

# Living on the Edge: Can Eurasian Red Squirrels (*Sciurus vulgaris*) Persist in Extreme High-elevation Habitats?

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## Abstract

Studying intraspecific spatiotemporal variation in vital rates among populations over a range of environmental conditions is essential to reveal intrinsic and extrinsic factors affecting population dynamics. Mammal populations living at higher elevations often have higher adult survival, shorter breeding seasons, and lower reproductive output per season than at lower elevations. We studied dynamics of a Eurasian red squirrel (*Sciurus vulgaris*) population in high-elevation, mountain pine (*Pinus mugo*) forest with extreme winters, in the Central Italian Alps, and compared vital rates with populations in more productive habitats at lower elevations. Average density was  $0.14 \pm 0.07$  squirrels  $\text{ha}^{-1}$  (range 0.07–0.30  $\text{ha}^{-1}$ ), and numbers typically increased in summer–autumn as a result of seasonal reproduction and immigration. Mean persistence time was only 12.5 months, and there was a nearly complete population turnover in only two years. Local survival and recruitment rate were correlated with seasonal population growth rate, and partial effect of survival explained 80% of variation in growth rate. While reproductive rate in mountain pine habitat was more similar than in more productive habitats at lower elevations, density and autumn–winter survival were much lower. Thus, red squirrels did not show the adaptations observed in several other mammal species, but might invest heavily in early reproduction to compensate for short life expectancy.

## Introduction

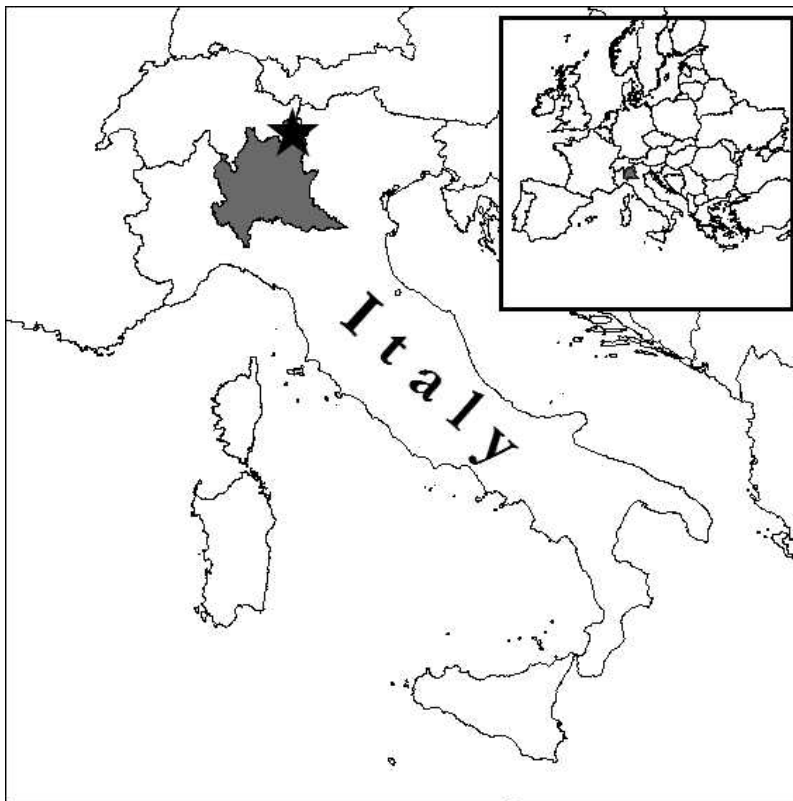
A major objective of population ecology is to determine the mechanisms underlying spatiotemporal variation in population growth rate (Krebs, 2001; Turchin, 2003; Morrison and Hik, 2007). This variation is caused by intrinsic and extrinsic factors that affect vital rates such as reproduction, juvenile recruitment, and (adult) survival, which differ in their relative importance among mammals (e.g. Dobson and Oli, 2001; Aars and Ims, 2002; Wauters et al., 2004; Gaillard et al., 2005). But variation in vital rates also exists among populations of the same species living under different environmental conditions. Such intraspecific spatial variation of the relative importance of vital rates has been mainly demonstrated for ground squirrels (e.g. Dobson and Oli, 2001; Oli et al., 2001; Oli and Armitage, 2004; Gillis et al., 2005) or other small mammals living in (sub)alpine habitats (Yoccoz and Ims, 1999; Millar and McAdam, 2001; Morrison and Hik, 2007). Usually, populations of mammals living at higher elevations have higher adult survival, shorter breeding seasons, lower reproductive output per season, and older ages of first reproduction than populations of the same species at lower elevations (Spencer and Steinhoff, 1968; Millar and Innes, 1985; Zammuto and Millar, 1985; Ferguson and McLoughlin, 2000; Badyaev and Ghalambor, 2001). One of the most commonly observed adaptations on constrained reproduction in alpine populations of small mammals, compared with populations in more temperate environments, is in fact delayed maturation, sometimes linked with compensatory enhanced survival (e.g. Zammuto and Millar, 1985; Yoccoz and Mesnager, 1998).

