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## Forest Ecology and Management

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# Annual variation in predation and dispersal of Arolla pine (*Pinus cembra* L.) seeds by Eurasian red squirrels and other seed-eaters

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### ARTICLE INFO

#### Article history:

Received 8 April 2010

Received in revised form 11 May 2010

Accepted 11 May 2010

#### Keywords:

Cone counts

Eurasian nutcracker

Scatterhoarding

*Sciurus vulgaris*

Subalpine forest

### ABSTRACT

Seed predation and dispersal are key processes in the survival and distribution of plant species. Many animals cache seeds for later consumption, and, failing to recover some of these seeds, act as seed dispersers, influencing post-dispersal seed and seedling survival. Both animal and plant benefit from scatterhoarding and natural selection of seed characteristics and adaptations of seed predators (and dispersers) is one of the most important examples of co-evolution and mutualism. We studied the producer–consumer Arolla pine (*Pinus cembra*)–red squirrel (*Sciurus vulgaris*) system in a subalpine forest in the Italian Alps. Arolla pine produced large seed-crops (masting) at irregular intervals, followed by years with poor or moderate seed production. Squirrel density fluctuated in synchrony with the food resource, eliminating the time-lag normally present when resources are produced in pulses. In all years except 2009 (a mast-crop year), all Arolla pine cones were harvested (their seeds consumed and/or cached) by September to late October by different species. Both squirrels and nutcrackers (*Nucifraga caryocatactes*) fed on seeds, and their relative pre-dispersal predation rates (on cones in the canopy) differed between years. Overall, nutcrackers consumed more seeds between July and October than squirrels, but in 1 year squirrels took the largest number of seeds. Pre-dispersal seed predation by squirrels tended to be lower in years with large seed-crop size and there was a positive correlation, over the entire study period, between density of recovered hoards and Arolla pine seed density of the previous year. We conclude that (i) squirrels and nutcrackers are important pre-dispersal seed predators and seeds dispersers; (ii) squirrels are also post-dispersal seed predators, and (iii) the proportion of cached seeds consumed by squirrels increased with the size of the Arolla pine seed-crop, suggesting that red squirrel is a conditional mutualistic scatterhoarder of Arolla pine seeds.

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## 1. Introduction

Plant seeds are often subject to high predation by organisms, such as fungi, insects and vertebrates (Janzen, 1971). Seed dispersal can be regarded as a key process in the survival and distribution of plant species. The process may affect parent and offspring plant fitness through its effects on seed density, the distance seeds are moved from the parent tree, and the habitat where seeds are dispersed (Vander Wall, 1990; Tamura et al., 2005). It will also influence post-dispersal seed and seedling survival by affecting incidence of predation or attack by seeds eaters, and the types of

plants with which the seedling will compete (Willson and Traveset, 2000).

Many animals temporarily cache seeds for later consumption, and occasionally fail to recover some of these seeds, thereby acting inadvertently as seed dispersers, called synzoochory (Vander Wall, 1990). There are two types of caching that differ in the spatial distribution of cached seeds: larderhoarding and scatterhoarding (Smith, 1970; Smith and Reichman, 1984; den Ouden et al., 2005). Scatterhoarding is more favourable for plant dispersal (Vander Wall, 1990; Steele et al., 2005). Animals benefit from scatterhoarding because of the decreased probability that seeds will be found and consumed by other intra- and interspecific competitors (Smith and Reichman, 1984; Steele et al., 2005). This benefit can increase the animals' survival over the period of food scarcity, and, subsequent, reproductive success (Wauters et al., 1995). Potential advantages for the plant are: (1) escape from high seed and seedling mortality caused by distance, or density-dependent factors near parent tree; (2) coloni-

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sation of rare, unpredictable or ephemeral sites, such as tree fall gaps; and (3) directed dispersal to particular microhabitats suitable for seed survival and seedling germination (Willson and Traveset, 2000). Hence, natural selection of seed characteristics of plants and the adaptations of animals acting as seed predators and seed dispersers is a typical example of co-evolution, and one of the most important systems of mutualism in nature (Smith and Reichman, 1984; Vander Wall, 1990; Benkman, 1995; Benkman et al., 2003; Siepielski and Benkman, 2008).

In genus *Pinus*, there are approximately 110 species which can be classified into two groups according to the modes of their seed dispersal, i.e. wind-dispersed and animal-dispersed pines (Tomback and Linhart, 1990; Lu and Sun, 1996). The former have small, light seeds with relatively large wings which can be carried over considerable distances by wind, while the latter often have large, edible and wingless or nearly wingless seeds (Willson and Traveset, 2000). These heavy seeds are retained in cones, either by indehiscence or restraining flanges after cones dehisce. Large-seeded *Cembrae* pines, occur in barren or xeric habitat, or in mountains at high elevations, where environmental conditions are often stressful and/or highly variable (Tomback and Linhart, 1990).

