Demography of alpine red squirrel populations in relation to fluctuations in seed crop size

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Vertebrate population dynamics, social organisation and space use often are closely associated with the distribution of critical resources, such as food. Tree squirrels are ideal models to study these relationships, since both key demographic parameters (reproduction, survival and dispersal) and spatio-temporal variation in food supplies (measured as seed-crop size) can be reliably estimated. In this paper we test the following two predictions underlying the association between annual food abundance and demography in six alpine red squirrel populations, both with and without time-lag effects: 1) between-season and between-year fluctuations in survival rate, population density and increase parallel those in food availability; and 2) individuals follow a resource tracking strategy and increase in density mainly the year after a rich seed-crop. Red squirrels occurred at higher densities in Scots pine forest, characterised by stable seed-crops, than in Norway spruce with more abundant but more variable seed crops. Fluctuations in numbers were positively correlated with food availability, measured as annual conifer seed-crop sizes. Overall, adult survival rates were higher than those of subadults, and survival substantially fluctuated between seasons and years. Autumn densities and rates of population increase (summer-autumn) were strongly correlated with the same year’s autumn seed-crop, while correlations with the previous year’s seed-crop (time-lag models) were either weak (population density) or absent (population increase). Results of this paper show that fluctuations in red squirrel densities in habitats with strong temporal variation in seed production are more closely linked with food availability than in more stable habitats. In addition, in the Alpine conifer forests squirrel population sizes, in autumn, increase in synchrony with food resources, eliminating the population lag normally present when resources are produced in pulses.

In vertebrate populations, dynamics, social organisation and space use often are associated with the abundance and distribution of critical resources (Turchin 1999, Julliard et al. 1999, Dobson and Oli 2001). Conceptual models of producer-consumer systems predict how important resources (in particular food resources) affect different population processes and/or multi-species interactions (Curran and Leighton 2000, Ostfeld and Keesing 2000, Satake and Bjornstad 2004). Alternative, but not mutually exclusive, models on population regulation consider the relative importance of exogenous factors (that have no dynamic feedback with population density, such as food, nest sites and weather conditions) and endogenous factors (that represent dynamic feedbacks affecting population numbers, possibly involving time lags) on population demography (Dobson 1995, Turchin 1999, Hixon et al. 2002, Wauters et al. 2004).

Other hypotheses predict how variation in spatio-temporal abundance and predictability of food resources determine spacing behaviour and degree of territoriality in vertebrates (Carpenter and MacMillen 1976, Maher and Lott 2000, McLoughlin et al. 2000). Moreover, in many mammal species, from large polygynous carnivores and herbivores to small, promiscuous rodents, social organisation, aggressiveness and space use patterns differ between males and females, and polygynous or promiscuous mating systems result in differential use of critical resources by the two sexes to enhance fitness (Ostfeld 1985, 1990, Clutton-Brock et al. 1985, 2002, Ims 1988, Lambin 1994, Albon et al. 2000, Wauters et al. 2004).

To fully understand how social structure and space use may affect habitat and food utilisation by individuals and, consequently, population demography, empirical study of the predictions underlying food availability-space use
models is required (McLoughlin et al. 2000, Wauters et al. 2005). When conducted across a wide range of landscapes and/or habitat types, such study may offer insight into population processes that are of prime importance for wildlife and landscape management and conservation. For instance, the long-term survival of the European red squirrel *Sciurus vulgaris* is currently threatened by competition for food with the dominant, invasive grey squirrel *Sciurus carolinensis* (Lurz et al. 2001, Wauters et al. 2001a, Bertolino and Genovesi 2003, Tattoni et al. 2006).


The dynamics of most Holarctic tree squirrels, and the majority of vertebrate seed predators, is closely linked to fluctuations in the size of seed-crops of conifers and/or large-seeded broadleaf trees, in a “bottom-up” producer-consumer system with time-lags (Smith 1970, André and Lemnell 1992, Lurz et al. 1995, 2000, Wauters and Lens 1995, Gurnell 1996, Kenward et al. 1998, Humphries and Boutin 2000, but see Boutin et al. 2006). Several long-term studies have revealed interesting relationships between fluctuations in food supplies and tree squirrel demography, in particular reproductive output, using populations occurring in one to maximum three different high-quality habitats (Wauters and Lens 1995, Gurnell 1996, Humphries and Boutin 2000, Wauters et al. 2004, Boutin et al. 2006). All basic consumer-resource population models portray consumer rates of increase, and consequently density, as a function of current or past rather than future resource availability (Ostfeld and Keesing 2000). However, at least two species of squirrels, Eurasian red squirrel *Sciurus vulgaris* and American red squirrel *Tamiasciurus hudsonicus*, are capable of increasing reproductive output (second litters) in anticipation of upcoming resource pulses, before mast seeding (the intermittent, synchronous production of large seed crops by a population of plants), whereby increasing population size in synchrony with resources and eliminating the population lag normally present when resources are produced in pulses (Boutin et al. 2006).