Eurasian red squirrels (*Sciurus vulgaris*) have a wide Palearctic distribution, occurring under very different environ-

mental conditions, from boreal or subalpine conifer forests, over temperate mixed or deciduous forests to mediterranean woodland habitats (Lurz et al., 2005). Their population dynamics and inter-population variation in vital rates have been well studied in mixed temperate woods (Wauters and Dhondt, 1995; Wauters and Lens, 1995; Kenward et al., 1998; Wauters et al., 2004; Boutin et al., 2006), and demographic data are also available for boreal and subalpine populations (Andrén and Lemnell, 1992; Bertolino et al., 2003; Wauters et al., 2008). However, very little is known of the occupancy of marginal habitats and of the demography of populations at the edge of the species' distribution. During a wide-scale survey of Eurasian red squirrels in montane and subalpine forest habitats in the Central Italian Alps, the species' presence was temporally documented in at least three sites of high-elevation dwarf mountain pine (*Pinus mugo*) wood and shrubland (Mari et al., 2008; Molinari et al., 2008). Here we present 3-year data of squirrel population dynamics in one of these sites. We predict that Eurasian red squirrels can persist in this marginal habitat characterized by extreme winter conditions and strong temporal variation in pine-seed production, but that they will occur at a lower density, and have a lower reproductive rate, possibly compensated by higher survival, than in populations living at lower elevations and/or in habitats with higher food availability.

## Study Area

Red squirrels were monitored at Cancano (CAN; 46°33'N, 10°15'E, elevation from 1940 m to 1970 m a.s.l.) in the Stelvio National Park, Central Italian Alps (Fig. 1, Lombardy Region, N. Italy). The study site (60 ha), located at the bottom of a high-



**FIGURE 1.** Location of the study area (black star, 46°33'N, 10°15'E) and the Lombardy region (dark gray) in Italy. Inset: Italy in Europe.

elevation valley near the artificial lakes of Cancano, is almost entirely composed of a pioneer homogeneous dwarf mountain pine (*Pinus mugo* Turra) woodland. The understory consists mainly of winter heath (*Erica herbacea* L.), European blueberry (*Vaccinium myrtillus* L.), mountain cranberry (*Vaccinium vitis-idaea* L.), and common juniper (*Juniperus communis* L.). The CAN study site is characterized by having a single major food resource for squirrels, the seeds of dwarf mountain pine which mature inside small cones in September and are dispersed by wind the next spring (late April–early May). Mean energy content per cone of this species is 5.9 kJ (our unpublished data).

CAN has a high-altitude continental climate typical of the Central Alps, with mean annual temperatures below 3 °C (2006–2008: mean  $\pm$  SD = 2.7  $\pm$  0.3 °C), relatively moderate precipitation occurring mostly in summer, and long, cold winters (mean monthly temperatures below 0 °C from November to April, mean  $\pm$  SD = -2.7  $\pm$  3.0 °C). Duration and depth of permanent snow cover varies annually but between 30 and 150 cm of snow tends to cover the study site between early November and late April–May (Cancano meteorological station, 1948 m a.s.l., A.E.M. Milan, unpublished data).