The Arolla pine or Swiss stone pine (*Pinus cembra* L.) occurs in the subalpine zone (mainly between 1500 and 2200 m a.s.l.) in the Alps and Carpathian Mountains of Central Europe where it often reaches the upper tree-line, forming mixed or pure stands. Cones are 4–8 cm long and contain 8–12 mm long seeds with a hard pericarp and a vestigial wing. It is a member of the white pine group (*Pinus*, subgenus *Strobus*), where most species have wingless or nearly wingless seeds and belong to the animal-dispersed pines (Tomback and Linhart, 1990). Mutualistic relationships and co-evolution between *Strobus* pines and their seed predators and dispersers have been well documented for some species (e.g. Korean pine, *Pinus koraiensis*, Hayashida, 1989; whitebark pine, *Pinus heldreichii*, Tomback, 1982; Mattson and Reinhart, 1997). Wheelwright and Orians (1982) suggested that dispersal by a variety of animal species is more advantageous to a plant. Mattes (1985) documented that Eurasian nutcrackers (*Nucifraga caryocatactes* L.) acted as seed predators and seed-dispersing agents of Arolla pine. However, in mixed alpine conifer stands, also Eurasian red squirrels (*Sciurus vulgaris* L.) cached and regularly fed on *P. cembra* seeds (Molinari et al., 2006), while great spotted woodpecker (*Dendrocopos major* L.) and nuthatch (*Sitta europea* L.) may occasionally act as seed predators and wood mice (*Apodemus* sp.) and voles can exploit seeds from partly opened fallen cones (Mattes, 1985). Since these seeds have deep dormancy, they survive in the soil litter until the next year, when the snowcover melts, and squirrels and nutcrackers seek for cached seeds on the ground. Molinari et al. (2006) suggested that cone and seed traits of *P. cembra* facilitate seed consumption by red squirrels which prefer seeds of this species (which have the highest energy-content per cone of all food types, except silver fir, *Abies alba* Mill., Salmaso et al., 2009), as the major food resources throughout late summer–autumn. Being a highly specialised seed predator, red squirrels probably consume large numbers of Arolla pine seeds; hence whether they play the role of antagonistic seed predator or mutualistic seed disperser is equivocal (Theimer, 2005; Steele et al., 2005).

In this paper, we monitored annual fluctuations in *P. cembra* seed production and squirrel density, pre- and post-dispersal seed predation by red squirrels, nutcrackers and other potential seed-eaters and estimated predation rates on seeds in indehiscent cones by different seed-eaters. Consumption of cones with immature or mature seeds occurred from late July to late October, while retrieval and consumption of cached seeds occurred (at least) during the entire period when ground is not covered by a permanent snow-layer (late April–early May to October–November). We hypothesise that red squirrel is a conditional mutualistic scatterhoarder (Theimer,

2005) of Arolla pine seeds. To test this hypothesis, we first explored if the Arolla pine–red squirrel relationship is typical for a pulsed resource system with population dynamics of the consumer fluctuating in parallel with producer dynamics (seed-crop size, Boutin et al., 2006). If this is the case and squirrels scatterhoard as conditional mutualists, we predict that squirrels mainly act as pre-dispersal seeds eaters, and that, based on rapid-sequestering hypothesis (Jenkins and Peters, 1992), scatterhoarding is a strategy to reduce food competition when squirrels face a rich but short-lived food resources. Thus, the proportion of seeds cached (and not directly predated) will increase with the size of the *P. cembra* seed-crop. This was measured by counting recovered caches, i.e. caches whose seeds were retrieved and consumed (Wauters and Casale, 1996), and correlating cache density in spring–summer with seed-crop of the previous year. Earlier work on squirrels showed that density of recovered caches was correlated with total cache density (Wauters and Casale, 1996) and thus is a reliable, indirect measure of number of seeds cached.

## 2. Methods

### 2.1. Study area, forest composition and seed-crop size

The study was conducted over 9 years (2001–2009) in a mature, subalpine mixed conifer forest at Bormio, Central Italian Alps (area BOR 46°27'N, 10°30'E, see also Di Piero et al., 2008; Wauters et al., 2008). The study area extends over 93 ha at elevations between 1950 and 2150 m a.s.l., the upper tree-line, and was dominated by Arolla pine, mixed with Norway spruce (*Picea abies* L.) and larch (*Larix decidua* Mill.).

To estimate tree-seed availability as our measure of food abundance, we first determined woodland composition by establishing a 20 m by 20 m (400 m<sup>2</sup>) vegetation sample-plot (hereinafter called VSP) around each trapping station across the trapping grid ( $N=20$ , Salmaso et al., 2009). Trapping stations, and consequently each VSP, were randomly distributed over the study site using the Random Point Generator version 1.3 for Arcview GIS (Jenness enterprises, 2005, <http://www.jennessent.com/>). In each VSP, we counted the number of trees of each species, and measured the diameter at breast height (DBH) of two trees of typical size for each species on the plot (forests consisted of large areas of even-age stands with trees of similar size), hereafter called 'sample trees'. Choice of sample trees was random amongst trees with canopy easily visible for counting cones. Dead trees were recorded separately since their presence indicated a naturally structured forest.

Each year, initial counts of developed fresh cones were conducted between 25 July and 5 August. Cones were counted in the canopy of all coniferous sample trees (*P. cembra*,  $N=40$ ; *P. abies*,  $N=30$ ; *L. decidua*,  $N=32$ ) from a fixed position using  $10 \times 40$  binoculars and scaled to estimate the total number of cones per tree (Salmaso et al., 2009). Four repeated counts by different observers of cones in the same tree showed that counting error was small (from 0 to 7% of mean,  $N=10$ ). Average numbers of seeds per cone and cone-energy value (kJ cone<sup>-1</sup>) were determined as in Salmaso et al. (2009). Data of average cone-energy value (Arolla pine 121.4 kJ, Norway spruce 51.1 kJ, larch 9.4 kJ), cones tree<sup>-1</sup> and tree density were combined to calculate total and species-specific seed-energy production per VSP (kJ ha<sup>-1</sup>, Salmaso et al., 2009). The mean energy production over all VSP was our estimate of annual seed production. We also estimated annual seed production by Arolla pine, as the dominant tree species.

### 2.2. Cone survival and predation

To monitor Arolla pine cone survival in the canopy, we returned to the same observation points every 2 weeks between 15 August

and the end of October to early November of each year (2004–2009) and counted the remaining cones in the marked sample trees. Because cones are indehiscent at maturity (mid-September) and rarely fall to the ground without vertebrate assistance, we were able to ascribe cone loss to one of two species in the majority of cases, by identifying and counting remains of eaten cones (recently cut cones or pecked/chewed cone cores) under the canopy. Current year status of partly or entirely consumed cones was determined by remains having purple cone scales and light-coloured, soft cores. Nutcrackers start to extract seeds while the cone remains attached to the branch, and cone remains fall to the ground when the birds start pecking on the basal part of the cones, leaving a characteristic dished-out cone after seed harvesting (Cheng and Wauters, pers. obs.). Red squirrels use their sharp teeth to cut the base of a single cone from the branch and eat most of it in situ. They gnaw the base of bracts and tear bracts off (see also Rima et al., 2007), leaving a clean-cut seed-coat attached to the cone core, or extracting the entire seed (with coat = pericarp) and leaving seed-coats cut in two symmetric halves (our own observations). In some cases, when characteristics of cone remains did not allow us to attribute them to nutcrackers or squirrels, they were classified in category 'others'.