Here we address two hypotheses on the relationship between spatio-temporal variation in seed crops and demographic properties of Eurasian red squirrels in six montane and subalpine forest types. First, we test the hypothesis that fluctuations in tree squirrel populations are mainly determined by annual variation in tree-seed productivity. In this case we predict that between-season and between-year fluctuations in survival rates, population densities and rates of increase will parallel those in food availability, measured as the size of conifer seed-crops produced each year in each study site. Assuming that higher-quality habitats have higher densities and more stable populations (Lurz et al. 1997, Wauters et al. 2001b, 2004, 2005, but see Wheatley et al. 2002) we further predict that differences in overall density among populations will be related to the average annual seed-crop size in the different habitats.

Second, based on the producer-consumer time-lag hypothesis (Curran and Leighton 2000, Ostfeld and Keesing 2000), we predict that squirrels will follow a resource tracking strategy and increase in density mainly the year after a rich seed-crop. However, we also explore the alternative hypothesis by Boutin et al. (2006) that summer increase is adjusted to future seed crops and autumn density increases is in synchrony with the same year’s resource pulse. To investigate this hypothesis, possible effects of overall annual food abundance are tested both without and with a time-lag. If squirrels “anticipate” reproduction so that young are weaned when seeds of the new mast-crop are mature, autumn density are expected to be correlated more strongly with the seed-crop of the same year (rather than of the previous year), and increase rates from summer to autumn can be expected to be affected by the size of the same year’s seed-crop only.

**Materials and methods**

We selected 6 study sites within mature, secondary montane and subalpine mixed conifer forests of the Italian Alps, with elevations ranging from 1100 to 2100 m a.s.l. (the upper tree-line). These areas are distributed over 2 geographic regions: two sites are located in the Cogne and Rhemes Valleys of the Gran Paradiso National Park (western Alps), while Cedrasco (CED), OGA, Valfurva (VAL), and Bormio (BOR) all occur in the Valtellina Valley in the Central Alps. Specific location and distances between study sites are presented elsewhere (Fig. 1 in Trizio et al. 2005). Rhemes (RHE, 69 ha) and VAL (78 ha) are dominated by Norway spruce *Picea abies*, OGA (47 ha) by Scots pine *Pinus sylvestris*, and BOR (93 ha) by Arolla pine *Pinus cembra*. Cogne (COG, 55 ha) is spruce-larch *Larix decidua* forest and at CED (76 ha) the forest is mainly composed of silver fir *Abies alba* and spruce with small proportions of larch, Scots pine and beech *Fagus sylvatica* at lower elevations (Table 1).

The proportion of spruce, silver fir, larch, Scots pine, and Arolla pine differed among study sites, but also varied within sites at a fine-grained level. Therefore, to estimate seed availability as our measure of food abundance, we first determined woodland composition by establishing a 20 by 20 (400 m²) vegetation plot around each trapping station across the trapping grid (n = 20–30). In each vegetation plot, we counted the number of trees of each species, and measured the diameter at breast height (DBH in cm) of 2 randomly chosen mature trees for each species on the plot (forests consisted of large areas of even-age stands with trees of similar size), hereafter called “sample trees” (Wauters
et al. 2005). Dead trees were recorded separately since their presence indicated a naturally structured forest. Each year in August, we counted green cones in the canopy of all coniferous sample trees from a fixed position (the best point to view cone crop) using 10 × 40 binoculars and scaled to estimate the total number of cones per tree (Wauters et al. 2005). The mean value of all vegetation plots was calculated as the measure of average annual tree seed abundance in each study site. In one study site, CED, we used two measures of food availability: the first estimated seed-crop size of all tree species (hereinafter called “seed-crop”), the second used only the Norway spruce seed-crop (hereinafter called “Norway spruce-crop”) because this was the dominant tree species which retains its seeds in closed cones from August to the next spring (April–May). Seed-fall in silver fir, in contrast, already occurs in autumn (October) soon after seed maturation (Konnert and Bergmann 1995) reducing seed availability (in the canopy) for squirrels to only 2–3 months.

Squirrels start feeding on immature green cones in summer (July–August) and continue to consume conifer seeds, except those of silver fir, throughout autumn-winter and until cones open in April-May of the next spring (Steele et al. 2005, Molinari et al. 2006). Hence, seeds produced in the summer-autumn of year t were considered available for the squirrels during the following “squirrel year” (Wauters and Lens 1995), i.e. from August of year t to July of year t+1.

**Study design**

An important objective of this study was to compare population parameters derived from “traditional” methods, such as minimum number alive (MNA) used in most tree squirrel studies (Smith 1970, Wauters and Lens 1995, Lurz et al. 1997, 2000, Wauters et al. 2001a, b, 2004, 2005, Gurnell et al. 2004, Boutin et al. 2006) with estimates from capture-mark-recapture (CMR) analysis that provide confidence intervals for the different parameters. Squirrels were live-trapped in three separate sessions per year, starting

![Fig. 1. (a) Relationship between squirrel densities based on minimum numbers alive (MNA) and capture-mark-recapture analysis (POPAN, full line), linear regression Y=X (dotted line); (b) spatio-temporal variation in squirrel densities based on MNA estimates between July 2000 and April 2005 in populations OGA (filled squares), VAL (filled triangles), CED (open triangles), RHE (filled circles), COG (open circles) and BOR (filled diamonds).](image)