## Methods

### ESTIMATING FOOD AVAILABILITY

Tree seed abundance of dwarf mountain pine was estimated as described in detail elsewhere (Salmaso et al., 2009). Briefly, we determined woodland composition in 20 vegetation plots of 20  $\times$  20 m (400 m<sup>2</sup>), 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. Shrubs and trees of dwarf mountain pine were counted separately. Each year (between 25

July and 5 August), the new (current year) maturing pine cones were counted in the canopy of all sample trees from a fixed position using 10 $\times$ 40 binoculars. Average numbers of seeds per cone and cone-energy value (kJ/cone) were determined as in Salmaso et al. (2009). The mean number of cones/tree, or the mean energy production, over all plots was our estimate of annual tree-seed production (Salmaso et al., 2009).

### TRAPPING AND HANDLING SQUIRRELS

Trapping was carried out in four to five periods per year, from April 2006 to April 2009. A trapping session involved the use of 31 ground-placed Tomahawk “squirrel” traps (models 201 and 202, Tomahawk Live Trap, Tomahawk, Wisconsin, U.S.A.). Traps were placed on a grid, with distances of ca. 150 m between traps and average trap density of 0.6 traps/ha. Traps were pre-baited with sunflower seeds and hazelnuts 4 to 6 times over a 30 days period, and then baited and set for 7–10 days, until no new, unmarked squirrels were trapped for at least 2 consecutive days (Wauters et al., 2008). Traps were checked two–three times per day.

Each trapped squirrel was flushed into a light cotton handling bag with a zipper or a wire-mesh “handling cone” to minimize stress during handling, and individually marked using numbered metal ear-tags (type 1003 S, 10  $\times$  2 mm, National Band and Tag, Newport, Kentucky, U.S.A.). It was weighed to the nearest 5 g using a spring-balance (Pesola AG, Baar, Switzerland), and the length of right hind foot (without nail) was measured (0.5 mm) with a thin ruler (Wauters et al., 2007). Sex and age class were determined on the basis of external genitalia and body mass, with juveniles weighing less than 250 g (Wauters and Dhondt, 1995). Reproductive condition was scored as active (reproducing) or not active (non-reproducing). Non-reproducing males had abdominal testes and a small and unstained scrotum (juveniles and

subadults), or a small, dark-stained scrotum (sexually non-active adult males). Sexually active males had scrotal testes and scrotum >25 mm. Non-reproducing females were in anestrus (vulva small, no longitudinal opening, not lactating). Sexually active females were in estrus or post-estrus (vulva partly or strongly swollen with longitudinal opening, enlarged abdomen during late pregnancy), or lactating (nipples large, milk excretion can be stimulated; Wauters and Dhondt, 1995). Each year, between 60 and 90% of adults were radio-collared (type M1640 radio-collar, ATS Inc., Isanti, Minnesota, U.S.A.). 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.

#### DEMOGRAPHIC PARAMETERS

The minimum number of animals known to be alive (MNA), from capture-mark-recapture (CMR), radio-tracking, and observations during each trapping period was used as an estimate of population size. Previous studies on a wide range of tree squirrel populations have shown that these estimates realistically represent true squirrel densities (e.g. Kenward et al., 1998; Wauters et al., 2001, 2004, 2008; Wheatley et al., 2002; Boutin et al., 2006). Resident squirrels were recorded as the number of adults and subadults present in April (spring density) or October (autumn density) of each year, that had been marked previously.

Seasonal estimates of local survival, or persistence, including subadults and adults, were made from 1 October year  $t$  to 1 April year  $t+1$  (winter survival), and from 1 April year  $t$  to 1 October year  $t$  (summer survival). To allow a staggered entry design (Krebs, 2001), we used the Kaplan-Meier estimate of finite survival rate for each 6-month period,

$$S_K = 1 - (d_i/r_i), \quad (1)$$

where  $d_i$  = number of adult squirrels that disappeared between time  $i$  and time  $i+1$ , and  $r_i$  = number of adult squirrels alive at time  $i$ .