### 2.3. Cache recovery

Recovery of cached Arolla pine seeds was monitored every 2 weeks from May to October (2005–2009). At each count, four VSP were visited and in each VSP a sampling-circle with 0.80 m diameter (0.50 m<sup>2</sup>) was randomly thrown four times, producing four repeated measures of cache density per VSP, extrapolated to number of recovered caches/m<sup>2</sup>. For each count of caches we measured distance from the circle-centre to nearest tree. Each VSP was visited twice per year (once during May to July, a second time during August to October). Caches recovered by red squirrels were easily recognisable as small, round holes on the forest floor, about 3–6 cm deep (diameter 2–4 cm), in most cases with empty pericarp of Arolla pine near the hole (see also Wauters and Casale, 1996). Since this study was originally centred on squirrels, we did not search systematically for caches retrieved by nutcrackers (e.g. Hayashida, 2003).

### 2.4. Trapping and handling squirrels

Trapping was carried out in three periods per year (May, July and September to October), from 2002 to 2009. A trapping session involved the use of 20 ground-placed Tomahawk "squirrel" traps (models 201 and 202, Tomahawk Live Trap, WI, USA). Traps were pre-baited with sunflower seeds and hazelnuts 4–6 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 to 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 minimise stress during handling, sexed (based on external genitalia), and individually marked using numbered metal ear-tags (type 1003 S, 10 by 2 mm, National Band and Tag, Newport, KY, USA). The minimum number of animals known to be alive (MNA), from trapping, radio-tracking and observations, during each trapping period was used as an estimate of population size (total squirrel density). Since demographic patterns may differ between the sexes (Wauters et al., 2004), we also determined density for each sex separately. Previous studies on tree squirrel populations showed that these estimates realistically represent true squirrel densities (e.g. Lurz et al., 1995; Wauters et al., 2004, 2008; Boutin et al., 2006). The number of squirrel captures in a given trap during year  $t$  was used as an index of squirrel abundance in the VSP for year  $t$ : for each VSP it estimates how frequent that area of forest is used by squirrels.

### 2.5. Statistical analyses

We explored annual variation in tree-seed production with a General Linear Model (GLM) using total seed-energy production of the three conifer species (Arolla pine, spruce and larch) as dependent variable, and year as fixed effect, adding vegetation plot (VSP) as a random factor. The proportion of total variance explained by the random factor (VSP) was estimated and its significance was calculated using the Likelihood Ratio Test, which produces a value of  $\chi^2$  with one degree of freedom (Verbeke and Molenberghs, 2000). We also used the same model to explore annual variation in the size of the Arolla pine seed-crop. Significance of pairwise differences between annual means were tested using the differences of least squares means (hereinafter DLSM).

We analysed our data on cone survival in the canopy using a generalized linear mixed model (GLMM) using the proportion of surviving cones as dependent variable. Day, *P. cembra* density and squirrel abundance were added as continuous covariates. Year was added as fixed factor. We are mainly interested in how the decrease in the survival of cones with time (the association between the proportion cones surviving and day) differed between years and is affected by local squirrel abundance and *P. cembra* density. We therefore tested for the significance of two-way interactions between day and year, day and squirrel abundance, and day and *P. cembra* density. The three-way interaction between day, *P. cembra* density and squirrel abundance was also included and tested. Because the same plots were sampled repeatedly, plot and interactions with day and year were added as random effect. Significance tests were based on likelihood ratio tests and performed in R (R Development Core Team, 2009) using the lmer function in the lme4 package (Bates and Maechler, 2009).

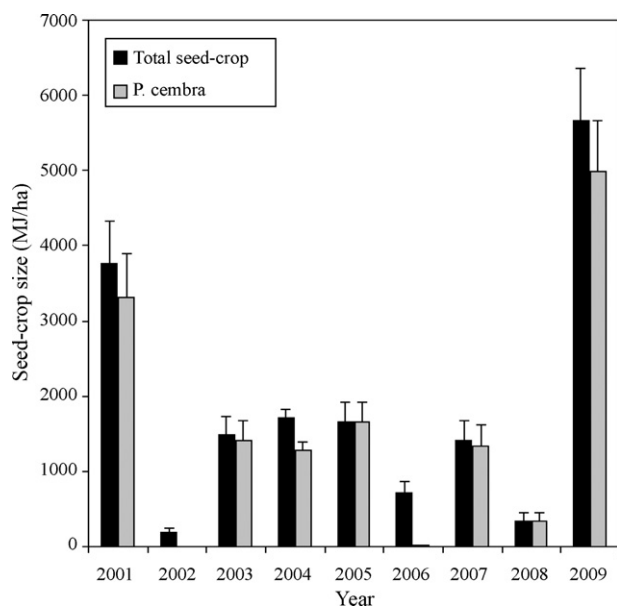
We used a log-linear model (PROC GENMOD with binomial distribution and Wald Type3 Chi-square, SAS, 1999) to explore annual patterns of the proportion of pre-dispersal seed predation (cone consumption) by the three seed-eaters (squirrel, nutcracker, and others). In a second analysis we only compared cone consumption by squirrels and nutcrackers.

