Differences in access to resources also can be important, although males tended to have more cones, not fewer, hoarded in their primary middens (Donald and Boutin 2011). We also found lower rates of survival in older squirrels (within the 2008 data set), consistent with previous findings for this population (McAdam et al. 2007).

Compared to adults, juveniles had smaller territories with fewer cones on trees and within their middens. Although we predicted that cone supply would be a crucial determinant of survival during a squirrel's 1st winter, we initially found no relationship between territory size or territory-wide cone production and overwinter survival for juveniles. However, in 2008, we found that both juveniles that died had failed to hoard any cones. A critical determinant of juvenile survival in low-cone years might be associated with their ability to acquire a territory with a preexisting hoard from a previous territory owner. Although juveniles are likely to be competitively inferior and unable to evict an existing territory holder, empty territories will become available due to mortality, as evidenced by the declining population density from 2002 to 2004. The increase in territory size across years coincided with a decrease in the density of squirrels on the study grids. Density had increased again by 2008, likely due to a moderate masting event that occurred in the fall of 2005 (Krebs et al. 2012). It also is possible that juvenile red squirrels will attempt to survive in suboptimal areas on small territories with few cones until better territory sites become vacant (Kemp and Keith 1970).

White spruce cone production is both temporally and spatially variable (Nienstaedt and Zasada 1990; Greene et al.

2002; LaMontagne and Boutin 2007; Fletcher et al. 2010), which directly influences the availability of cones within a territory. We acknowledge that sources of error in our maps of cone availability will exist based on imperfect sampling of basal area density of trees and variation in cone production that would propagate into our estimates of cone availability within territories. However, we did directly measure the diameter at breast height of 5,582 trees in 55,800 m^2 of our study area, we cross-validated our maps of basal area and cones per unit basal area, and we spent considerable time throughout the study area each year, and qualitatively the map of cone production reflected areas that appeared to have high cone production and low cone production (J. M. LaMontagne, pers. obs.).

In this study, we mapped the distribution of the primary food resource (white spruce cones) and individual territories across 4 nonmast (i.e., low-food) years in a population of persistently territorial food-hoarding red squirrels. We found high levels of spatiotemporal variation in the production of cones, combined with intraspecific variation in territory sizes, which resulted in large individual variation in access to cones on trees. Juvenile territories were smaller with fewer cones on trees. However, overwinter survival was not related to cone production within a territory but was affected by the supply of hoarded cones available in middens. Our results suggest that territory size and cone production on the territory may not be an effective measure of territory quality in cone-hoarding species.

ACKNOWLEDGMENTS

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