<table>
<thead>
<tr>
<th>Site</th>
<th>CED</th>
<th>OGA</th>
<th>VAL</th>
<th>BOR</th>
<th>RHE</th>
<th>COG</th>
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<tr>
<td>(a) Tree species (%)</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Norway spruce</td>
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<tr>
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<td></td>
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<tr>
<td>Scots pine</td>
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<td>88.7</td>
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<td>Larch</td>
<td>3.2</td>
<td>2.5</td>
<td>1.9</td>
<td>17.8</td>
<td>11.0</td>
<td>54.0</td>
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<tr>
<td>Arolla pine</td>
<td></td>
<td>6.2</td>
<td>73.2</td>
<td></td>
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<td>3.0</td>
<td>1.0</td>
<td>4.0</td>
<td>1.0</td>
</tr>
<tr>
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<td>9</td>
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<td>75</td>
<td>47</td>
<td>62</td>
<td>65</td>
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April, July and October. Thus, the interval between successive capture sessions per site was either three or six months. Capture sessions were deliberately spaced out to include spring, summer and autumn, and to maximise the number of encounters and time interval between successive encounters. The former ensured that population parameter estimates were as representative as possible, while the latter was key to furnishing sufficient statistical power for analyses in program MARK. In four study sites (COG, OGA, CED and RHE), there were 15 capture sessions over a six-year period, running from July 2000 to April 2005, whilst in the remaining two sites (VAL and BOR) trapping only begun in July 2002, making a total of nine sessions over four years (also until April 2005) (Table 1).

A trapping session involved the use of 20–30 ground-placed Tomahawk traps (models 201 and 202, Tomahawk Live Trap, WI, USA). Traps were placed on a grid, with distances of 100–150 m between traps and average trap density of 0.6–0.7 traps ha⁻¹. Traps were pre-baited with sunflower seeds and hazelnuts four to six times over a 30-d period, and then baited and set for 8–12 d, until no new, unmarked squirrels were trapped for at least two consecutive days. Traps were partly covered by dark plastic to give shelter from rain or cold, and checked two-three times per day. Each trapped squirrel was flushed into a light cotton handling bag with a zipper (Wauters et al. 2007), or a wire-mesh “handling cone” to minimise stress during handling, and individually marked using numbered metal ear-tags (type 1003 S, 10 by 2 mm, National Band and Tag, Newport, KY, USA). It was weighed to the nearest 5 g using a Pesola spring-balance (Pesola, Baar, Switzerland), and the length of the right hind foot (without nail) was measured (0.5 mm) with a thin ruler (Wauters et al. 2007). Sex, age, and reproductive condition were recorded following Wauters and Dhondt (1995). All squirrels first caught as juveniles (six weeks–four months old, body mass below 250 g, Wauters et al. 2004, 2007) were defined as locally-born offspring (Wauters and Dhondt 1995).

"Traditional" estimates of demographic parameters using minimum number alive (MNA)

Eurasian red squirrels in alpine populations may have one or two litters per year. Seasonal changes in numbers are caused by spring reproduction and dispersal, resulting in an increase in numbers in May–June, followed by mortality of juveniles and emigration over summer. In September–October, summer reproduction and autumn immigration result in a second increase phase, which again is followed by a decrease in numbers through autumn-winter mortality of locally born juveniles and emigrants (Wauters and Lens 1995, Wauters et al. 2004, 2005). We used the minimum number of animals known to be alive from trapping, radiotracking or observations (MNA, Wauters and Lens 1995, Kenward et al. 1998, Wauters et al. 2001b, 2004, Bertolino et al. 2003, Gurnell et al. 2004, Boutin et al. 2006) during each trapping period as an estimate of population size. Residents were recorded as the number of adults and subadults present in April–May (spring density), July (summer density) or October (autumn density) of each year that previously had been marked.

Since most reproduction and dispersal occurred in two distinct periods, spring and summer-autumn, and mortality has been hitherto found to differ between seasons (Wauters et al. 2004), all population parameters were analysed seasonally. Population increase rate was estimated as the number of newly tagged animals (immigrants and locally born juveniles) divided by the number of residents in each trapping period. Since sex-specific samples sizes were small and the most parsimonious capture-recapture models did not retain a significant sex-effect (see Results), sexes were pooled when estimating rates of population increase and MNA.

Estimation of recapture and survival probabilities

MNA-based estimates of population size (see higher) were supplemented with estimates from capture-mark-recapture analysis with program MARK (White and Burnham 1999). All captured squirrels were marked and released, hence encounter histories were composed of live recaptures only. We used a Cormack-Jolly-Seber (CJS) routine to model effects of area (CED, OGA, VAL, BOR, RHE, COG), sex (male, female) and age (adult, young) on recapture and survival probabilities, taking into account variation in time interval between successive capture sessions (three or six months). In order to include data from all six sites, each individual record consisted of nine encounter histories, corresponding to the nine capture sessions in the least trapped site, VAL (Table 1). The saturated (global) model was defined as \[ \text{Phi}_{site \times sex \times age \times time} \times \text{P}_{site \times sex \times age \times time} \], with Phi being the three-monthly survival probability and p the three-monthly recapture probability. Time was incorporated into the models either as "time" (all capture occasions separately), "season" (summer, winter), or "season-year" (where the seasons were separated by year). We used a parametric bootstrap procedure (goodness-of-fit test, GOF) to test whether the saturated model adequately fitted the data and no assumptions were violated. First, we simulated the model deviance by running 100 iterations. Next, we calculated parameter \( \hat{c} \) (c-hat) by dividing the observed model deviance by the mean deviance of the simulated models to estimate overdispersion. Ideally, the \( \hat{c} \) value is close to 1 if the model assumptions are met. If the null hypothesis (\( \hat{c} = 1 \)) is rejected but \( \hat{c} < 3 \), it suggests little overdispersion in the data that can be corrected for by inflating variances of parameter estimates, \( \hat{c} \)-values \( > 3 \) indicate that the model inadequately fits the data.