Variation between years and period (date when hoards were counted) in hoard density (caches/m<sup>2</sup>) was investigated using GLMM (PROC MIXED, SAS, 1999) with the four counts in each VSP added as a repeated measure to account for pseudoreplication (Verbeke and Molenberghs, 2000). We also explored the fixed effects of tree density, proportion of Arolla pine, local squirrel abundance and Arolla pine seed-crop size (cones/tree), all measured at the level of the VSP, and the distance to the nearest tree of the sampling-circle containing recovered caches. To account for potential annual variation in the factors affecting hoard density, the two-way interactions of year with all other fixed effects were added. We started from a saturated model and used Schwarz's Bayesian information criterion (BIC) to find the correlation structures of the residual correlation matrix that best fitted the data (Verbeke and Molenberghs, 2000). The model with compound symmetry (CS) correlation structure had the smallest value of BIC, indicating a correlation between measures in the same VSP that does not vary over time (Verbeke and Molenberghs, 2000). After selecting the CS correlation structure, we continued testing fixed effects and performed model selection using a backward procedure. Degrees of freedom and standard errors of  $F$ - and  $t$ -tests were obtained using Kenward–Rogers method (Verbeke and Molenberghs, 2000).

## 3. Results

### 3.1. Forest composition and seed production

The proportion of spruce, larch, and Arolla pine varied between vegetation plots, thus at a fine-grained level. Of



**Fig. 1.** Annual variation in mean ( $\pm 1$  SE) tree-seed production ( $\text{MJ ha}^{-1}$ ) of all tree species and of *P. cembra*.

506 trees counted in the 20 vegetation plots (average tree density =  $633 \pm 201$  trees  $\text{ha}^{-1}$ ), 390 were *P. cembra* (mean  $\pm$  SD =  $76.6 \pm 15.0\%$ , range 45–100%), 65 *L. decidua* ( $13.0 \pm 12.1\%$ , range 0–36%), 43 *P. abies* ( $8.6 \pm 6.9\%$ , range 0–22%), and 8 (1.8%) were dead trees. Mean size (DBH) of *P. cembra* was  $36.7 \pm 10.1$  cm and all mature trees were more than 100 years old.

Overall tree-seed production varied markedly between years (Fig. 1,  $F_{8,152} = 33.6$ ,  $p < 0.0001$ ). Variance of the random factor (VSP) was significant (24% of total variance,  $\chi^2 = 20.6$ , one-tailed  $p < 0.001$ ), indicating variation at a fine-grained scale. Both 2009 and 2001 were mast years with seed-energy production higher than in all other years (DLSM, all  $p < 0.0001$ ). There was no difference in seed production between 2003, 2004, 2005 and 2007 (DLSM all  $p > 0.50$ ) or between these years and 2006 (DLSM, all  $p > 0.05$ , Fig. 1). In 2002 and 2008, poor seed-crops produced less seed-energy than in all other years (DLSM, all  $p < 0.05$ ), except 2006 (DLSM,  $p > 0.20$ ). Also *P. cembra* seed production varied between years (Fig. 1,  $F_{8,152} = 30.7$ ,  $p < 0.0001$ ; variance random factor explained 24% of total variance,  $\chi^2 = 21.6$ , one-tailed  $p < 0.001$ ). In 2009 and 2001 *P. cembra* produced mast-crops that were larger (DLSM, all  $p < 0.01$ ) than the seed-crops in 2003, 2004, 2005 and 2007. Few seeds were produced in 2006 and 2008, with a complete seed-crop failure in 2002 (Fig. 1, 2002, 2006 and 2008 against all other years, DLSM all  $p < 0.05$ ).

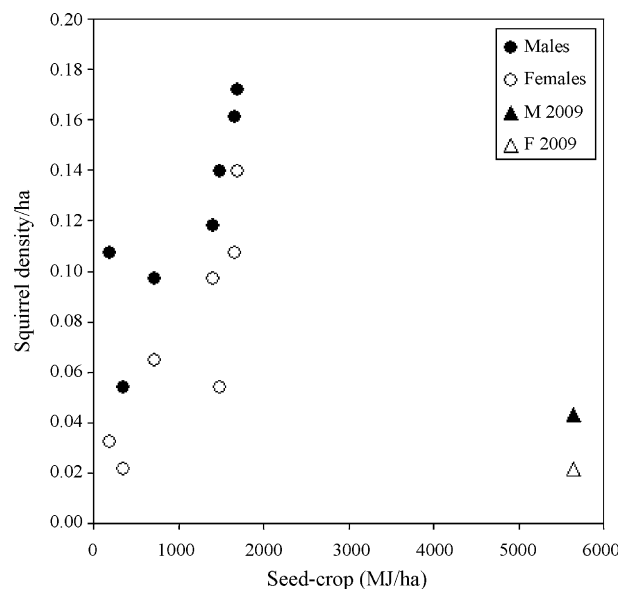
**Table 1**

Cones partly or entirely consumed found under the tree canopy as a measure of pre-dispersal Arolla pine seed predation. Average annual cone density (cones/tree) and squirrel density in summer (ind/ha). % Cones eaten is the percentage of eaten cones taken by each of the three seed predators.

Year	Cones/tree (total cones) <sup>a</sup>	Squirrel density/ha	% Cones eaten (number of cones eaten) <sup>b</sup>			
			All seed-eaters	Squirrels	Nutcrackers	Others
2004	33.0 (660)	0.24	50.6 (334)	11.8	33.0	5.8
2005	26.8 (1071)	0.33	44.2 (473)	13.5	28.8	1.9
2006	4.3 (172)	0.16	76.2 (131)	33.7	41.3	1.2
2007	24.8 (992)	0.17	28.3 (281)	11.5	13.5	3.3
2008	5.4 (214)	0.09	13.1 (28)	12.6	0.5	0.0
2009	79.6 (3182)	0.03	3.7 (117)	0.4	3.1	0.2

<sup>a</sup> Total cones = cones counted in canopy of all sample trees at August 1 (see Section 2) between brackets.

<sup>b</sup> Total number of eaten cones found under tree canopy of sample trees between brackets.