Since most females had only a single litter per year, we estimated annual reproductive rate as the ratio of the number of reproducing females to the number of resident females present in spring–summer.

Seasonal recruitment rate was calculated as the number of new squirrels trapped in April–June (spring) or October–February (autumn) and present for at least 3 months divided by the number of resident squirrels in April (spring) or in October (autumn), respectively. Annual recruitment rate for year  $t$  was the ratio of newly tagged squirrels that remained in the study site for at least three months and trapped between April $_t$  and February $_{t+1}$ .

Population growth over the summer of year  $t$  (1 April–1 October) was calculated as

$$r_{\text{sum}} = (\ln N_{\text{autumn}} - \ln N_{\text{spring}}), \quad (2)$$

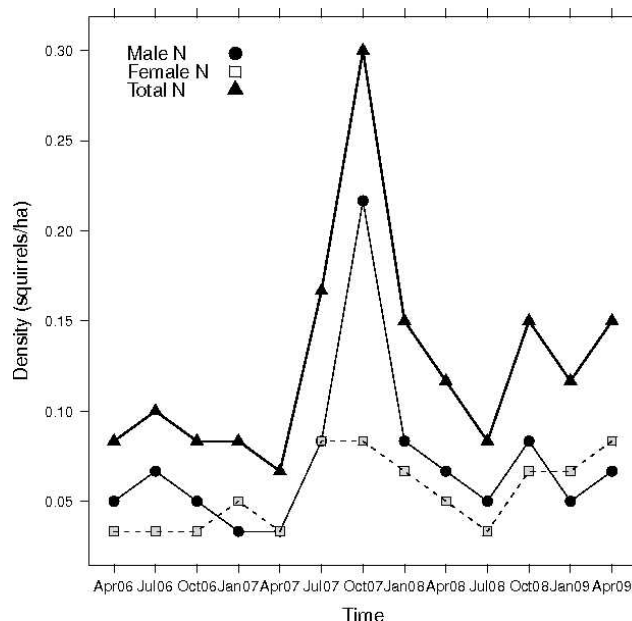
while over the winter of year  $t$  to  $t+1$  (1 October year  $t$  to 1 April year  $t+1$ ) it was calculated as

$$r_{\text{win}} = (\ln N_{\text{spring } t+1} - \ln N_{\text{autumn } t}) \quad (3)$$

(Millar and McAdam, 2001).

## Results

Dwarf mountain pine trees produced an average of (mean  $\pm$  SD)  $15 \pm 11$  (range 2–42),  $22 \pm 12$  (2–43), and  $42 \pm 15$  (10–74) cones per tree in 2006, 2007, and 2008, respectively. This



**FIGURE 2.** Density (squirrels  $\text{ha}^{-1}$ ) fluctuations of red squirrels (males, females, and total densities) in mountain pine forest.

corresponded with a seed-energy production of, respectively,  $276 \pm 202$ ,  $404 \pm 220$ , and  $767 \pm 274$  MJ  $\text{ha}^{-1}$ .

In three years we trapped 47 different squirrels (29 males, 18 females) for a total of 139 captures and recaptures. Males were trapped 82 times (mean  $\pm$  SD =  $2.8 \pm 3.9$  captures/male, range 1–18), females 57 times (mean  $\pm$  SD =  $3.2 \pm 4.7$  captures/female, range 1–21). Low mean number of captures per individual suggest high turnover rate in this population. Of the 25 males trapped the first time before 2009, five were only caught as pre-weaned young in the maternal nest, 16 were trapped one to two times, and only 4 were trapped  $\geq 5$  times. Among 14 females trapped the first time before 2009, three were only caught as pre-weaned young in the maternal nest, 8 were trapped one to three times, and only 3 were trapped  $\geq 5$  times.

