

## Seed predators in south Swedish deciduous woods: a field experiment \*

Jon LOMAN\*\*

Department of Animal Ecology, Lund University, SE-223 62 Lund, Sweden

**Abstract** Seeds from oak, horse chestnut, hawthorn, and sloe were exposed to seed predation during one week in autumn and over winter (for 6 months) in two different years. Three different exposure treatments were used and designed to exclude (1) small mammals and birds or (2) birds or (3) none. Insects and slugs had access to all exposures. 16 replicate experiments were set up in different deciduous woods and small woodlots. The pattern of seed loss from the different treatments suggest that small mammals were the quantitatively most important seed predators on chestnut, acorns and sloe nuts. Invertebrates probably had some importance as predators on hawthorn nuts. Birds appeared to be of less importance. This conclusion was valid for both woods and small woodlots. In one year, total predation rates were significantly higher in small woodlots than in large woods [*Acta Zoologica Sinica* 52 (3): 462-468, 2006].

**Key words** Small mammals, Birds, Insects, Acorn, Nuts

## 瑞典南部落叶林动物对种子捕食的实验研究 \*

Jon LOMAN\*\*

Department of Animal Ecology, Lund University, SE-223 62 Lund, Sweden

**摘要** 在瑞典南部落叶林, 于 1985 年和 1986 年秋季分别研究了不同动物对欧洲七叶树、夏栎、山楂和黑刺李等 4 种种子的捕食作用, 即种子释放 1 周后被动物捕食的情况。实验分以下 3 种处理: 排除小兽和鸟、排除鸟和对照 (小兽和鸟均不排除), 但昆虫可进入所有处理。在不同落叶林和小型林地共建有 16 个重复实验, 即每个林分类型于每年秋季各设 4 个重复。在所有林分 (包括落叶林和小型林地), 不同处理的种子捕食表明: 小兽是欧洲七叶树、夏栎和黑刺李等植物种子的主要捕食者, 而无脊椎动物则是山楂种子的重要捕食者, 但鸟类很少取食上述种子, 因而捕食作用极小。在其中 1 年, 动物对种子的总捕食率在落叶林和小型林地存在较大差异, 以小型林地较高 [动物学报 52 (3): 462-468, 2006]。

**关键词** 小兽 鸟 昆虫 橡子 坚果

Seed predation is an important process that may govern the distribution pattern and population dynamics of many rodent (Jensen 1982; Diaz et al., 1993; Ostfeld et al., 1996) and bird species (Enoksson, 1990) and is a major cause for bird irruptions (Ulfstrand, 1963). Predation can also shape plant communities, both as a cause for mortality (Hay and Fuller 1981; Ostfeld et al., 1997; Manson et al., 2001; Clarke and Kerrigan, 2002) and as part of the plant's dispersal strategy (O'Dowd and Hay, 1980; Herrera, 1995; Masaki et al., 1998; Fuentes, 2000; Andresen, 2002). Seed predation can be either

pre-or post-seedfall (Janzen, 1971). Pre-seedfall predation on trees and shrubs is mainly from birds (Courtney and Manzur, 1985) and insects (DeSousa et al., 2003) although also some mice may climb to take nuts in trees (Hoffmeyer 1976; Ida et al., 2004). After seedfall, seeds are more available to and used by mammals, mainly rodents (Watts, 1968; Gurnell, 1993; Masaki et al., 1998) but also deer and wild boar are locally important (Bosch 1997; Focardo et al., 2000).

Although small mammals are usually named the main post-seedfall seed predators in temperate decidu-

Received Dec. 09, 2005; accepted Apr. 17, 2006

\* The research was funded by a grant from Swedish National Environmental Protection Board

\*\* E-mail: jon.loman@zoekol.lu.se

© 2006 动物学报 *Acta Zoologica Sinica*

ous forests, there are in this and similar habitat also present several birds that feed on tree and shrub seeds found on the ground (Bossema, 1969; Enoksson, 1988; Stapanian et al., 1994; Hulme, 1997; Walther and Gosler, 2001). Over time, seeds may also decay or disappear due to the activities of invertebrates and fungi (Nilsson and Wästljung, 1987; Kelbel, 1996). Given this diversity of potential seed predators and the importance for the plant community, it is important to learn what groups of animals are important seed predators in different habitats and regions.

Seed predation rates may vary within a landscape (Hulme and Kollmann, 2005); effects of patch area (Nilsson and Wästljung, 1987; Wästljung, 1989; Santos and Telleria, 1994) and distance to habitat where potential seed predators can find cover (Hay and Fuller, 1981; McCormick and Meiners, 2000) have been found. To evaluate studies on landscape effects, it is thus important to know what groups of seed predators are potentially important in a region.