**Fig. 2.** Relationship between seed-crop size and sex-specific squirrel density in autumn.

### 3.2. Seed-crop size and squirrel density

Autumn density of red squirrels ranged from 0.07 to 0.31 animals  $\text{ha}^{-1}$  (mean  $\pm$  SD =  $0.18 \pm 0.09$ ). Male densities fluctuated between 0.04 and 0.17  $\text{ha}^{-1}$  (mean  $\pm$  SD =  $0.11 \pm 0.05$ ), female densities between 0.02 and 0.14  $\text{ha}^{-1}$  ( $0.07 \pm 0.04$ ). Over all years there was no positive effect of seed-crop size on autumn density of male and females squirrels, or on total squirrel density (Fig. 2, each sex,  $N = 16$ ,  $r = -0.21$ ,  $p = 0.44$ ; total density,  $N = 8$ ,  $r = -0.24$ ,  $p = 0.57$ ). However, if 2009, an outlier with very low densities despite a mast-crop, was eliminated, autumn density increased with seed-crop size of the same year (Fig. 2, each sex,  $N = 14$ ,  $r = 0.72$ ,  $p = 0.004$ ; total density,  $N = 7$ ,  $r = 0.89$ ,  $p = 0.008$ ). In the latter case, a GLM with sex and seed-crop size explained 79% of variation in autumn density of male and female squirrels ( $F_{2,11} = 21.3$ ,  $p = 0.0002$ ) with densities of males higher than females (sex effect  $F_{1,11} = 14.7$ ,  $p = 0.003$ ; seed-crop  $F_{1,11} = 27.9$ ,  $p = 0.0003$ ).

### 3.3. Pre-dispersal seed predation of Arolla pine cones

Pre-dispersal seed predation (cones partly or entirely consumed in or under the canopy) varied between 4 and 76% of the total cone-crop ( $N = 6$ , mean  $\pm$  SD =  $36 \pm 27\%$ ). Consumption by squirrels varied from 0.4 to 34% of total cone-crop (Table 1,  $N = 6$ ,



mean  $\pm$  SD =  $14 \pm 11\%$ ) and was correlated with percentage pre-dispersal seed predation by all seed-eaters ( $r = 0.87$ ,  $p = 0.025$ ). There was a weak negative relationship between percentage cones eaten by squirrels and cone-crop size ( $r = -0.77$ ,  $p = 0.075$ ). Pre-dispersal seed consumption did not increase with squirrel (summer) density ( $r = 0.27$ ,  $p = 0.60$ ).

Nutcrackers took between 0.5 and 41% of total cone-crop (Table 1,  $N = 6$ , mean  $\pm$  SD =  $20 \pm 17\%$ ) and consumption by nutcrackers was strongly correlated with percentage pre-dispersal seed predation by all seed-eaters ( $r = 0.97$ ,  $p = 0.0013$ ). There was no relation between percentage cones eaten by nutcrackers and cone-crop size ( $r = -0.37$ ,  $p = 0.47$ ).

Proportion cones taken by different seed-eaters changed between years (Table 1, year  $\times$  species interaction  $\chi^2 = 161.6$ ,  $df = 10$ ,  $p < 0.0001$ ) and, overall, nutcrackers took a larger proportion than squirrels, and both took more cones than other seed-eaters (species  $\chi^2 = 694.4$ ,  $df = 2$ ,  $p < 0.0001$ ; pairwise-species comparisons all  $p < 0.001$ ). In a second step, we only considered squirrels and nutcrackers. Proportion cone consumption by each species varied between years (year  $\times$  species interaction  $\chi^2 = 130.5$ ,  $df = 5$ ,  $p < 0.0001$ ). Comparing proportion cones eaten by squirrels and nutcrackers for each year separately, nutcrackers consumed more cones in 2004, 2005 and 2009 (all  $p < 0.0001$ ) while squirrels consumed more cones in 2008 ( $\chi^2 = 20.9$ ,  $df = 1$ ,  $p < 0.0001$ ; Table 1). There were no differences between the two species in proportion cones eaten in 2006 and 2007 (all  $p > 0.05$ ).

### 3.4. Cone survival

All mature Arolla pine cones disappeared from the canopy by the end of October in all years except 2009. Since intact cones did

not fall down, this indicated that all cones were harvested by seed-eaters before the onset of winter.

The decrease in survival of cones with time in the canopy of *P. cembra* differed between years (year  $\times$  day interaction  $\chi^2 = 735.3$ ,  $df = 5$ ,  $p < 0.0001$ ), but was not affected by variation in squirrel activity (squirrel activity  $\times$  day interaction  $\chi^2 = 0.01$ ,  $df = 1$ ,  $p = 0.99$ ) or by variation in tree density (*P. cembra* density  $\times$  day interaction  $\chi^2 = 0.57$ ,  $df = 1$ ,  $p = 0.45$ ) or a combination of both (squirrel activity  $\times$  *P. cembra* density  $\times$  day interaction  $\chi^2 = 2.00$ ,  $df = 1$ ,  $p = 0.15$ ). Patterns of cone survival with time differed greatly between years (Fig. 3). Cones were removed most quickly from the canopy in 2007 and 2008 (the latter being a year with very poor cone-crop). 80% of cones were removed in about 1 month (by 1 September) in 2005 and 2006, while it took squirrels and nutcrackers about 2 months to remove 80% of cones in 2004. Only in 2009, when the squirrel population had crashed, cone survival was very high and less than 20% were removed by early November, when the study site was covered by deep snow-cover ( $>50$  cm) that remained throughout winter (Fig. 3). The average percentage of cones surviving in the canopy for 30 days (cones in canopy at 1 September) was  $43.8 \pm 40.9\%$  ( $N = 181$ , range 0–100%), and mean 30-day cone survival per year was positively correlated with mean annual cone-crop size ( $N = 6$ ,  $r = 0.84$ ,  $p = 0.037$ ).

