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Nutcrackers become choosy seed harvesters in a mast-crop year

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As an efficient seed-disperser, Eurasian nutcrackers (*Nucifraga caryocatactes*) generally consume and hoard mature, edible pine seeds for future use. In 2009, when the Arolla pine, *Pinus. cembra*, produced a mast-crop, we investigated cones discarded by nutcrackers. Most cones were only partly eaten and some mature seeds remained in the distal part. This was in contrast to years of lower seed production when nearly all seeds were harvested from the majority of cones. To determine whether nutcracker cone-discarding behaviour maximised intake rate, seed kernels and the aborted seeds rate were measured from the different cone parts. In 2009, seeds from cone-tops were on average 17% lighter than in the base and middle sections, and the proportion of aborted seeds in the top part was 81% higher than in the other sections. There was no difference in seed mass and proportion of aborted seeds in cone-tops of intact cones and cones handled by nutcrackers. Regarding each cone as a patch, cone discarding behaviour can be considered as an optimal cone-leaving rule, maximising rate of energy-intake, supporting the Marginal Value Theorem. Hence, we suggest that increased food abundance leads to more selective seed harvesting in nutcrackers.

KEY WORDS: *Nucifraga caryocatactes*, *Pinus cembra*, partial consumption, patch model, mast-crop.

INTRODUCTION

Many predators do not consume prey entirely. If these foragers feed on progressively less valuable portions of each prey item, they might maximise their net rate of energy intake by leaving an item while some material still remains, to search for more rewarding portions of another item (SIH 1980). In this case, a prey item may be viewed

as a patch with decreasing intake rate as a function of time spent in that patch, i.e. a patch model can be applied. The general prediction of this model is that a predator should leave a patch when its immediate intake rate of net energy drops below average across the entire habitat, this prediction has become known as the "Marginal Value Theorem (MVT)" (CHARNOV 1976; PYKE et al. 1977; STEPHENS & KREBS 1986). Examples of patch assessment rules (GREEN 1984) have been found in crossbills (leave a cone when kernel mass declines; BENKMAN 1989) and hummingbirds (PYKE 1978).

In 2009, Arolla pine produced a mast-crop in the central Italian Alps (ZONG et al. 2010). During the summer and autumn, we observed Eurasian nutcrackers, *Nucifraga caryocatactes*, foraging and hoarding seeds of *P. cembra* in almost all daylight hours. In nearly all cases, the nutcracker discarded the top one-third (or smaller) part (distal part) of a handled cone which still contained some mature and edible seeds (Fig.1). All seeds from the basal part of the handled cones were eaten or removed for caching. Since in 2009 nearly all cones used by nutcrackers had the distal part intact, which was not the case in previous years, this behaviour deserved consideration.

Based on MVT, increasing prey availability or value and decreasing search and handling costs should decrease the optimal time spent feeding on each item (SCHOENER 1971). An item's value should be its maximum possible net energy intake per unit handling time rather than the intake rate from consuming an entire item (SIH 1980). In this case, each Arolla pine cone can be viewed as a patch, and assuming that nutcrackers should try to maximise rate of energy intake and minimise time necessary to obtain nourishment by leaving the cones with edible seeds in the distal part, we predict that (1) nutcrackers will use all seeds from a cone in years with a poor or average seed production, but will take only the heavier seeds from each single cone during a mast-crop. If this is the case, we further predict that in a mast-crop (2) total seed mass and seed kernel mass will be higher for seeds from the basal part than from the distal end of a cone. Third, the proportion of aborted seeds (undeveloped seeds containing only the seed coat, thus without edible embryo), a cone-trait which acts to deter predators (e.g. BENKMAN 1995; BENKMAN et al. 2003), is likely to be higher in the distal part of cone than in the rest of the cone (HAYASHIDA 2003).

Fig. 1. — *P. cembra* cone discarded by Nutcracker after removal of seeds for feeding and/or caching.

MATERIALS AND METHODS

The study was conducted in a mature, subalpine mixed conifer forest at Bormio, Central Italian Alps (area BOR 46°27′N, 10°30′E; see also WAUTERS et al. 2008; ZONG et al. 2010). The study area extends over 93 ha at elevations between 1950 and 2150 m a.s.l., the upper tree-line, and is dominated by Arolla pine (77% of tree cover), mixed with Norway spruce (*Picea abies* L., 9%) and Larch *(Larix decidua* Mill., 13%). Average tree density is 633 trees/ha (ZONG et al. 2010). Nutcracker density was not known.

We established 20 m by 20 m (400 m^2) vegetation sample-plots hereinafter called VSP ($n = 20$, SALMASO et al. 2009) that 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). From August to October 2006, 2007 and 2009, we searched each VSP and collected the remains of cones used by nutcrackers (Table 1). Nutcrackers start to extract seeds (see also JACKOWIAK et al. 2010) while the cone remains attached to the branch. 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 (ZONG et al. 2010). In 2009, we also collected 111 intact cones from trees in the VSP to compare the seed characteristics between discarded and intact cones (containing all seeds).

