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Research Article

Habitat effects on hoarding plasticity in the Eurasian red squirrel (*Sciurus vulgaris*)

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Abstract

Hoarding patterns can be classified into two general types: scatter-hoarding and larder-hoarding, but there are intermediate types. Various factors affect hoarding patterns. Animals hoarding identical seeds in different habitats may use different hoarding patterns to adapt to habitat variation. We used a sample-plot investigation method to study cache features and recovery rate of seeds of Arolla pine (*Pinus cembra*) by Eurasian red squirrels (*Sciurus vulgaris*) in 2009 and 2010 in two subalpine forests with different tree-species composition in the Italian Alps. Hoarding patterns of red squirrels varied among habitats: the typical scatter-hoarding pattern with most caches including 2-6 seeds is found in spruce (*Picea abies*) dominated forest, while a combination of few large caches ($\geq$10 seeds) and many small caches (less than 10 seeds) is found in Arolla pine dominated forest. Consequently, average number of seeds/cache was higher in the latter habitat. Among five microhabitats, shrubs, grass, moss, fallen leaves, and stone, Eurasian red squirrels preferred fallen leaves and moss as hoarding substrate. Cache recovery investigation indicated that recovery rate was 62% in spruce forest and only 21% in Arolla pine forest. A lower availability of suitable hoarding microhabitat resulted in changes in hoarding patterns of red squirrels in *Pinus cembra* dominated forest. We suggest that the main factor influencing differences in recovery rate was a higher cone production per tree in *Pinus cembra* forest.

Introduction

Hoarding behavior is a specialized foraging behavior by which animals control part of their food resources to adapt to the spatio-temporal heterogeneity of food distribution in natural environments (Vander Wall, 1990). Hoarding animals have several patterns of food storage from complete concentration to complete dispersal. Scatter-hoarding means food is stored in scattered caches, with only small amounts in each cache; larder-hoarding means food resources are concentrated in a single location such as a burrow or a midden (Vander Wall, 1990; Steele, 1998; Steele et al., 2005). Scatter-hoarding and larder-hoarding are only two extreme types and there are many intermediate forms between them (Jiang, 1996; Steele et al., 2005). Tree squirrels in the Holarctic have two major hoarding patterns: scatter-hoarding in the non-territorial *Sciurus* species such as gray squirrels (*S. carolinensis*), fox squirrels (*S. niger*) , Japanese squirrels (*S. lis*), and Eurasian red squirrel (Stapanian and Smith, 1978; Kato, 1985; Gurnell, 1987; Kenward and Holm, 1989; Wauters et al., 1992; Suselbeek et al., 2013); and larder-hoarding in the territorial species American red squirrels (*Tamiasciurus hudsonicus*) and Douglas Squirrels (*T. douglasii*) (Smith, 1968; Steele et al., 2005; Archibald et al., 2013). Although tree squirrels build several dreys (e.g. Bosch and Lurz 2013), seeds are mainly hoarded on the ground.

Hoarding patterns of animals depend on their abilities to protect the stored food resources (Smith and Reichman, 1984; Preston and Jacobs, 2001; Dally et al., 2006). Larder-hoarding occurs when animals can protect their food resources from competitors. In contrast, if hoarders have low abilities to protect food, they will mainly use scatter-hoarding which can avoid catastrophic loss of all hoarded food due to pilfering animals (Vander Wall, 1990). However, some species have more complex hoarding behavior. The western and eastern populations of American red squirrels show different hoarding patterns (Layne, 1954; Smith, 1968; Smith and Reichman, 1984; Dempsey and Keppie, 1993; Archibald et al., 2013). Ord's kangaroo Rats (*Dipodomys ordi*) and yellow pine squirrels (*Tamias amoenus*) scatter-hoard in summer but behave as larder-hoarders in winter (Kuhn and Vander Wall, 2009; White and Geluso, 2012). Geographic locations, different seasons and habitat types can influence the intraspecific variation of hoarding behavior (Hurly and Robertson, 1990; Dempsey and Keppie, 1993; Steele, 1998; Kuhn and Vander Wall, 2008; White and Geluso, 2012). Moreover, population density of intraspecific or interspecific competitors and human disturbance may cause changes in hoarding patterns (Stapanian and Smith, 1978; Hurly and Robertson, 1987).