Squirrel numbers were relatively stable from April 2006 to April 2007, followed by a 3-fold increase of density during summer–autumn 2007 (Fig. 2). This strong increase was caused by high levels of reproduction, with four females producing offspring between May and August (Table 1). Density decreased over winter and spring 2007–2008, followed by a slight increase in autumn 2008, linked with immigration of subadult and adult squirrels (Fig. 2). Spring (pre-breeding) densities varied from 0.07 to 0.15 squirrels  $\text{ha}^{-1}$ . Average density over the entire study period was very low:  $0.14 \pm 0.07$  squirrels  $\text{ha}^{-1}$  ( $0.08 \pm 0.05$  males  $\text{ha}^{-1}$  and  $0.06 \pm 0.02$  females  $\text{ha}^{-1}$ ) and fluctuated between a minimum of 0.07 and a maximum of 0.30 animals  $\text{ha}^{-1}$  (Fig. 2). The sex-ratio was male-biased in eight out of 13 trapping sessions (Fig. 2).

Between 50 and 100% of male squirrels were sexually active from February until early summer (July). In contrast, all had abdominal testes in September–October. All females were in anestrus between October and February, with the earliest date of estrus mid-March. In all years, lactating females were found between late April and late September.

We used persistence time, the number of months a subadult or adult individual remained in the study site, as a measure of local survival. We included only subadults and adults, since juvenile squirrels tend to disperse from the natal range from 4 months old onwards (Wauters and Dhondt, 1993; Wauters et al., 1993). In this subset, 5 out of 14 males (36%) and 2 out of 8 females (25%)

TABLE 1

Population parameters for Eurasian red squirrels, broken down by season and year. Mean and variance (coefficient of variance in % of mean) of each parameter throughout the three-year study period.

Population parameter	Spring–Summer (Apr <sub>t</sub> –Oct <sub>t</sub> )	Autumn–Winter (Oct <sub>t</sub> –Apr <sub>t+1</sub> )	Annual (Apr <sub>t</sub> –Apr <sub>t+1</sub> )
Population growth	0.58 (138%)	-0.39 (127%)	0.20 (200%)
2006	0.00	-0.22	-0.22
2007	1.50	-0.94	0.56
2008	0.25	0.00	0.25
Local survival rate	0.77 (27%)	0.35 (11%)	0.32 (28%)
2006	0.60	0.40	0.25
2007	1.00	0.33	0.43
2008	0.71	0.33	0.29
Annual reproductive rate			0.60 (29%)
2006			0.50
2007			0.80
2008			0.50
Recruitment rate	0.63 (123%)	0.37 (51%)	1.25 (69%)
2006	0.40	0.40	0.80
2007	1.50	0.17	2.25
2008	0.00	0.55	0.71

occurred in only one trapping session. Since they might have been transient animals trapped during dispersal movements, we did not include them in persistence analysis. Average persistence time did not differ between the sexes (males  $12.3 \pm 6.8$  months, females  $13.3 \pm 12.2$  months; *t*-test equal variance  $t = 0.20$ ,  $df = 13$ ,  $p = 0.84$ ; Figure 3).

Of the 20 males and 10 females trapped in 2007 only one animal of each sex was still present in April 2009, suggesting a nearly complete population turnover in only two years. The male was a subadult trapped for the first time in October 2007, probably born in April–May. The female was already present at the start of the study, in April 2006, as a primiparous female, thus most likely born in 2005.

Overall, population growth was positive in summer and negative in winter (Table 1). Over the whole year, it was negative in 2006, but positive in the next two years (Table 1). Local survival rate and recruitment rate were both correlated with seasonal population growth rate ( $n = 6$ ,  $r = 0.90$ ,  $p = 0.015$ ; and  $r = 0.81$ ,  $p = 0.049$ , respectively). In a multiple linear regression model, both parameters explained 91% of variation in growth rate ( $F_{2,3} = 14.4$ ,  $P = 0.029$ ). The partial effect of survival was stronger than of recruitment (partial  $p$ ,  $p = 0.07$  and  $p = 0.17$ , respectively), and variation in survival alone explained 80% of variation in growth rate.