### 3.5. Hoard recovery

Variance in density of recovered hoards caused by repeated measures in VSP was small and not significant (0.6% of total variance,  $\chi^2 = 0.28$ ,  $df = 1$ ,  $p = 0.60$ ). Overall, hoard density varied greatly between years and many interactions of year with other fixed effects were significant (Fig. 4 and Table 2), indicating that fac-

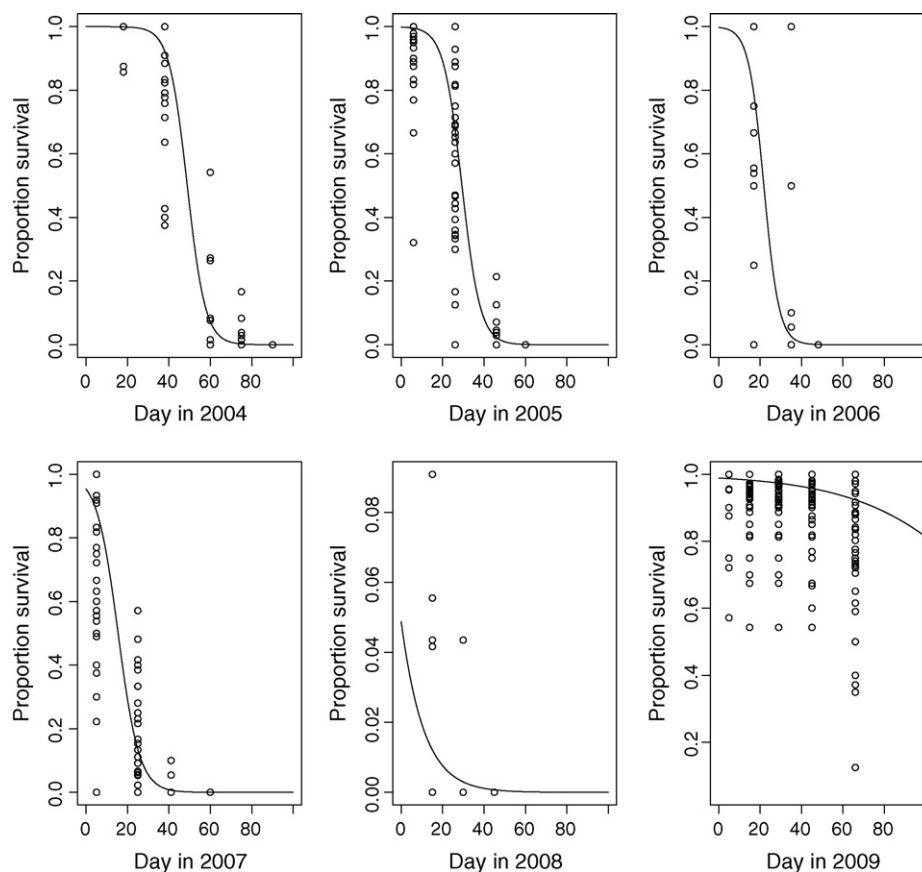
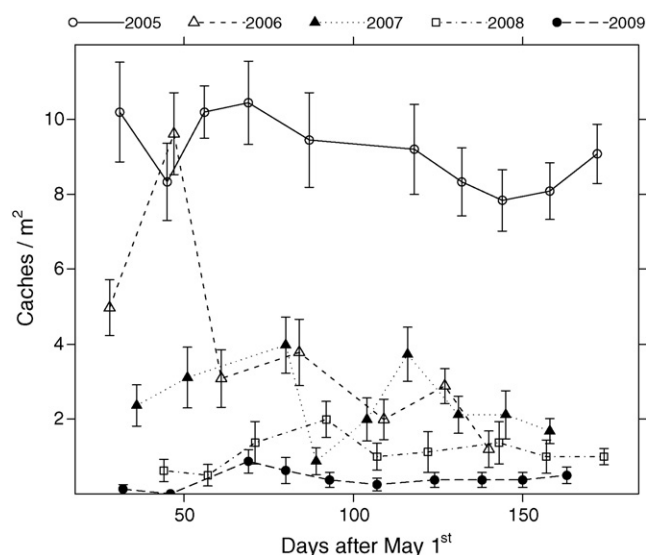


Fig. 3. Estimates of survival of *P. cembra* cones in the canopy per year. Estimated association of survival with day (slope  $\pm$  SE) for each year: 2004,  $-0.229 \pm 0.015$ ; 2005,  $-0.226 \pm 0.012$ ; 2006,  $-0.270 \pm 0.034$ ; 2007,  $-0.195 \pm 0.012$ ; 2008,  $-0.103 \pm 0.056^*$ ; 2009,  $-0.032 \pm 0.008$ ; all  $p < 0.0001$  except  $*p = 0.065$ .



**Fig. 4.** Mean ( $\pm$ SE) number of recovered caches/ $\text{m}^2$  over the spring–autumn period per year.

tors affecting hoard density differed among years. There was also a period effect and a year by period interaction (Table 2), suggesting that recovery of hoards by squirrels varied over the season (May to October, Fig. 4). Over all years, density of recovered hoards increased with cone density (the size of Arolla pine seed-crop) of the previous year, suggesting that squirrels cache more intensively when seed availability of *P. cembra* is high (Table 2, and linear regression coefficient of mean density of recovered hoards on cones/tree for entire study period  $b = 0.079 \pm 0.013$ ,  $p < 0.0001$ ). Hoard density also increased with tree density and there was tendency of finding more hoards at smaller distances from the nearest tree (Table 2). However, also interactions of these factors with year were significant (Table 2) indicating that patterns varied among years. Therefore, in a second step, we analysed the fixed effects for each year separately (Fig. 4).