Intact cones were divided into three sections: the distal part, the cone-middle and the cone-base. To allow comparison of cones handled by nutcrackers with an intact distal part, we defined the distal part as the top part of a cone with three rows of scales; the cone-base and cone-middle are, respectively, the lower and middle one-third of the entire cone. In total, 1116 seeds of the cone-base (BC), 994 seeds of the cone-middle (MC), and 854 seeds of the distal part (TC) were collected. Another 679 seeds from distal part of cones handled by nutcracker (TN) were collected.

Because mature seeds of *P. cembra* are light, the traditional water selection method to discriminate aborted (floating) from full seeds (sinking) is unsuitable. We used 90% ethanol to discriminate aborted seeds. We randomly selected 30 seeds as a unit to measure the proportion of aborted seeds and then sampled 20 times from each of the four groups (BC, MC, TC and TN, see above, total number of samples $n = 80$ for a total of 2400 seeds).

From each of the four groups, 200 seeds were randomly selected. Fresh total seed mass (with seed coat) and seed kernel mass were measured with an electronic balance (precision 0.01 g).

Data on total seed mass and seed kernel mass in the different cone sections met the assumptions of normality (Shapiro-Wilk's test, all $W > 0.90$). We used one-way ANOVAs with the seed mass parameters as dependent variables and group (the section of a cone from where seeds were taken: cone-base, cone-middle, distal part) as factor. Differences between means were further explored with the Tukey's Studentized Range test. The proportion aborted seeds was arcsine square-root transformed to normalise data (Shapiro-Wilk's $W > 0.90$) and the transformed values were used as a dependent variable in a General Linear Model (GLM) with group as factor. To determine whether intact cones were representative of cones that were foraged on, seed mass, seed kernel mass and proportion of aborted seeds were compared between intact distal parts (group TC) and distal parts

Table 1.

Mean Arolla pine cone production per tree (from ZONG et al. 2010) and number of collected cones eaten by nutcrackers in different years and, within this sample, those with intact cone top.

Year	Cone production (per tree)	Collected consumed cones	
		Eaten by nutcracker	Eaten but with intact distal part (%)
2006	4.3	71	5 (7%)
2007	24.8	134	22 (16%)
2009	79.6	170	165 (97%)

of cones handled by nutcrackers (group TN). Next, each seed trait was compared between distal part, cone-middle and cone-base of intact cones. All tests of significance were two-tailed and the significance level was set at 0.05. Values are presented in the text as mean ± SE using original data.

RESULTS

The proportion of cones handled by nutcrackers with the distal part left intact was much higher in 2009 than in the other years (Table 1, $\chi^2 = 263.4$; df $= 2$; $P < 0.0001$).

The distal part contained, on average, $20.4 \pm 0.5\%$ ($n = 111$) of all seeds in a cone. An Arolla pine cone contained on average $5.4 \pm 0.7\%$ of aborted seeds ($n = 60$, range 0–20%).

The mean total seed mass (Fig. 2A, $F_{1,398} = 0.90$, $P = 0.34$), mean seed kernel mass (Fig. 2B, $F_{1,398} = 0.06$, $P = 0.81$), and average proportion of aborted seeds (Fig. 3,
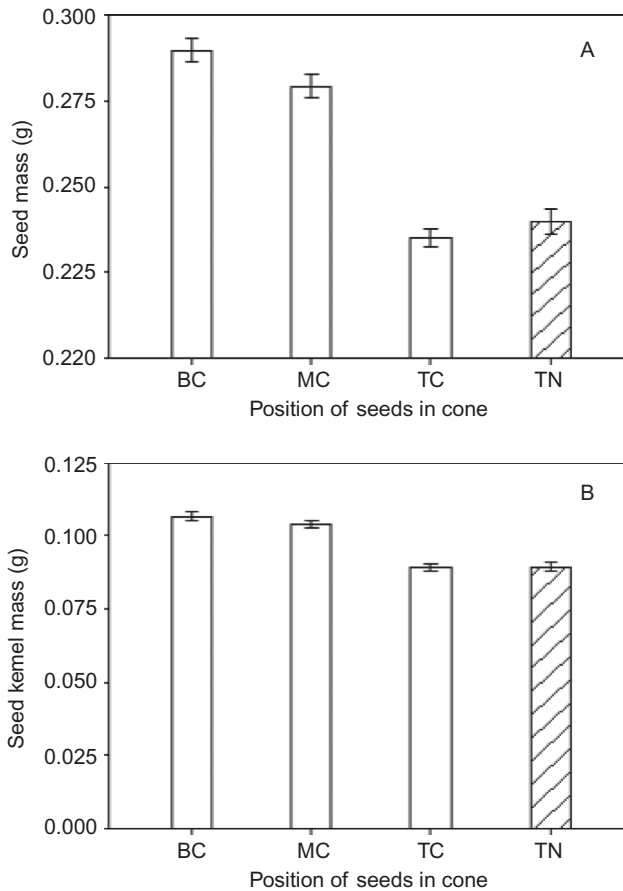