We have been studying Eurasian red squirrels (*Sciurus vulgaris*) in two subalpine conifer forests (named Valfurva and Bormio), with different tree-species composition and at different elevations, in the Central Italian Alps since 2002 (Wauters et al., 2007, 2008; Salmaso et al., 2009). The dominant tree species in Valfurva is Norway spruce (*Picea abies*) with a small number of Arolla pine (*Pinus cembra*) and larch (*Larix decidua*), while Arolla pine is the dominant species in Bormio. The substrate microhabitats in the two study area are different: mainly moss and fallen leaves in Valfurva, while Bormio has more microhabitat types including moss, shrub, grass and fallen leaves.

In this paper we explored if these differences in habitat affected the density and size of caches made by red squirrels, and whether this resulted in different hoarding strategies in the two study areas. We also investigated whether red squirrels selected particular microhabitats for

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caching, and whether different hoarding patterns influenced their cache recovery rate.

Methods

Study area

Our study was conducted in mature subalpine mixed conifer forests in the Stelvio National Park, central Italian Alps (Fig. 1). Valfurva (46°27′ N, 10°31′ E, elevation 1650-1870 m) is a 78 ha area dominated by Norway spruce (89%) with some scattered larch (2%), Arolla pine (6%), and dead trees (3%). The surface vegetation is mainly moss and litter layer (leaves of coniferous trees). Bormio (46°27′ N, 10°30′ E, elevation 1950-2130 m) is on the same mountain slope but at higher elevation, reaching the upper tree-line. It covers 93 ha and is dominated by Arolla pine (73%) with some larch (18%), Norway spruce (8%) and few dead trees (1%). The undergrowth vegetation was alpine roses (*Rhododendron ferrugineum*), bilberry (*Vaccinium myrtillus*), and Poaceae plants (see also Molinari et al. 2006; Zong et al. 2010). This study is part of a low-budget long-term monitoring project of red squirrels in the Italian Alps, highlighting the importance of continuity and multi-disciplinarity in field-research projects (Cagnacci et al., 2012).

Hoarding and cache recovery

Hoarding investigation was conducted in Bormio and Valfurva in September and October 2009. We established 20 by 20 m (400 m^2) vegetation sampling plots, one around each trapping station across the trapping grid (n=20) (hereinafter called VSP, see Salmaso et al. 2009 for details), with sample tree as centre (Fig. 1). Trapping station were placed on a 150 m × 150 m grid or were randomly distributed over study area using the Random Point Generator version 1.3 for ArcView GIS (Jennuss Enterprises, 2005 http://www.jennessent.com). For each cache sampling, a circle with 0.80 m diameter (0.50 m^2) was randomly thrown four times in each VSP (hereinafter called small-sample plot, SSP). All VSPs were monitored four times each month, resulting in a total of 320 SSPs in Valfurva and 640 in Bormio. The difference in SSP sample size between study areas was due to *Pinus cembra* being present in all 20 VSP in Bormio but in only 10 VSP in Valfurva.

We searched for caches made by squirrels in SSP by carefully digging through litter and soil to a depth of ca. 10 cm. The size of each cache (number of *P. cembra* seeds) was recorded (Wauters and Casale, 1996) and microhabitat factors, such as forest type, substrate type and cache depth were measured. At the end, we replaced litter and soil to restore the SSP to its initial appearance.

Squirrels typically leave two lines of clear teeth marks on the seed-shell when pulling the seeds out of *P. cembra* cones. We used this feature to distinguish caches of red squirrels from those of Eurasian nutcrackers (*Nucifraga caryocatactes*) in Liangshui Nature Reserves in China (Zong et al., 2007), and this method was also used in this study. The major native seed predators which fed on Arolla pine seed in the two study sites are red squirrels and Eurasian nutcrackers (Zong et al., 2010, 2012).

Because thick snow cover made it impossible to visit study sites in winter, the recovery of caches was studied in May-June 2010. Every two weeks four VSP were visited so that all 20 VSP were checked once during the 2-month period. In each VSP a sampling-circle with 0.8 m diameter (0.5 m^2) was randomly thrown four times, producing four repeated measures of cache density per VSP extrapolated to number of recovered caches/m^2. Caches of red squirrels were easily recognized as small and round holes on forest ground, about 3-6 cm depth and 2-4 cm diameter, and always with seed shell fragments near the holes (Wauters and Casale, 1996; Zong et al., 2010). In both hoarding and recovery experiments, we did not search for caches retrieved by nutcracker systematically, since the study was originally concentrated on squirrels.

Microhabitat of caches

Microhabitat surveys were done in September and October 2009. We classified microhabitat types in five categories: fallen leaves, moss, grass, shrubs (present in both study sites), and under stones (only in Bormio site). Microhabitat types were patchily distributed: we determined availability of each category by measuring the composition of microhabitat types in all SSPs (8 in each VSP in both study sites).