In 2005, when density of recovered hoards was the highest of the entire study period, none of the effects was significant (all  $p > 0.10$ ). In 2006, hoard recovery was most intense in May to July (period  $F_{6,38} = 13.9$ ,  $p < 0.0001$ ) decreased with increasing distance from nearest tree ( $F_{1,133} = 9.14$ ,  $p = 0.003$ ), increased in VSPs with higher tree density ( $F_{1,10} = 5.61$ ,  $p = 0.039$ ) and with higher cone production the previous year ( $F_{1,10} = 9.61$ ,  $p = 0.012$ ). In 2007, most hoards were recovered in late May to early July (period,  $F_{8,67} = 2.13$ ,  $p = 0.045$ ) and hoard density decreased with increasing distance from the

nearest tree ( $F_{1,148} = 7.49$ ,  $p = 0.007$ ), while in 2008 a peak of hoard recovery occurred by late June (period,  $F_{8,64} = 2.05$ ,  $p = 0.054$ ), and hoard density decreased with increasing distance from the nearest tree ( $F_{1,149} = 17.1$ ,  $p < 0.0001$ ). Finally, in 2009 density of recovered hoards was highest in VSPs with a higher cone production the previous year ( $F_{1,18} = 8.15$ ,  $p = 0.01$ ).

## 4. Discussion

### 4.1. Masting by Arolla pine: a predator satiation strategy?

The multi-annual pattern of seed production by Arolla pine in our study site was typical for a pulsed resource system where mast years (the synchronous production of large seed-crops by a population of plants, Silvertown, 1980) occurred at irregular intervals, followed by years with poor or moderate seed production. One of the most widely accepted explanations for masting, a common phenomenon in plants whose seeds are dispersed (and cached) by animals (Vander Wall, 2002), is the predator satiation hypothesis: plants experience increased survival of seeds through satiation of specialist insect and/or vertebrate seed consumers, resulting in a greater proportion of seeds surviving in mast years (Janzen, 1971; Vander Wall, 2002). In this study, however, and in agreement with producer–tree squirrel dynamics in other habitats, we found that autumn density of Eurasian red squirrels fluctuated in parallel with Arolla pine seed-crop size. Thus, population size increased in synchrony with the food resource, eliminating the time-lag normally present when resources are produced in pulses (Boutin et al., 2006; Wauters et al., 2008). It was suggested that when consumers respond without a time-lag, masting by the producer will be less efficient as a seed predator satiation strategy (Boutin et al., 2006). This view was further supported by our data showing that the removal rates of seeds handled (both eaten and cached) by scatterhoarders was relatively stable and that the entire seed-crop was removed from the canopy by early November in all years except 2009.

We must underline that the producer–consumer dynamics pattern was disrupted in 2009 when Arolla pine produced a mast-crop, that followed the seed-crop failure of 2008, and squirrel numbers had not yet recovered from the population crash (during autumn–winter 2008–2009), caused by the poor seed availability in summer–autumn 2008 (see Fig. 1). In 2008, seed-crop failure was synchronous in the three conifer species in the study site (Arolla pine, larch and Norway spruce) eliminating strategies of diet shifts from preferred to less preferred tree-seed species (e.g. Wauters and Dhondt, 1987; Steele et al., 2005). This rare combination of a poor seed-crop causing a strong reduction in population size of predators, followed by a large seed-crop satiating the few predators left illustrates the presumed advantage of masting on increased plant recruitment.

Although some studies in mixed coniferous or mixed conifer–broadleaf woods showed that fewer seeds were predated and more cached seeds survived to germination after masting (e.g. Vander Wall, 2002; Steele et al., 2005; Theimer, 2005), our data do not allow to conclude that masting in Arolla pine increases subsequent seed germination. In contrast, we showed that density of recovered hoards increased with previous year cone density, suggesting that squirrels consumed more cached seeds after a good cone-crop. We admit that density of recovered hoards is only an indirect measure of density or proportion of seeds of the previous year's seed-crop that were cached and that additional studies are needed to show that squirrel seed caching increases after good seed-crops.

These results indicate the importance of examining tree-seed dispersal strategies over longer time periods. For example, monitoring the fate of seeds from the 2009 mast-crop, and counting Arolla pine seedlings of different age in relation to past (2001–2009)

**Table 2**

GLMM exploring the effects of year, period and continuous variables on density of recovered hoards. See Section 2 for model details.

Variables and factors removed	Statistics
Year $\times$ tree density	$F_{4,550} = 1.00$ , $p = 0.41$
Year $\times$ % Arolla pine	$F_{4,657} = 1.03$ , $p = 0.39$
% Arolla pine	$F_{1,19} = 1.39$ , $p = 0.25$
Selected model	
Year	$F_{4,463} = 20.8$ , $p < 0.0001$
Period	$F_{9,487} = 2.61$ , $p = 0.0061$
Year $\times$ period	$F_{31,439} = 4.16$ , $p < 0.0001$
Distance nearest tree	$F_{1,714} = 6.29$ , $p = 0.012$
Tree density	$F_{1,24} = 4.95$ , $p = 0.036$
Cone density	$F_{1,43} = 5.50$ , $p = 0.024$
Squirrel activity	$F_{1,109} = 0.84$ , $p = 0.36$
Year $\times$ distance nearest tree	$F_{4,720} = 3.53$ , $p = 0.007$
Year $\times$ cone density	$F_{4,239} = 7.07$ , $p < 0.0001$
Year $\times$ squirrel activity	$F_{4,263} = 2.60$ , $p = 0.036$

estimates of seed-crop size will be necessary to explore whether masting in Arolla pine is an efficient seed predator satiation strategy that increases the tree's reproductive success. Finally, our results suggest that large-scale landscape structure, affecting the seed predator's mobility and its ability to move and switch between different habitats to make use of local food abundance, may be important.