## Discussion

Total number of trapped squirrels and animals present at any one time in our study area was not particularly large, but the densities of Eurasian red squirrels in subalpine conifer forests are generally low (Wauters et al., 2008; this paper). Despite small sample size, resident animals were monitored intensively over three years, producing reliable estimates of persistency and reproduction. Studying low-density populations is rarely done and therefore is of great interest to understand demographic patterns in low-quality habitats (Hurly, 1987; Lurz et al., 1995, 1997; Gillis et al., 2005). Moreover, although we did not replicate CMR in other *P. mugo* habitats, squirrel surveys using hair-tubes in two other *P. mugo* sites in the Lombardy Alps (elevations 1650–1800 m and 2000 m a.s.l.) confirmed the presence of persisting

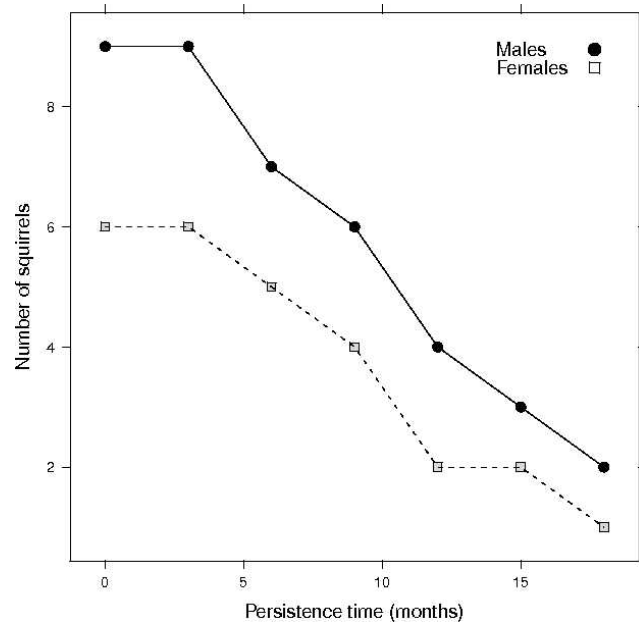


FIGURE 3. Persistence time of individual red squirrels (males and females) in mountain pine forest.

populations (over three years; Molinari et al., 2008; our unpublished data). Finally, at one site, estimated pre-breeding densities ( $0.10$ – $0.12$  squirrels  $ha^{-1}$ ) were similar to this study (Molinari et al., 2008). Therefore, we believe that the findings of this study offer insights into the dynamics of Eurasian red squirrels in marginal, high-elevation habitats and merit discussion.

Continuous presence of Eurasian red squirrels throughout this study confirmed our hypothesis that the species can persist in a high-elevation dwarf mountain pine wood. Average density ( $0.14 \pm 0.07$  squirrels  $ha^{-1}$ ) was much lower than in populations in deciduous and in mixed woodlands in North Belgium, southern Britain, and North Italy, and than in other, boreal or subalpine conifer forests, mainly dominated by Norway spruce and/or Scots pine (Table 2). Lowland woods of Scots (*Pinus sylvestris*) and Corsican pine (*P. nigra*) had much higher densities, but in mixed, montane silver fir (*Abies alba*)–Norway spruce (*Picea abies*) forests similar low densities were found in some years (Table 2). In the latter case, low densities are due to the fact that silver fir seeds are only rarely used by feeding squirrels, which select other conifers (Molinari et al., 2006; Wauters et al., 2008). We believe the low densities in Cancano were caused by a combination of cold winters, with mean monthly temperatures below  $0^\circ C$  for 5 to 6 months with continuous deep snowcover, and relatively poor seed production which might limit population processes such as (winter) survival and reproductive rate. Adverse weather conditions are likely to increase energy expenditure (Humphries et al., 2005), forcing squirrels to increase foraging effort in order to meet daily energy requirements. Data on activity patterns and rate of energy intake (handling times of consumption of pine cones) throughout the year (Wauters and Dhondt, 1987) will be gathered to test this hypothesis.