When scaling down from the global model to the most parsimonious one (i.e. representing the data most adequately with the least number of parameters, we first modelled recapture probabilities whilst retaining the most saturated survival function \( \text{Phi}_{site \times sex \times age \times time} \). Next, survival was modelled using the most parsimonious recapture function. Models were initially selected based on the Akaike information criterion AIC (or quasi-AIC when the quasi-likelihood parameter, \( \hat{c} \), was applied). However, to minimise the chances of excluding significant effects from parameter estimation, all models with \( \Delta QAIC < 7 \) that were nested with the lowest QAIC model were tested using likelihood ratio tests (LRT’s) in MARK.
Estimation of densities

We used the POPAN model in MARK to estimate population size and increase rates. The following parameters are estimated from POPAN models: 1) \( \phi \) (apparent survival), 2) \( p \) (recapture probability), 3) \( \text{pent} \) (probability of entry into the population for this occasion), and 4) \( N \) (super-population size, i.e. the total number of individuals present within the population during the entire study period). Thus, for \( t \) occasions, POPAN generates \( t-1 \) estimates of \( \phi \), \( t \) estimates of \( p \), \( t-1 \) estimates of \( \text{pent} \) (corresponding to the probability of entry for occasions 2, 3, \ldots, \( t \)), and one estimate of \( N \). The population size for each occasion was derived from the super-population size estimate in four steps (White and Burnham 1999). First, the probability of being in the population on the first occasion was estimated as \( \text{pent}(0) = 1 - \sum \text{pent}(i) \). Second, the number of animals in the population on occasion 1 was estimated as \( N(1) = \text{pent}(0) \text{times \ N (super-population size)} \). Third, the number of new animals (the increase rate \( B \), representing both locally born individuals and immigrants in our case) entering the population prior to occasions \( i = 2, 3, \ldots, t \) was estimated as \( B(i) = \text{pent}(i-1) \text{times \ N} \). Fourth, the population size on occasion \( i = 2, 3, \ldots, t \) was estimated as \( N(i) = [N(i-1) - \text{losses on capture}] \text{times \ } \phi(i-1) + B(i) \).

Data were arranged into 12 groups assigned to site (CED, OGA, VAL, RHE, COG, BOR) and sex (M, F). Time was incorporated into the models either as “time” (all capture occasions separately), “season” (winter and summer) or “season-year” (yearly variation across seasons). In modelling, the important group and time effects on \( \phi \) and \( p \) inferred from the survival analyses were retained and used to model the key parameters of interest. We used the MLogit-link function to estimate \( \text{pent} \), Logit-link to estimate \( N \), and Sin-link to estimate \( \phi \) and \( p \). The Akaike’s information criterion (AIC) was applied for model selection from the set of candidate models incorporating group and time dependence.

Statistical analyses

Effects of annual food abundance on demographic parameters were tested both in absence and presence of a time-lag effect. In the former case, effects of seed-crop size in year \( t-1 \) were related to demographic parameters in April and July of year \( t \) (Wauters and Lens 1995, Wauters et al. 2004, 2005), while seed-crop in year \( t \) was related with demographic parameters in October of the same year \( t \). In the latter case, seed-crop size in year \( t-1 \) was related with demographic parameters in all seasons (April, July and October) of the next year \( t \). Data of seed-crop and Norway spruce crop were log transformed to approach homogeneity of variances and normality of errors (Shapiro-Wilk tests, \( p > 0.05 \)).

To account for dependence of food abundance measures across seasons per year, we used mixed models with estimated squirrel density as the dependent variable, seed-crop (or Norway spruce crop) and study site as main effects, and season in year as a repeated measures subject (procedure MIXED, SAS 1999). Similar modelling was done with increase rate \( B \) as the dependent variable. Statistical inference of density effects among study sites was based on least square means (DLSM) values. When small sample size and/or skewed distributions resulted in violations of normality assumptions, non-parametric tests were used.

Results

Food availability

Tree seed production varied between years and study areas (year \( F_5, 21 = 7.07, p = 0.0005 \), area \( F_5, 21 = 5.35, p = 0.0025 \), see also Fig. 1 in Wauters et al. 2007). Overall, 1999 and 2004 had the largest crops, while 2003, and especially 2000, had poor crops. The largest seed-crops were produced at CED and VAL, the smallest at BOR and OGA, and seed-crops of pines at OGA and BOR were less variable than spruce and larch crops at the other sites. The year-effect explained 41% of variation in food abundance and the area-effect explained 31%.