Fig. 2. — Comparison of mean seed mass with pericarp (A) and mean seed kernel mass (B) in different position of a cone. BC, base of intact cone ($n = 200$); MC, middle of intact cone ($n = 200$); TC, top of intact cone ($n = 200$); TN, distal part discarded by nutcracker ($n = 200$).
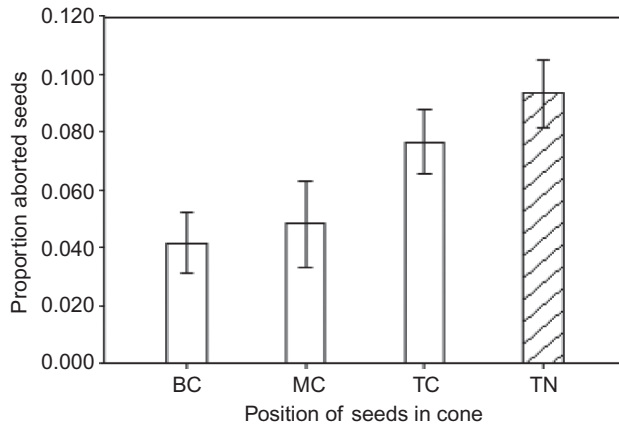
Fig. 3. — Comparison of proportion of aborted seeds in different sections of a cone (see Fig. 2 for abbreviations).

Table 2.

Seeds-traits in different sections of *P. cembra* cones.

Section of cone	Seed mass (g)	Seed kernel mass (g)	Proportion of aborted seeds
Distal part ($n = 200$)	0.235 ± 0.003	0.090 ± 0.001	0.077 ± 0.011
Cone-base and middle ($n = 400$)	0.284 ± 0.002	0.105 ± 0.002	0.045 ± 0.009

$F_{1,38} = 0.85$; $P = 0.36$) did not differ between intact distal parts (TC) and distal parts of cones handled by nutcrackers (TN), suggesting that intact cones were representative of those consumed by nutcrackers.

In intact cones, mean total seed mass (Fig. 2A, $F_{2,597} = 80.7$, $P < 0.0001$), mean seed kernel mass (Fig. 2B, $F_{2,597} = 53.2$, $P < 0.0001$) and proportion of aborted seeds (Fig. 3, $F_{2, 57} = 4.67$, $P = 0.013$) differed with position in the cone. Seed mass and seed kernel mass were lower, while proportion of aborted seeds was significantly higher in the distal part than in the lower sections (cone-base and cone-middle; all $P < 0.05$). Therefore, in further analysis we compared the seeds of the distal part with the rest of the cone.

The average seed mass in distal part was 17% lighter than in the rest of the cone (difference between means $F_{1, 598} = 154.8$, $P < 0.0001$), and there was the same trend for seed kernel mass (15% lighter, difference between means $F_{1, 598} = 103.4$, $P < 0.0001$). Moreover, the proportion of aborted seeds in distal parts was higher than in the rest of the cone (Table 2, difference between means $F_{1,58} = 9.07$, $P = 0.004$).

DISCUSSION

Direct observations of nutcrackers feeding on Arolla pine seeds confirmed that, in 2009, the birds nearly always dropped cone remains with an intact distal part,

indicating that not taking the seeds from the distal part was not the result of inadvertently dropping the cones. Moreover, it is unlikely that the phenomenon is related to a limited transport ability of nutcrackers while carrying seeds in the sublingual pouch. The capacity of the sublingual pouch was estimated at 42.4 ml, and Eurasian nutcrackers were observed to carry up to 134 *P. cembra* seeds at a single time (MATTES 1982). In our study, the average number of seeds per cone of *P. cembra* was 82, thus a nutcracker is potentially capable of transporting seeds of more than one cone per trip. Previous studies also showed that nutcrackers are efficient seed harvesters capable of discriminating edible from aborted seeds and selectively transporting and caching only edible seeds (HAYASHIDA 2003). All of the Pinon pine, *Pinus edulis*, seeds found in Clark's nutcracker, *Nucifraga columbiana*, pouches were mature and edible (VANDER WALL & BALDA 1977), and only three of 500 pine seeds from pouches of the Eurasian nutcracker were aborted or eaten by insects (REIMERS 1959). Thus, avoiding parts of cones with empty seeds is probably adaptive.

