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Original article

Living on the edge: Space use of Eurasian red squirrels in marginal high-elevation habitat

Claudia Romeo, Lucas A. Wauters*, Damiano Preatoni, Guido Tosi, Adriano Martinoli

Dipartimento Ambiente, Salute, Sicurezza (DASS), Università degli Studi dell'Insubria, Varese, Via J.H. Dunant 3, I-21100 Varese, Italy

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ABSTRACT

In marginal habitats located at the edge of a species' range, environmental conditions are frequently extreme and individuals may be subject to different selective pressures compared to central populations. These so-called edge or marginal populations tend to have lower densities and reproductive rates than populations located in more suitable habitats, but little is known about local adaptations in spacing behavior. We studied space use and social organization in a population of Eurasian red squirrels (*Sciurus vulgaris*) in a high-elevation marginal habitat of dwarf mountain pine (*Pinus mugo*) and compared it with spacing patterns in high-quality Scots pine (*Pinus sylvestris*) forest at lower-elevation. Home ranges and core areas were larger in the marginal habitat. In both habitats, males used larger home ranges than females, but sex differences in core area size were significant only in the edge population. Patterns of core area overlap were similar in both habitats with intra-sexual territoriality among adult females and higher degrees of inter-sexual overlap, typical for the species throughout its range. However, low densities in the edge population resulted in higher female by males overlap in spring-summer, suggesting males increased home ranges and core areas during mating season to augment access to estrus females. Thus, in the marginal habitat, with low food abundance and low population densities, linked with extreme winter conditions, squirrels, especially males, used large home ranges. Finally, squirrels responded more strongly to variation in food availability (inverse relation between home range size and seed abundance), and even to fluctuations in density (inverse relation between core area size and density of animals of the same sex), in the marginal than in the high-quality habitat, suggesting high behavioral plasticity to respond to the ecological constraints in marginal habitats.

1. Introduction

Limits to species' distribution can be imposed by geographical barriers or, more often, by ecological conditions that become suboptimal for their survival. Hence, in so-called 'marginal habitats' located at the border of a species' range, environmental conditions are frequently extreme and individuals are subject to different selective pressures compared to central populations (reviewed in Kawecki, 2008).

Populations living in such marginal habitats at the edge of the species' distribution are often referred to as edge populations (or marginal populations). They are usually sink-populations (reviewed in Dias, 1996) that have lower densities and reproductive rates than populations located in more suitable habitats (Vucetich and Waite, 2003; Sagarin et al., 2006), and are therefore more affected by small changes in ecological factors (Gonzalez-Megias et al., 2005; Manier and Arnold, 2005). On the other hand, if these populations are enough isolated and immigration and gene flow are reduced, they can develop local adaptations to such extreme habitats, diverging from central, source-populations (Garcia-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997; Case and Taper, 2000; reviewed in Kawecki, 2008). For both these reasons, studying marginal populations can be very interesting to understand contraction and expansion mechanisms of geographic ranges and, in general, species' response to climate and habitat alterations (Thomas et al., 2001; Wiens and Graham, 2005; Parmesan, 2006).

Several studies explored variability in vertebrate's population dynamics along altitudinal or latitudinal gradients and compared vital rates of central and marginal populations (e.g. Spencer and Steinhoff, 1968; Millar and Innes, 1985; Zammuto and Millar, 1985; Ferguson and McLoughlin, 2000; Badyaev and Ghalambor, 2001; García and Arroyo, 2001), but few have focused on behavioral adaptations in edge populations involving space or habitat use

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* Corresponding author. Tel.: +39 0332 421538; fax: +39 0332 421446.
E-mail address: l.wauters@uninsubria.it (L.A. Wauters).

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(Smith, 1974 on pikas; Mehlman, 1989 on primates; Sound and Veith, 2000 on western green lizards; Caudron et al., 2001 on grey seals; Sunde et al., 2001 on Tawny owls).

The aim of this study was to investigate space use by Eurasian red squirrel (*Sciurus vulgaris*) in a high-elevation forest with low resource abundance (Rodrigues et al., 2010) in order to understand if living on the edge can affect species' spatial behavior. Eurasian red squirrel is a widespread arboreal mammal that exploits a wide variety of forest habitats along a wide geographical ranges (Lurz et al., 2005). Species' demography, social behavior and space use are strongly affected by its main food resource, tree seeds, whose availability is highly variable in seasons and years (Wauters and Dhondt, 1992; Wauters and Lens, 1995; Lurz et al., 2000; Wauters et al., 2004; Boutin et al., 2006; Zong et al., 2010). We collected radio-tracking data and estimated food availability in two populations living in different conifer forests. One is an edge population located at the upper elevation limit of squirrel's distribution in a dwarf mountain pine (*Pinus mugo* Turra) wood with extreme weather conditions (Rodrigues et al., 2010) hereinafter called mountain pine forest; the second one is a high density population (Wauters et al., 2008) in a lower-elevation, montane Scots pine (*Pinus sylvestris*) forest (hereinafter called Scots pine forest).

In studies carried out in single sites, spatio-temporal variation in squirrel home ranges is negatively correlated with the availability of tree seeds (e.g. Lurz et al., 2000; Wauters et al., 2005; Di Pierro et al., 2008). Therefore, we predict that in mountain pine forest, where food availability is lower, squirrels have larger home ranges and core areas than in Scots pine forest. We explore the partial effects of food availability and (intra-sexual) squirrel densities on home range (core area) size in both habitats.