Statistical analyses

All tests were carried out using R (R Core Team, 2013). One-sample goodness-of-fit tests were used to compare availability of microhabitat types against an expected homogeneous distribution. Bonferroni confidence intervals (CI) were calculated to explore whether a given microhabitat type was available more or less than expected. Chi-square tests were used to compare frequency of occurrence of microhabitat types between study areas and the Bonferroni confidence interval (CI) to test whether squirrels selected certain soil-cover types for caching pine seeds. Tree density and number of cones/tree were compared between the two areas using a Student t-test with Satterthwaite correction of degrees of freedom for samples with unequal variance. A generalised linear model with Poisson error structure was used to test effects of study area, microhabitat type and their interaction on cache size (number of seeds hoarded). Pearson Chi-square test was used to analyze recovery intensity difference in different habitats. Quantitative data were described as mean ± standard deviation, and significant level was 0.05.

Results

Cone abundance and microhabitat availability

In Bormio, tree density and cone production of Arolla pine were higher than in Valfurva, but there was no difference in the number of seeds per cone between the two areas (Tab. 1). Hence the availability of Arolla pine seeds for hoarding was much higher in Bormio than Valfurva. In Bormio, fallen leaves (pine needles) covered more of the soil than expected (29%), grass (20%), shrub (20%) and moss (18%) occurred as expected, and stone (13%) less than expected (One-sample goodness-of-fit test χ^2=47.2; df=4; p<0.0001 and Bonferroni CI). In Valfurva, fallen leaves (34%), grass (35%) and moss (29%) occurred more than

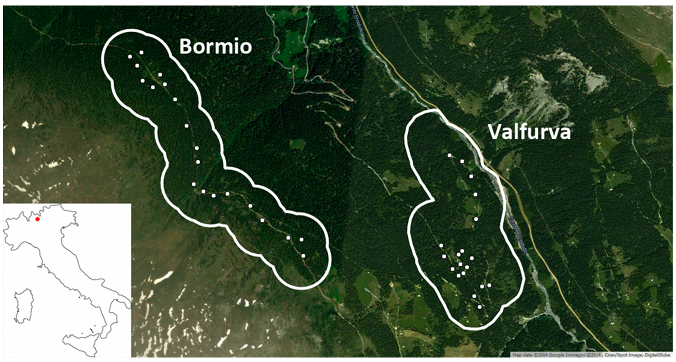

Figure 1 – Map of the two study areas in Stelvio National Park. Dots indicate trapping stations and their relative vegetation sampling plots (VSPs, see Methods).

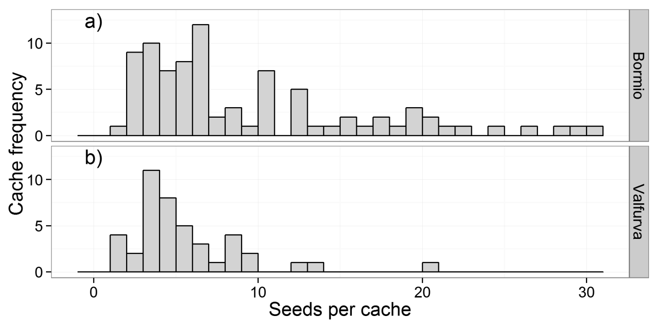

Figure 2 – The number of Arolla pine seeds hoarded by red squirrels per cache in (a) Bormio and (b) Valfurva study areas.

Table 1 – Mean (±SD) number of *P. cembra* trees/ha, mean (±SD) number of cones/tree in 2009 and mean number of seeds/cone in the two study areas. Student's t-test for differences between means.

Study area	*P. cembra* trees/ha	*P. cembra* cones/tree	Seeds/cone
Bormio	466±160	84±46	73±10
Valfurva	34±35	14±9	69±12
t-test	t=11.8; df=21; p<0.0001	t=9.12; df=45; p<0.0001	t=1.12; df=38; p=0.27

expected, while shrub (2%) occurred only rarely and there was no soil covered with stones (One-sample goodness-of-fit test χ^2=196.8; df=4; p<0.0001 and Bonferroni CI). Hence, study areas differed in the availability of different microhabitat types (χ^2=130.1; df=4; p<0.0001), with grass and moss relatively more common in Valfurva, and shrub and stone more common in Bormio.