Seed productivity in our mountain pine site was higher than in man-made conifer forests in northern England ( $26$ – $36$  MJ  $ha^{-1}$ ; Lurz et al., 2000; Wauters et al., 2000). Nevertheless, in the latter, Eurasian red squirrel (pre-breeding) densities were higher than in our site (Table 2), suggesting that extreme winter conditions at high elevations negatively affected squirrel numbers.

TABLE 2

Review of Eurasian red squirrel population parameters according to habitat type and geographic location. Pre-breeding densities (Density, D) = squirrels/ha. Reproductive rate (RR) = number of litters per year/numbers of adult females (mean  $\pm$  SE). Survival rate = proportion subadults and adults surviving seasonally (Sum: from April to October; Win: from October to April next year) or annually.

Habitat description (location)	Density (D) and Reproductive rate (RR) <sup>1</sup>	Survival rate (mean $\pm$ SE)	References
Deciduous and mixed woodlands (N. Belgium)	D 0.70–1.70 RR 0.60 $\pm$ 0.09	Sum 0.76 $\pm$ 0.06 Win 0.86 $\pm$ 0.05 Annual 0.63 $\pm$ 0.04	Wauters et al. (1994, 2004); Wauters and Lens (1995)
Deciduous and mixed woodlands (S. England)	D 0.60–1.00 RR 0.51 $\pm$ 0.06	Annual 0.82 $\pm$ 0.06	Kenward et al. (1998)
Deciduous and mixed woodlands (N. Italy)	D 0.39–0.58 RR 1.25 $\pm$ 0.09	Annual 0.55 $\pm$ 0.06	Wauters et al. (2001)
Lowland woods of Scots and Corsican pine (N. Belgium, S. England)	D 0.83–1.17 RR 0.58 $\pm$ 0.05	Sum 0.77 $\pm$ 0.05 Win 0.83 $\pm$ 0.03 Annual 0.61 $\pm$ 0.04	Wauters and Lens (1995); Kenward et al. (1998); Wauters et al. (1994, 2004)
Mixed conifer plantations (N. England)	D 0.26–0.29 RR 0.76 $\pm$ 0.10	Annual 0.49 $\pm$ 0.09	Lurz et al. (1995); Wauters et al. (2000)
Boreal and alpine forests dominated by Norway spruce and Scots pine (Sweden, Italian Alps)	D 0.28–0.53 RR 0.81 $\pm$ 0.08	Sum 0.67 $\pm$ 0.05 Win 0.60 $\pm$ 0.07	Andrén and Lemnell (1992); Wauters et al. (2005, 2008)
Mixed Silver fir–Norway spruce forests (Italian Alps)	D 0.10–0.23 RR 0.42 $\pm$ 0.10	Sum 0.65 $\pm$ 0.05 Win 0.62 $\pm$ 0.05	Bertolino et al. (2003); Wauters et al. (2008)
Dwarf mountain pine forests (Italian Alps)	D 0.07–0.15 RR 0.60 $\pm$ 0.12	Sum 0.77 $\pm$ 0.15 Win 0.35 $\pm$ 0.03 Annual 0.32 $\pm$ 0.07	This study

<sup>1</sup> RR can be more than 1 if many females have two litters/year.

In general, squirrels occur at higher densities in “stable,” high-quality habitats than in habitats characterized by a high degree of temporal and spatial variation in food availability (Lurz et al., 1997, 2000; Wauters et al., 2004). For example, densities of Eurasian red squirrel populations in West Europe and North Italy have been shown to be higher in mixed conifer woods than in more productive, yet more variable, mixed broadleaf woods (seed production mixed conifer woods 500–5600 MJ ha<sup>-1</sup>; mixed broadleaf woods 2500–20,000 MJ ha<sup>-1</sup>; Wauters and Lens, 1995; Kenward et al., 1998; Wauters et al., 2001, 2004; and Table 2). In Canada, during years of poor seed crop, white spruce (*Picea glauca*) forests characterized by high but unpredictable resource abundance had densities of American red squirrels (*Tamiasciurus hudsonicus*) similar to those typical for mixed coniferous or pine-dominated forests with lower but more stable resource abundance (Wheatley et al., 2002). Longer time-series will have to be gathered to explore the food–demography relationships in squirrels in dwarf mountain pine forests at high elevations, and in other nearby conifer forests that might act as source habitats, to explore whether *P. mugo* is a sink habitat, where the population cannot survive without regular immigration from other populations (Pulliam, 1988).