Recapture and survival estimates

Dividing the deviance of the saturated model by the mean deviance of all simulated models resulted in a \( \hat{c} \)-value of 1.248. Hence, the saturated model did not violate the CJS model assumptions. Because the \( p \)-value associated with this \( \hat{c} \)-value reached significance (\( p = 0.001 \)), the null hypothesis that \( \hat{c} \) value = 1 was rejected and overdispersion was accounted for by adjusting the \( \hat{c} \)-value to inflate variances. When modelling recapture probability, models with \( p_{site} \) and \( p_{c} \) (where “c” signifies no group or time effects) were the most parsimonious. Because the LRT between them was highly significant (\( \chi^2 = 20.1, p = 0.0053 \)), site was retained in the final recapture model. In general, recapture probabilities were relatively high at all sites (all \( p_{site} > 0.79 \), Appendix 1). Survival was modelled starting from \( \phi_{site \times sex \times age \times time} \) \( p_{site} \) producing a most parsimonious model of \( \phi_{season \times season-year} \). This indicates that survival rates differed between adults and subadults only and fluctuated over seasons and years. Hence, survival for a given age-class in each season-by-year combination did not differ among sites. Three-monthly survival estimates were generated based on this model. Six-month survival probabilities representing entire summer (April–September) and winter (October–March) periods were calculated by raising these estimates by a factor of two (Appendix 1). On average, seasonal local survival of adults was higher than of subadults (mean \( \Delta \) SD = 0.66 ± 0.08 and 0.54 ± 0.17, respectively, Wilcoxon matched-pairs signed-ranks test, \( n = 6, p = 0.062 \), one-sided).

Density estimates: MARK and MNA

Based on the results from survival modelling, we started with the global model \( \phi_{season-yr} p_{site} \text{pent}_{site \times sex \times time} N_{site \times sex} \) which was simplified down to \( \phi_{season} p_{site} \text{pent}_{site \times time} N_{site \times sex} \) (least AIC model). Only one other model (\( \phi_{season-yr} p_{site} \text{pent}_{site \times time} N_{site \times sex} \) had a ΔAIC
<7. However, as the AIC weight was significantly larger for the least AIC model (0.88) compared to the second model (0.035), the former was selected for parameter estimation (Appendix 2).

Population estimates based on MNA and capture-recapture analysis were highly intercorrelated (population density: \( r = 0.91, n = 54, p < 0.0001 \), population increase: \( r = 0.82, n = 46, p < 0.0001 \), Fig. 1a). MNA-based density estimated over all sites, seasons and years was 0.31 ± 0.11 squirrels ha\(^{-1}\) (n = 78). However, MNA densities differed between sites and fluctuated with season and year (Fig. 1b). POPAN-based densities ranged from 0.13 to 0.68 squirrels ha\(^{-1}\) (n = 54, mean ± SD = 0.39 ± 0.14, Appendix 2), hence were slightly higher than those based on MNA (Fig. 1a). The level of population increase B (n = 46) was estimated at 7.1 ± 4.2 individuals (range: 1–16 individuals) and was positively correlated with density (\( r = 0.44, n = 46, p = 0.0024 \), Fig. 2).

**Food availability and population parameters**

**Relationship with population density**

Population density significantly differed between sites and was significantly related with seed-crop size (site F\(_5, 17 = 37.8, p < 0.0001 \), log seed-crop size F\(_1, 17 = 5.65, p = 0.03 \), estimated slope ± SE = 0.085 ± 0.036). Average population density in OGA was higher than in all other sites except VAL (DLSM: other sites, p < 0.001, with VAL p = 0.068), while densities in CED and BOR were lower than in all other sites (all p < 0.01). On average, VAL had higher densities than RHE and COG (p < 0.05) where densities did not differ significantly (p = 0.06) (Fig. 3) The model fitted better (ΔAICc with previous model = −3.7) when selecting Norway spruce seed-crop as measure of food abundance in CED (site F\(_5, 17 = 36.5, p < 0.0001 \), log Norway spruce seed-crop F\(_1, 17 = 9.57, p = 0.007 \), estimated slope ± SE = 0.12 ± 0.04). Including a time-lag effect in models of food abundance increased the respective AICc values (log seed-crop size AICc = 102.8, log Norway spruce seed-crop AICc = 105.2).

To further explore relationships between food abundance and autumn density, we used a general linear model with autumn density as dependent variable, and study site, log Norway spruce seed-crop same year, and log Norway spruce seed-crop previous year as factors. The model explained 94% of variation in autumn density among sites and years (F\(_7, 10 = 24.1, p < 0.0001 \), R\(^2\) = 0.94). Overall, autumn densities were higher at OGA than at VAL, RHE and COG, while the lowest densities were at BOR and CED (site effect F\(_5, 10 = 27.6, p < 0.0001 \)). Seed-crop size of Norway spruce from the same (F\(_1, 10 = 16.7, p = 0.002 \), slope = 0.28 ± 0.07) and previous years (F\(_1, 10 = 9.99, p = 0.01 \), slope = 0.20 ± 0.06) positively affected autumn density, yet the partial effect of same year’s seed-crop turned out to be stronger.