In addition, it is unlikely that seeds from the distal part are more difficult to extract than those from the lower sections of the cone. The second most important seed predator, the red squirrel, always starts extracting seeds from the distal part, cutting or stripping the distal part scales (ZONG et al. 2010). Crossbills (*Loxia curvirostris*) handle cones leaving them attached to the branch, and consume seeds only from the middle section of the side of the cone directed upwards, leaving a horizontal C-shaped cone-remain with intact scales (L. WAUTERS pers. obs.).

Nutcrackers processed most cones entirely in 2006 (93% of all handled cones) and 2007 (84%), years with a poor and a medium seed-crop. In contrast, only 3% of consumed cones from the 2009 mast-crop had all seeds removed, confirming our first prediction that nutcrackers become choosy seed predators and/or dispersers only when saturated by a rich seed-crop. Moreover, we found that the edible part (kernel) of seeds in the distal part was on average 15% lighter than in the rest of the cone, confirming our second prediction. Finally, in agreement with our third prediction, the proportion of aborted seeds in the distal part was 81% higher than in the rest of the cone. Hence, by discarding distal parts with a high proportion of aborted seeds, nutcrackers are likely to increase their foraging rate in a given period of time. Furthermore, since the mass of edible seeds in the distal part was lower, the rate of energy intake will increase when birds only feed on seeds from the base and middle sections of cones.

Other hypotheses have been proposed to explain why a forager might not consume an entire prey item; for example predator satiation models predict that a lower proportion of each item should be eaten if food availability is higher (JOHNSON et al. 1975). However, note that the mechanisms involved here are quite different. The satiation model predicts partial consumption even when the net rate of energy intake is constant, whereas in the marginal value theorem, patches (cones) are left sooner when travel time between patches decreases. Thus, nutcrackers should leave cones earlier (before complete depletion) during large cone crops than during small cone crops because travel time between cones is shorter during large cone crops. This assumes decelerating intake rates (i.e. the gain function) as the nutcracker begins to forage at the distal end of the cone, due to smaller and often empty seeds. Therefore, nutcrackers are more likely to leave seeds in the distal end of the cone as cone production increases.

Benefits of specialisation for the nutcracker are apparent. Nutcrackers spend considerable time during the autumn months collecting and storing pine seeds and may fly long distances in doing so. Since related energy costs must be considerable (VANDER WALL & BALDA 1977), the benefits of caching must be high. These benefits can be increased by selectively caching seeds of better quality (seeds with higher mass, more

nutrients; TOMBACK & LINHART 1990) which will result in more efficient exploitation of cached seeds during the next breeding season (VANDER WALL & BALDA 1977). For *P. cembra*, the nutcracker is the most effective dispersal agent (MATTES 1982), and seedling establishment depends mainly on nutcracker caches (HOLTMEIER 1986) and on germination of seeds scatter-hoarded by red squirrels (ZONG et al. 2010). Therefore, selective caching of heavy seeds by nutcrackers is likely to increase the proportion of vigorous seeds in the seed-bank and, subsequently, favour germination and seedling establishment (e.g. WESTOBY et al. 1996).

Discarding distal parts, which still contain some mature seeds, may favour other seed eaters. In montane and subalpine conifer forests of the Alps, passerines, such as willow tits, *Poecile montanus*, and crested tits, *Lophophanes cristatus*, were observed tracking red squirrels foraging on Scots pine, *Pinus sylvestris* and Norway spruce, *Picea abies* seeds (L. WAUTERS pers. obs.). While handling cones, squirrels always drop some viable seeds (WAUTERS & DHONDT 1987; WAUTERS et al. 1992) and tits search the ground for these seeds and feed on them. Similarly, in Japan, tits and Eurasian nuthatch, *Sitta europea,* were unable to open the intact cones of *Pinus pumila* but wrecked the scales of the tops of cones partly opened by nutcracker to feed on the remaining seeds (HAYASHIDA 2003). Also in our study area, coal tits, *Periparus ater,* fed on seeds left in the distal parts discarded by nutcrackers.

Both red squirrels and nutcrackers are major predators and hoarders of Arolla pine seeds (ZONG et al. 2010). Previous studies showed that one of the most important advantages of the caching behaviour of the nutcracker may be the avoidance of competition with other seed predators (TOMBACK 1982; SMITH & REICHMAN 1984; TOMBACK & LINHART 1990; VANDER WALL 1990). Based on the rapid-sequestering hypothesis (JENKINS & PETERS 1992), abandoning the distal part with more aborted and/or low-quality seeds can be considered an optimal foraging strategy, maximising the trade-off between energy gain and time costs. Nutcrackers might obtain a competitive advantage over red squirrels by harvesting more and better quality seeds of a finite food resource.

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