I here report on an experiment to evaluate the relative importance of different groups of seed predators in south Swedish woodland habitats. Because there may be landscape effects on the set of predators that are quantitatively important in a habitat, I conduct the study at two ranges of wood sizes.

## 1 Materials and methods

Seeds were distributed on the forest floor in the autumns of 1985 (October 14th to 16th) and 1986 (October 20th to 25th). The number of seeds remaining after one week and after six months was counted. In both years, eight sites in the central and southwestern part of the province Skåne, in south Sweden, were used (different sites in the two years, for a total of 16). In each year, four of these sites were in small woodlots (each 0.04–0.30 ha in size) and four sites were in larger woods. These were at least 25 ha of forest or part of a larger area with predominantly forest. In each wood, one site was used. At the sites, two or three sets of seeds were distributed.

The different sets at one site were subject to either of two or three treatments. One set (open) was uncovered, open to all forms of seed predation. One set (partly covered) was covered by a metal wire net with a mesh width of 10 mm, shaped like an up side down 15 cm deep pan. Between the rim of the pan and the ground, metal stands produced a space of about 2 cm that was left clear. This treatment was open to rodent predation but designed to keep birds out. One set (full cover) was completely covered by a metal wire net, also with a mesh width of 10 mm. This surrounded the set and was dug down to a depth

of 25 cm. The top of the set was also covered by a net. This treatment was designed to keep birds and rodents out but to allow invertebrate predation and natural decay, including effects of fungi. This last treatment was only successfully undertaken in the second year. In the first year, the below ground part of the net was more shallow and there were signs of rodent penetration (tunnelling, earth heaps) at most sites. This treatment was thus not analyzed for the first year. Also, the number of seeds in the completely covered treatment was only counted after 6 months. Dismounting the cover after one week when very little predation was to be expected (as the seeds were accessible to invertebrates only) was not deemed motivated.

Each set of seeds was evenly scattered within 0.5 m<sup>2</sup> and the sets were within a few meters from each other. All seed were placed partly covered by leaves which mimics the natural situation at this time of the year. By placing the seeds thus, rather than open on trays, and in moderate densities, I assured that only animals naturally foraging in the forest litter would find them. They could not be detected from a distance, as might have been the case with a more concentrated food source.

Each set contained 10 seeds from horse-chestnut *Aesculus hippocastanum* and 20 seeds each from oak *Quercus robur*, hawthorn *Crataegus* sp. and sloe *Prunus spinosa*. The average size of these seeds was 20 mm, 12 mm, 5 mm, and 7 mm, respectively. The first is a naturalized species while the other are indigenous.