#### 4.2. The conditional mutualism between red squirrel and Arolla pine

Co-evolved mutualism between the Eurasian nutcracker (*N. caryocatactes*) and large-seeded pines (*Pinus*, subgenus *strobus*) have been well-documented with at least four species of Eurasian pines (*P. cembra*, *P. koraiensis*, *P. pumila* and *P. sibirica*; Mattes, 1985; Hayashida, 1989, 2003; Hutchins et al., 1996; Lu and Sun, 1996; Kondrashov, 2004; McKinney et al., 2009). Our results showed that Eurasian nutcracker took, in most years, more Arolla pine seeds than other seed-eaters, and there was no relation between percentage seeds eaten and seed-crop size, indicating that Eurasian nutcracker is the most important Arolla pine seed predator. In the following years, additional data will have to be gathered on number of nutcrackers and on the amounts of seeds cached and retrieved by this species to investigate whether it is the primary mutualistic Arolla pine seed disperser in the Alps.

Where nutcrackers were observed flying over considerable distances carrying Arolla pine seeds in their sublingual pouch, often to different habitats (lower elevation Norway spruce forest, higher elevation wooded alpine grasslands, Mari and Zong, pers. obs.), red squirrels scatter-hoarded seeds inside their home range within the Arolla pine forest (our unpubl. data). Thus, also squirrels acted as an important pre-dispersal seed predator and, by scatterhoarding seeds for consumption the next spring–summer (assuming incomplete seed recovery), as seed disperser.

In the Arolla pine forest in this study, squirrels consumed a relatively stable proportion of seeds in the pre-dispersal period (between 12 and 34%, excluding 2009), and cached seeds in large quantities on the forest floor. In fact, we found high densities of recovered caches where seeds were consumed by squirrels within our sampling plots, indicating high post-dispersal seed predation. Although we do not know over which range of distances groups of seeds are carried before caching, we found that after intermediate (2005 and 2007) and poor seed-crop years (2006) there was tendency of finding more retrieved caches at shorter distances from the nearest parent tree. These data suggested that squirrels performed Rapid-Sequestering seed harvest strategy (Jenkins and Peters, 1992) for a limited food resource. This type of caching, moving seeds over short distances from parent trees, is unlikely to enhance opportunities for colonisation or to escape distance-responsive seed predators. Hence, seed burial may be the only benefit to Arolla pine from scatterhoarding by squirrels (e.g. Steele et al., 2005).

Conditional mutualistic relationship between animals and plants occurs when: (i) mutualism is facultative rather than obligate; (ii) a third species is involved in the interaction; and (iii) the benefit of the interaction is a function of the relative abundance of the partners (Bronstein, 1994; Theimer, 2005). Two of these conditions were met by the red squirrel–Arolla pine interaction. First, Arolla pine seed dispersal by squirrels could be facultative, since squirrels also fed on other resources such as Norway spruce and larch seeds, as well as on flowers, shoots and buds of several conifers and on hypogeous and epigeous fungi (Bertolino et al., 2004; Molinari et al., 2006). Second, squirrel numbers fluctuated in parallel with seed-crop dynamics and squirrels recovered more caches, and probably scatter-hoarded more Arolla pine seeds, when Arolla pine produced rich seed-crops.

In conclusion, our data supported our predictions that (i) as non-exclusive seeds disperser, squirrels simultaneously acted as important pre- and post-dispersal seeds eaters; and (ii) the proportion of cached seeds consumed by squirrels increased with the size of the Arolla pine seed-crop, suggesting that red squirrel is a conditional mutualist scatterhoarder of Arolla pine seeds.

#### 4.3. Management implications

Arolla pine is a species endemic to the Alps and restricted areas of the Carpathian Mountains (Casalegno et al., 2010), and subalpine forest of *P. cembra*, are listed as priority habitats for conservation in the EC Habitat directive (Annex I, habitat 9420). In the Italian Alps, Arolla pine occurs in patches or as sparsely distributed trees in mixed subalpine conifer forests or as dominant species near the upper tree-line (Theurillat and Guisan, 2001; Casalegno et al., 2010). The current increase in temperature, combined with land abandonment, result in upward shifts of species' maximum altitudinal limit and thus in changes in forest diversity and composition (Theurillat and Guisan, 2001; Parmesan and Yohe, 2003; Walther et al., 2005; Chauchard et al., 2010). Consequently, inter-specific competition of Arolla pine with fast regenerating conifer species is likely to increase (e.g. Chauchard et al., 2010). We showed that seed dispersal, and thus subsequent seedling establishment and natural regeneration of Arolla pine, depend on hoarding activity by Eurasian nutcracker and Eurasian red squirrel. Having more than one species involved in seed dispersal is likely to be advantageous for the tree since it increases the range of habitats and distances over which seeds will be transported, favouring Arolla pine regeneration both at the local scale (seeds that survived caching by squirrels in partly open patches near parent tree) and in the wider subalpine mixed forest ecosystem (seeds that survived long-distance caching by nutcrackers). We recommend that Arolla pine forest management should plan for selective felling of mature trees with high timber quality, creating small opening in the mature pine-dominated stands to enhance seedling establishment from cached seeds, and that conservation should aim to maintain the overall forest structure and extension. Finally, natural colonisation, from cached seeds, of alpine grassland above the current upper forest limit (Didier, 2001) should be monitored.

#### Acknowledgements

We thank Ambrogio Molinari and Stefania Martini for help with the fieldwork. Constructive comments by two anonymous referees greatly helped to improve the paper. This study is part of the ASPER (Alpine Squirrel Population Ecology Research) project, funded by the province of Sondrio (Servizio Agricoltura, Caccia e Pesca, Settore Risorse Ambientali), the Stelvio National Park and the Parco Regionale delle Orobie Valtellinesi to Istituto Oikos NGO, Milan. Additional financial support was given by MIUR (Ministero dell'Istruzione, dell'Università della Ricerca, project COFIN 2003, number 2003053710-006) to Insubria University of Varese. C. Zong held a research grant for extra-European researchers from the Commission for International Relations of the Insubria University, Varese. 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. This is paper #19 of the ASPER project.

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