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**Table 2. Cormack-Jolly-Seber models with ΔQAIC < 7 and the likelihood ratio test (LRT) results for nested models, the model used in parameter estimation is shown in bold. Phi = survival probability; p = capture probability.**

<table>
<thead>
<tr>
<th>Model</th>
<th>QAICc</th>
<th>ΔQAICc</th>
<th>No. par</th>
<th>QDeviance</th>
<th>LRT</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1236.7</td>
<td>0.0</td>
<td>10</td>
<td>733.838</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>1238.3</td>
<td>1.6</td>
<td>18</td>
<td>718.934</td>
<td>1and2: p = 0.061</td>
</tr>
<tr>
<td>3</td>
<td>1238.6</td>
<td>1.9</td>
<td>8</td>
<td>739.795</td>
<td>1and3: p = 0.051</td>
</tr>
<tr>
<td>4</td>
<td>1239.3</td>
<td>2.6</td>
<td>8</td>
<td>740.492</td>
<td>1and4: p = 0.034</td>
</tr>
<tr>
<td>5</td>
<td>1241.4</td>
<td>4.7</td>
<td>10</td>
<td>738.535</td>
<td>2and3: p = 0.022</td>
</tr>
<tr>
<td>6</td>
<td>1241.7</td>
<td>5.0</td>
<td>12</td>
<td>734.757</td>
<td>2and6: p = 0.015</td>
</tr>
<tr>
<td>7</td>
<td>1242.2</td>
<td>5.7</td>
<td>10</td>
<td>722.802</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>1242.4</td>
<td>5.7</td>
<td>10</td>
<td>739.501</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>1243.6</td>
<td>6.9</td>
<td>22</td>
<td>715.903</td>
<td></td>
</tr>
</tbody>
</table>

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![Fig. 2. Relationship between rate of population increase (B) and population densities (POPAN) in six alpine red squirrel populations: OGA (filled squares), VAL (filled triangles), CED (open triangles), RHE (filled circles), COG (open circles) and BOR (filled diamonds).](image1)

![Fig. 3. Relationship between food availability and population density (POPAN) in populations OGA (filled squares), VAL (filled triangles), CED (open triangles), RHE (filled circles), COG (open circles) and BOR (filled diamonds).](image2)
Relationship with population increase

Food abundance, with and without time-lag, was significantly correlated with increase rate B (p = 0.06 and 0.0053, respectively), but not with MNA- and POPAN-based population densities (all p > 0.22) (Table 3). However, when we selected Norway spruce seed-crop size in CED and total seed-crop size in all other sites, food abundance was positively correlated with density (Table 3). Associations of food abundance with both population density and increase rate B were consistently stronger in absence of a time-lag effect (Table 3). In a mixed model, there was a significant effect of Norway spruce crop size, but not of study site (log Norway spruce crop F1, 11 = 17.3, p = 0.002, site F5, 11 = 2.50, p = 0.096).

Like for density modelling above, we run a GLM with summer-autumn increase rate B as dependent variable, and study site, log Norway spruce seed-crop same year, and log Norway spruce seed-crop previous year as factors. There was a stronger increase in the squirrel populations in autumns with a rich Norway spruce seed-crop size (F1, 10 = 13.2, p = 0.0046, slope = 17.0 ± 4.7), while partial effects of study site (F5, 10 = 2.54, p = 0.10) and previous year’s seed-crop (F1, 10 = 3.32, p = 0.10) were not significant. Thus, whereas autumn density was affected both by the same year’s and the previous year’s seed-crop, autumn increase rate only was affected by the size of the same year’s seed-crop. Sex ratios tended to be male-biased (female proportions: CED 0.45, OGA 0.40, VAL 0.47, RHE 0.46, COG 0.43, BOR 0.35) (Appendix 2) but only significantly deviated from 1:1 in BOR (one-way Fisher’s exact tests: BOR p = 0.023, all other p-values > 0.10).

Parameters contributing to population increase

The proportion of locally born young among the newly tagged animals, thus the proportion of population increase due to reproduction in the study sites, differed among seasons (ANOVA F2, 65 = 14.8, p < 0.0001). Early spring litters were rare, hence proportion young in April–May trapping sessions was lower than in other seasons (proportion young per trapping session mean ± SD: spring 0.06 ± 0.12, n = 24; summer 0.28 ± 0.32, n = 21; autumn 0.43 ± 0.24, n = 23). Juveniles trapped in spring and summer were of early litters (born between March and May) while those trapped in autumn were of summer litters (born in June–July). Therefore, we explored the relative contribution of immigration and local reproduction to population increase (B) separately for the spring-summer period (April and July) and for autumn (October).

In spring and summer, number of locally born offspring was not correlated with population increase B (r = 0.17, n = 28, p = 0.39), while B was strongly correlated with number of immigrants (r = 0.95, n = 28, p < 0.0001). When taking account of variation between sites, there was a weak tendency for the number of local offspring trapped in spring-summer to increase when the seed-crop of the previous year was abundant (Table 4, slope 1.14 ± 0.56). In contrast, there was no effect of study site on number of immigrants, which increased with the previous year’s seed-crop (Table 4, immigrants = −4.3 (± 3.7) + 3.42 (± 1.27) Ln seed-crop).