2. Materials and methods

2.1. Study area

We studied red squirrels and counted cones at two study sites in the central Italian Alps, Lombardy, N. Italy. Distance between the two areas is 11 km. Cancano (CAN the mountain pine forest, 46°33′N, 10°15′E, elevation from 1940 m to 1970 m a.s.l.) is located in the Stelvio National Park in a high-elevation valley. The study site (60 ha, mean tree density ± SD = 2888 ± 1128 trees ha^{-1}) is almost entirely composed of a homogeneous dwarf mountain pine (*P. mugo* Turra) subalpine woodland. *P. mugo* seeds, representing the major and almost unique food resource for squirrels, mature inside small cones in September and are dispersed by wind the next spring. Mean energy content per cone is 5.9 kJ (our unpubl. data).

The second study site, Oga (OGA, the Scots pine forest, 46°28′N, 10°22′E, elevation from 1280 m to 1450 m a.s.l.), is part of a mature mixed montane conifer forest (47 ha, mean tree density ± SD = 765 ± 251 trees ha^{-1}), dominated by Scots pine (*P. sylvestris*, 88.7% tree cover) with some Norway spruce (*Picea abies*, 8.8%) and larch (*Larix decidua*, 2.5%). Both Scots pine and larch seed-dispersal starts in late spring, after snow melting, while Norway spruce cones ripen in autumn and seed fall occurs from winter until late spring. Mean energy content per cone is 7.5 kJ for Scots pine, 51.1 kJ for Norway spruce and 9.4 kJ for larch (Salmaso et al., 2009).

The two sites are characterized by a continental pluviometric regime typical of the central alpine region, with low to moderate annual precipitation (2003–2009: mean ± SD = 564 ± 226 mm in Cancano, 809 ± 233 mm in Oga) occurring mostly in summer. The mountain pine forest has a high-elevation climate with mean annual temperature below 3 °C (2003–2009: mean ± SD = 2.6 ± 0.5 °C) and long, cold winters (mean monthly temperatures below 0 °C up to 6 months a year). Duration and depth of permanent snow cover vary annually, but between 30 and 150 cm of snow tend to cover the study site between early November and late April–May (Cancano meteorological station, 1948 m a.s.l., A.R.P.A. Lombardy). Due to its lower altitude, the Scots pine forest has a warmer climate with higher mean annual temperatures (2003–2009: mean ± SD = 8.1 ± 0.6 °C) and mean monthly temperatures below 0° for no more than 3 months a year (Bormio meteorological station, 1230 m a.s.l., A.R.P.A. Lombardy). In most years, snow covers the ground from December till late March.

2.2. Estimating food availability

Tree-seed abundance of conifers was estimated as described elsewhere (Salmaso et al., 2009). Briefly, we determined woodland composition in 20 vegetation plots of 20 by 20 m (400 m^2), centered on the trapping stations. In each plot, the number of trees was counted, and the diameter at breast height (DBH in cm) of two randomly chosen mature trees, hereinafter called "sample trees", was measured. Each year (between 25 July and 5 August), the new (current year) maturing cones were counted in the canopy of all sample trees from a fixed position using 10 × 40 binoculars. Average numbers of seeds per cone and cone-energy value (kJ $cone^{-1}$) were determined as in Salmaso et al. (2009). The mean energy production, over all plots, was our estimate of annual seed production (Salmaso et al., 2009). Overall seed-crop size (mean ± SE) was 276 ± 202 MJ ha^{-1}, 404 ± 220 MJ ha^{-1}, and 767 ± 274 MJ ha^{-1}, respectively in 2006, 2007 and 2008 in the mountain pine forest (Rodrigues et al., 2010), and 1732 ± 419 MJ ha^{-1}, 391 ± 82 MJ ha^{-1}, 557 ± 85 MJ ha^{-1}, 735 ± 153 MJ ha^{-1} and 525 ± 85 MJ ha^{-1} in 1999, 2000, 2001, 2002 and 2003, respectively, in the Scots pine forest (Wauters et al., 2008).

In a second step, we estimated food availability in each squirrel's home range (home range quality) as the mean food abundance (kJ ha^{-1}) of all vegetation plots within the 95% home range area using the kernel estimator (KDE, see below). Seeds produced in summer–autumn of year t were considered available for squirrels during the following 'squirrel year' (see Wauters and Lens, 1995), i.e. from August of year t to July of year t + 1.

2.3. Trapping and radio-tracking

Trapping was carried out in four to five periods per year, from April 2006 to April 2009 in CAN, and in three periods per year (April, June–July, October) from April 2000 to April 2006 in OGA. A trapping session involved the use of 31 (mountain pine forest) or 25 (Scots pine forest) ground-placed Tomahawk "squirrel" traps (models 201 and 202, Tomahawk Live Trap, WI, USA). Traps were placed on a grid, with distances of 100–150 m between them and average density of 0.6–0.7 traps ha^{-1}. Trapping and handling were carried out as in Wauters et al. (2008). Each trapped squirrel was individually marked using numbered metal ear-tags (type 1003S, 10 by 2 mm, National Band and Tag, Newport, KY, USA) and weighed to the nearest 5 g using a spring-balance (Pesola AG, Baar, Switzerland). Sex, age and reproductive condition (active = reproducing, or not active = non-reproducing) were recorded following Wauters and Dhondt (1989, 1995). Trapping and handling squirrels complied with the current laws on animal research in Italy and were carried out under permission of the Region of Lombardy.

The minimum number of animals known to be alive from capture-mark-recapture, radio-tracking and observations, during each trapping period was used to estimate population size and density of each sex. Previous studies on a wide range of tree squirrel populations have shown that these estimates are consistently close to true squirrel densities (e.g. Kenward et al., 1998; Wauters et al., 2004, 2008; Boutin et al., 2006).