In agreement with previous work on tree squirrel populations in marginal or fragmented habitats (Pulliainen, 1982; Hurly, 1987; Wauters et al., 1994), sex ratios in this study were male-biased. That different tree squirrel populations in marginal, or at least sub-optimal, habitat were characterized by having more males than females, may be related to the use of space by females being more strongly related with tree-seed abundance than males (Wauters and Dhondt, 1992; Lurz et al., 2000; Di Piero et al., 2008). Similar male-biased sex ratios have been documented in populations of reptiles (Hoare et al., 2006), birds (Legge et al., 2004; Githiru and Lens, 2006), and other mammals (Yoccoz and Mesnager, 1998; Smith et al., 2008) occurring in sub-optimal and/or fragmented habitats.

Breeding occurred in all three years but over a reduced period of time compared to populations at lower elevations. In this *P. mugo* wood, births of red squirrels occurred only from May to July. Eurasian red squirrels are seasonal breeders, and females normally produce one or two litters per year: one in February–March and a second one in June–July (Wauters et al., 1993; Wauters and Lens, 1995; Kenward et al., 1998; Gurnell et al., 2004). In other montane and subalpine mixed conifer forests of the Italian Alps, early spring litters were rare (March–May) and summer litters usually occurred in June–July (Wauters et al., 2008). Although the breeding season at Cancano was the shortest ever recorded, annual reproductive rate (60%) was similar in a variety of forest types (Table 2). Only in habitats where a high proportion of adult females produced two litters per year (mixed woodlands in North Italy and spruce or Scots pine dominated forests in the Alps; Table 2) were reproductive rates higher. Hence we found little support for our prediction of reduced reproduction in this marginal mountain pine habitat.

In this study, the average autumn–winter survival rate was much lower than in spring–summer. Spring–summer survival in the *P. mugo* wood was similar to populations in other habitats, but survival over winter was the lowest ever recorded (Table 2). Even in temperate climate in Belgium, cold winters tended to reduce densities the following spring (Wauters et al., 2004). Therefore, we believe that low winter survival in our study area was caused by regular episodes of extreme weather conditions (low temperatures, heavy rainfall or snowfall, long and permanent snow cover) during the autumn–winter period.

One of the most commonly observed adaptations on constrained reproduction in alpine populations of small mammals, compared with populations in more temperate environments, is delayed maturation, sometimes linked with compensatory enhanced survival (e.g. Zammuto and Millar, 1985; Yoccoz and Mesnager, 1998). In this study, comparing a high-elevation red squirrel population with populations at lower elevations, we found an

opposite trend. Our squirrels showed lower autumn–winter survival rates, shorter breeding season (absence of spring litters), but comparable annual reproductive rates. Populations of arctic ground squirrels (*Spermophilus parryii*) in high-elevation sites also presented significantly lower winter survival and greater reproductive output than at low elevation sites (Gillis et al., 2005). In effect, in Cancano Eurasian red squirrels survived on average for only one year; hence reproductive potential is limited in time, and both males and females should invest heavily in each single reproductive effort, as suggested by a record litter size of 7 young found in 2007 (Mari et al., 2008). Hence, the probability that squirrels only have one or two years to reproduce is high and in this case, the Williams' hypothesis predicts that females should adopt a trade-off between high reproductive investments when food abundance is high, against reduced survival (Williams, 1966; Descamps et al., 2006). Whether this strategy exists in our population will be further explored monitoring reproductive investment, combined with genetic parentage assignment, over longer time periods.

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