In autumn, both number of locally born offspring (r = 0.67, n = 18, p = 0.0025) and number of immigrants (r = 0.94, n = 18, p < 0.0001) were positively correlated with population increase B. Number of offspring was correlated with the same year’s seed-crop (r = 0.53, n = 26, p = 0.006) but not with previous year’s seed-crop (r = 0.03, n = 26, p = 0.87). In the GLM model only the effect of the same year’ seed-crop was significant (Table 4, juveniles = −3.8 (± 2.2) + 2.25 (± 0.74) Ln seed-crop). In contrast, the number of immigrants correlated with both same and previous year’s seed-crop (n = 26, r = 0.39, p = 0.05 and r = 0.41, p = 0.039, respectively). In the GLM model, both variables explained 34% of variation in the number of autumn immigrants (Table 4, immigrants = −16 (± 6) + 3.40 (± 1.38) Ln seed-crop + 3.38 (± 1.31) Ln seed-crop previous year).

Discussion

Spatio-temporal variation in food availability and squirrel demography

Alpine red squirrels occurred at higher densities in Scots pine forest, characterised by small annual variations in seed-crop size, than in Norway spruce dominated forests with more abundant but also more variable seed crops (i.e. during the duration of our study, Norway spruce produced mast crops in 1999 and 2004 and a seed-crop failure in 2000, Wauters et al. 2007). Likewise, densities of Belgian red squirrel populations have been shown to be higher in mixed conifer wood than in more productive yet more variable mixed broadleaf wood (Wauters and Lems 1995, Wauters et al. 2004). In Canada, during years of poor seed-crop, white spruce Picea glauca forests characterised by high but unpredictable resource abundance had densities of American red squirrels similar to those typical for mixed

Table 3. Pearson correlation coefficients and p-values of correlations between different measures of food abundance and red squirrel population parameters. * Norway spruce indicates that in site CED only size of Norway spruce seed-crop was used to estimate food abundance. (t – 1) food abundance estimated with a 1-yr time-lag (see Materials and methods). MNA = minimum number alive; POPAN = squirrel density estimated using the capture-mark-recapture analysis; B = population increase estimated from the capture-mark-recapture data.

<table>
<thead>
<tr>
<th>Estimates of food abundance</th>
<th>Population parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MNA (n = 78)</td>
</tr>
<tr>
<td>Log seed-crop</td>
<td>r = 0.14, p = 0.22</td>
</tr>
<tr>
<td>Log Norway spruce*</td>
<td>r = 0.42, p = 0.0001</td>
</tr>
<tr>
<td>Log seed-crop (t – 1)*</td>
<td>r = 0.12, p = 0.31</td>
</tr>
<tr>
<td>Log Norway spruce (t – 1)*</td>
<td>r = 0.395, p = 0.0003</td>
</tr>
</tbody>
</table>
coniferous or pine dominated forests with lower but more stable resource abundance and lower survival and juvenile production (Wheatley et al. 2002). Apart from providing very valuable input for single-species wildlife-habitat predictive models (Pulliam 1988) and GIS-based spatially explicit population dynamics models (SEPD, Pulliainen et al. 2001, Tattoni et al. 2006), these consistent findings question the assumption that animal densities reflect habitat quality (Van Horne 1983, Wheatley et al. 2002) as based on habitat-selection theory (Fretwell and Lucas 1969, Parker and Sutherland 1986).

Fluctuations in squirrel densities were positively correlated with food availability, measured as the size of conifer seed-crops produced each year in each study site, confirming our first prediction. Interestingly, relationships were stronger when food abundance at CED was estimated by Norway spruce seed-crop only. This suggests that fluctuations in silver fir seed-crop size, the most dominant tree species, had little effect on squirrel demography, despite it producing large seed-crops in three out of six years (>60 cones/tree, Wauters et al. unpubl.). Similar species-specific effects of seed-crop size on population density and demographic processes have been reported from studies on British red and grey squirrel populations (Kenward and Holm 1993, Lurz et al. 1995, Kenward et al. 1998). For example, in mixed oak-hazel woodlands, red squirrel densities correlated best with hazel-nut abundance, while grey squirrel densities correlated best with acorn abundance (Kenward et al. 1998), presumably because grey squirrels are physiologically better adapted at exploiting acorns (Kenward and Holm 1993). Hence, while tree squirrels are generally assumed to rank among the most specialised vertebrate seed predators (Smith 1970, Benkman et al. 2001, 2003, Mezquida and Benkman 2005, Steele et al. 2005, Molinari et al. 2006), Eurasian red squirrels do not seem to benefit from a high availability of silver fir seeds and numbers drop in years with poor Norway spruce but medium-good silver fir crops. To test this “maladaptive” hypothesis (Endler 1977, Dias 1996, Dias and Blondel 1996), red squirrel spacing behaviour and habitat selection currently is being studied under different levels of silver fir seed-availability in mixed spruce-fir forest.