Cache characteristics

We surveyed a total of 960 SSPs in two study areas, that contained 128 squirrel caches: 43 in Valfurva and 85 in Bormio. There was no difference between the areas in the number of caches found per sampling effort (χ^2=0.005; df=1; p=0.95), thus no difference in cache density. Squirrels were highly selective in the choice of microhabitat for caching pine seeds (Valfurva χ^2=23.7; df=3; p<0.0001; Bormio χ^2=42.9; df=4; p<0.0001). No caches were found under grass, shrub or stone in either study area. In Valfurva, 21 caches (49%) were found under fallen leaves and 22 (51%) under moss, while in Bormio there were more caches under fallen leaves (n=62, 73%) than under moss (n=23, 27%, difference between areas χ^2=7.28; df=1; p=0.007). Bonferroni CIs showed that in Valfurva moss was selected more than expected for caching but not fallen leaves, while in Bormio there was an opposite trend with significant selection for caching under fallen leaves but not under moss.

Mean cache size differed between areas ($F_{1,124}$ = 11.8; p=0.0008) but not between microhabitats ($F_{1,124}$ = 1.65; p=0.20) and there was no area by microhabitat interaction (Tab. 2, $F_{1,124}$ = 1.00; p=0.32). Average cache size (±SD) was 9.0±7.1 seeds in Bormio and 5.1±3.6 seeds in Valfurva (Tab. 2). There were 25 large caches (>10 seeds) in Bormio (29% of all caches) against only 3 in Valfurva (7% of all caches, Fig. 2, Fisher Exact test p=0.006).

Cache size was not significantly correlated with cache depth (r=0.16; n=128; p=0.067). Adding study area in a GLM with cache size as dependent variable and cache depth as explanatory variable, there was no effect of cache depth ($F_{1,124}$ = 1.23; p=0.27) and no area by cache depth interaction ($F_{1,124}$ = 0.41; p=0.52). These results suggest that larger caches are probably the result of squirrels adding seeds in subsequent visits enlarging the original cache.

Cache recovery

In the cache-recovery survey in May-June 2010, 18 out of 84 caches (21%) had been recovered by red squirrels in Bormio, against 40 out of 65 caches (62%) in Valfurva (χ^2=24.8, df=1, p<0.0001). The average number of eaten seeds in recovered caches did not differ between study sites (Bormio 4.7±2.0 seeds, Valfurva 4.0±2.1 seeds, t-test t=1.27, df=34, p= 0.21).

Discussion

Habitat effects on plasticity of hoarding pattern

Hoarding patterns of squirrels are often influenced by food distribution in habitats (Hurly and Robertson, 1990; Steele et al., 2005). Hurly and Robertson (1990) suggest that high concentration of food resources encourage larder-hoarding in American red squirrels. We suggest that larger average cache size of red squirrels in Bormio is related to the high density of Arola pine trees, combined with a high seed production per single tree in 2009, a mast year (see also Zong et al. 2010). In contrast, in Valfurva, Norway spruce is the dominant species and the number of Arolla pine trees is small. Moreover average seed production per tree was much lower than in Bormio. Hence, different food abundance and its non-uniform distribution in two study areas resulted in different hoarding patterns. We do not believe that habitat-related variation in space use has any effect on the observed differences in hoarding patterns. Red squirrel space use and home range (core-area) overlap are similar over a wide range of habitats and percentage core-area overlap did not differ markedly between spruce dominated and stone pine dominated forests (e.g. Di Pierro et al. 2008, 2011).

Whether a mast crop is the crucial factor for the occurrence of hoards with larger number of seeds (>10) than observed in the typical scatter-hoarding pattern (with few seeds/cache as in Valfurva) will be explored by studying hoarding patterns in poor and medium seed-crop years.

Hoarding microhabitat selection of red squirrels

Some previous researchers suggest that hoarding habitat is selected by hoarders (Hurly and Robertson, 1990; Dempsey and Keppie, 1993; Herrera et al., 1994; Liu and Zhang, 2004). Microhabitat preference of animals had an influence on the hoarding patterns (Debussche and Insemann, 1994; Herrera et al., 1994). Ordinary scatter-hoarding of Ord's kangaroo rats *Dipodomys ordii* is replaced by larder-hoarding pattern when lacking suitable hoarding sites due to snow cover and frozen soils in winter (White and Geluso, 2012). In our two study areas with different habitats, red squirrels displayed a marked microhabitat selection for hoarding, preferring to cache seeds in soil covered by fallen leaves or moss. The microhabitat fallen leaves occurred in similar proportions in the two study areas, but moss was more common in Valfurva.