Interestingly, sex-ratios tended to be male-biased in all six populations, although only significantly so in population BOR. Since our CJS-models did not reveal any sex-bias in capture probabilities, and since the sex-ratio of weaned, locally born offspring was even (Wauters et al. unpubl.), we feel confident that this skewed sex-ratio was not prejudiced by sampling biases. Similar male-biased sex-ratios have been documented in small red squirrel populations in fragmented woodlands in Belgium (Wauters et al. 1994a, b), in a dense population in an isolated conifer wood in southern Finland (Pulliainen 1982), in American red squirrels in heterogeneous fragmented habitats and in mixed conifer forests in Canada (Hurly 1987). The male-biased sex-ratio and low population density at BOR could suggest that, in most years, the Arolla pine habitat acts as a population sink within a dynamic interaction with surrounding (e.g. VAL) Norway spruce dominated forests. However, formally testing source-sink dynamics requires long-term monitoring of the availability and use of Arolla pine seeds (i.e. the major food supply at BOR), of reproductive and immigration rates, and gene-flow (Pulliam 1988, Dias 1996).

### Variation in survival rates

Comparable to other species of small rodents and large herbivores (Clutton-Brock et al. 1985, 2002, Ostfeld 1990, Julliard et al. 1999, Dobson and Oli 2001), adult squirrels showed higher survival rates than subadults, and survival substantially fluctuated between seasons and years. Juvenile and/or subadult survival rates of tree squirrels have earlier been shown to be more variable between years than adult survival. For instance, extreme weather conditions during winter or spring can drastically reduce juvenile/subadult survival (Koprowski 1991, Gurnell 1996), while survival and local recruitment of first-year individuals can be strongly affected by mast crops (Nixon et al. 1975, Gurnell 1996, Wauters et al. 2004). In contrast, subadult survival between spring and summer seems less strongly related to seed-crop size (Nixon et al. 1975, Gurnell 1996).

In most species and populations of Holarctic tree squirrels, adult survival typically varies seasonally, with often higher winter than summer survival in temperate forests (Wauters et al. 2004). Though variation in annual survival has been found to be related to the size of the previous year’s seed-crop (Nixon et al. 1975, Gurnell 1996), this effect is not always present (Barkalow et al. 1970). In many populations, patterns of (local) survival, or persistency, also differed between the sexes. For example, in a long-term study in high-density red squirrel populations, adult female survival was not related with food abundance, but was density-dependent in winter (October–March), while summer (April–September) survival of adult males increased with the previous year’s seed-crop (Wauters et al.
Mechanisms of resource tracking: increase rates or density?

In spring and summer, population increase was correlated with the previous year’s seed-crop, but this was no the case in autumn. Moreover spring-summer increases, those estimated in April and July, were mainly caused by higher immigration rates (particularly in spring) and less by new captures of weaned offspring from local spring litters. Redistribution of squirrels among populations in relation to food availability, with more animals settling in habitats with higher food-supplies, has been documented in the majority of tree squirrel populations (Wauters and Dhondt 1993, Gurnell 1996, Lurz et al. 1997, 2000, Münch 1998, Wauters et al. 2001b, 2004, Steele et al. 2005). Hence, in spring squirrels follow a resource tracking strategy with both spring reproduction and immigration increasing the year after a mast-crop (Boutin et al. 2006).

In contrast, squirrel densities and rates of population increase (parameter B) in autumn (thus new animals entering the population from August to October) were strongly correlated with the same year’s autumn seed-crop, while correlations with the previous year’s seed-crop (time-lag models) were either weaker (density) or absent (B). This contradicts our second prediction based on producer-consumer time-lag models (Curran and Leighton 2000, Ostfeld and Keesing 2000, Satake and Bjørnstad 2004), whereby squirrels were expected to follow a resource tracking strategy and increase in density mainly the year following a rich seed-crop. For squirrels, such time-lags have been shown from boreal squirrel populations in Sweden and montane beech-fir-spruce populations in Germany (Andrén and Lemnell 1992, Münch 1998). However, in alpine populations, the level of population increase between summer and autumn was only correlated with the upcoming seed-crop (of the same year). Moreover, we showed that in autumn both number of locally-born juveniles, hence birth rates during summer, and immigration rates increased with the upcoming seed-crops. Where immigration into habitats with higher autumn food-supply might be a direct response to the availability of maturing conifer seeds from early August onwards, much of the reproductive investment by resident females occurred before this new seed-crop became consumable (Boutin et al. 2006). Consequently, autumn density increased in synchrony with the same year’s resource pulse.

In conclusion, the hypothesis that fluctuations in tree squirrel populations are mainly determined by annual variation in tree-seed productivity was partly supported by our data. As predicted, fluctuations in numbers were positively correlated with food availability, measured as annual conifer seed-crop size. However, densities were not always higher in the habitat with the largest long-term average seed productivity, but red squirrels occurred at higher densities in Scots pine forest, characterised by stable seed-crops, than in Norway spruce with more abundant but more variable seed crops. Finally, both our data on annual variation in summer-autumn population increase and on fluctuations in autumn density supported the alternative hypothesis that red squirrel populations in montane and subalpine conifer forests increase population size in synchrony with resources, thereby eliminating population lags normally present when resources occur in pulses.

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