Why do red squirrels prefer fallen leaves and moss? We suggest that microhabitat selection is related to cache-recovery behavior. Our study areas are characterised by long and cold winter, with permanent deep snow-cover (>50 cm) from mid-November to next April in most years. These conditions make it impossible for squirrels to retrieve cached seeds. However, fallen leaves occur mainly close to tree trunks and under the densest part of the canopy where the snow-layer is thinner and melts earlier than in more exposed microhabitats. In fact, snow-free surface or soil with only a thin layer can be seen already in March allowing red squirrels to retrieve caches seeds earlier than in other microhabitats still covered with snow. Moreover, shrubs and grass microhabitat have dense surface vegetation, lack litter layer, and have a hard soil horizon, where digging is energetically more expensive than in soft soils (Luna and Antinuchi, 2006). Thus, cost of retrieving cached seeds in these microhabitats is likely to be higher than in fallen leaves and moss. Hence, we believe that selecting fallen leaves and moss reduces the energy consumption for hoarding and hoard recovery, which is an important determinant of hoarding behavior in environments with low temperatures (Briggs and Vander Wall, 2004; Zong et al., 2009).

Cache recovery rates in different habitats

Our results showed that cache recovery rate of red squirrels was significantly different between areas: 62% in Valfurva against 21% in Bormio. Recovery rate of hoarders in natural condition is always high. Recovery rate of chipmunks foraging in sand was up to 86% (Briggs and Vander Wall, 2004); recovery rate of yellow pine squirrels (*Tamias amoenus*) was 58%-74% (Vander Wall et al., 2006); and 79% of pine cones and acorn caches are recovered by the Eurasian red squirrels

Table 2 – Mean (±SD) seeds per cache according to study area and microhabitat.

Study area	Fallen leaves	Moss	all microhabitats
Bormio	8.4±6.4	10.8±8.6	9.0±7.1
Valfurva	5.0±4.1	5.1±3.1	5.1±3.6

in mixed conifer-broadleaf woods (Wauters and Casale, 1996). Compared with the previous study, recovery rate of red squirrels in Bormio was extremely low. Low recovery rate may be related to cache surplus emerged by the unusual death or emigration of hoarders (Steele et al., 2001). In our two study areas red squirrel population was stable but low before and after hoarding seasons in Bormio (density September 2009 0.13 squirrels/ha; May 2010 0.11/ha), or slightly increasing in Valfurva (density September 2009 0.18 squirrels/ha; May 2010 0.31/ha). Therefore ,we suggest that the cache surplus is unrelated to changes in population size in Bormio but could be related to the low density of squirrels during our study period as a consequence of the poor seed-crop in 2008 (Zong et al. 2010; L. Wauters, *unpublished data*). In mast-years, surplus seeds may increase the number of seeds cached resulting in more unretrieved caches becoming effective underground seed storage sites (Vander Wall, 1997; Steele et al., 2005). We believe that the 79% of caches not yet recovered in Bormio is related to different factors. First, the period in which we studied cache recovery was limited and other caches are likely to be retrieved after June, throughout the rest of summer. Second, cached seeds may remain dormant in the soil for a long time (Tachiki and Iwasa, 2010) and thus potentially can be retrieved also the two years after being hoarded. Third, after a mast-crop, some Arolla pine cones remained available for foraging in the tree canopy for an entire year (until next July). These remaining cones were easier to obtain compared with caches: thus because of abundant cone resources, red squirrels did not depend on underground caches after a mast-year, resulting in a low cache-recovery rate. In contrast, cone abundance of Arolla pines in Valfurva was much smaller, while population size of the two major Arolla seed predators, red squirrels and nutcrackers (*Nucifraga caryocatactes*), was similar or even higher than in Bormio (e.g. Zong et al. 2010, 2012). Consequently, all cones on trees were eaten or the seeds extracted for hoarding by the end of autumn, resulting in a more intense cache recovery. Red squirrels did not cache the cones or seeds of Norway spruce.

In conclusion, our results indicated that Eurasian red squirrels had different hoarding behavior in the different forest habitats of Bormio and Valfurva. In spruce-dominated forest with low density of Arolla pine (Valfurva), squirrels presented a typical scatter-hoarding pattern, while in the Arolla pine dominated forest of Bormio density of caches was similar but mean cache size was higher due to a larger number of seeds being hoarded in about 30% of caches. These differences were related to habitat dependent variation in food abundance and the distribution of Arolla pine trees, with larger caches occurring at high density of pine trees and high cone density per tree. To what extend variation between years in Arolla pine seed production affects the hoarding patterns of red squirrels in forests with different tree-species composition will be explored by monitoring seed consumption and hoarding over several years.

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