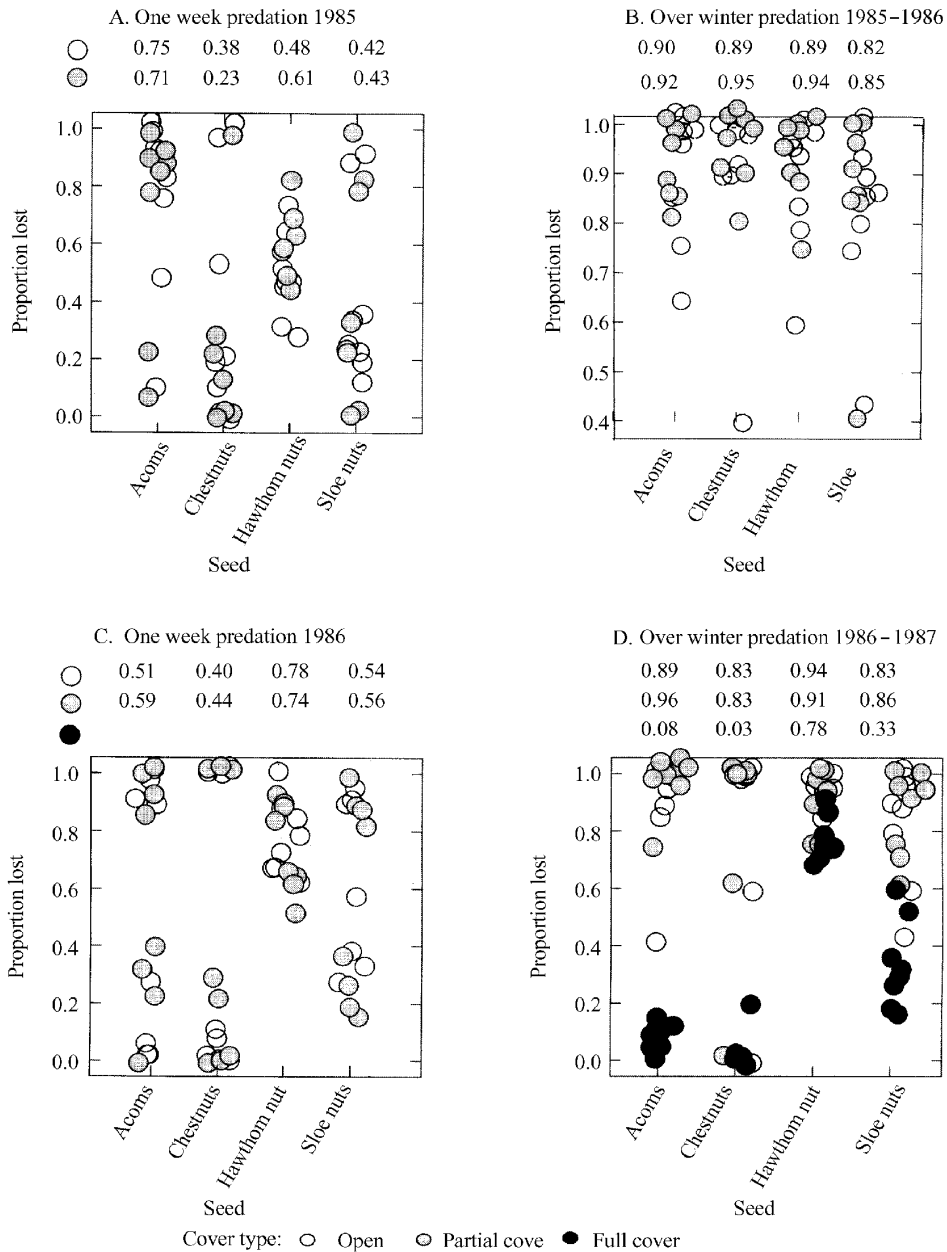
Predation, rather than exploitation (including removal), of seeds is the focus of this study. Thus, following some other seed predation studies (Masaki et al., 1998; Kollmann et al., 1998), fruit pulp was removed from fleshy-fruit seeds used.

The effects of seed species, cover treatment (within plot factors), and habitat type (between plot, random, factor) were analysed by a split plot ANOVA, where each site comprised one "plot". Predation rate (% seeds removed) were arcsine, square root transformed before analysis to improve normality.

## 2 Results

### 2.1 Treatment and seed species effects

In both years and after one week of exposure, the proportion of seeds lost was independent of the presence of cover treatment (Table 1, Figs. 1a and c). This response was true irrespective of seed species, as manifest by the lack of an interaction. However, there was a difference among species in the general level of predation. In 1985, more acorns than chestnuts and sloe nuts were lost (Tukey test,  $P <$



**Fig. 1** Effect of cover type (treatment) on seed predation rate

Data points refer to different sites (8 in each of two years) and treatments. Symbols have been slightly relocated ("jitter"). This was done to avoid complete overlap of some symbols. Mean values are given above each set of symbols, for each cover type separately.

0.001 and  $P = 0.013$ ). In 1986, more hawthorn nuts than chestnuts, sloe nuts and acorns were lost (Tukey test:  $P < 0.001$ ,  $P = 0.018$  and  $P = 0.021$ , respectively).

Also over the first winter, there was no difference in loss between the two treatments (Fig. 1b). In this time perspective (in contrast to one week), there was no difference among the four seed species. Over the second winter, fewer seeds were lost when fully covered than when open or partially covered (Table 1, last row, Fig. 1d) (Tukey test, both  $P < 0.001$ ). The losses in the other two treatments were similar; including only open and partly covered treatments in

the test, the effect of treatment was not significant ( $df = 1:6$ ,  $F = 0.02$ ,  $P = 0.88$ ). In this winter there was also a difference in the response of different seed species to the treatment, as manifest by a significant interaction (Table 1). More specifically, there were few losses of acorns and chestnuts from the fully covered treatment (Fig. 1d) but high and similar losses from the other two treatments. For hawthorn (especially) and sloe nuts, the difference between the losses from the fully covered seeds and those in the other treatments were less clear. Also general level of winter predation differed among seed species, though this was not quite significant for the first winter. The

**Table 1** Tests of cover treatment (open, partially covered and, for winter predation 1986 – 1987 only, also fully covered), seed type (acorn, chestnut, hawthorn and sloe) and patch size (small woodlots and large woods) effects, analysed as a split plot ANOVA

		One week predation		Winter predation	
		1985	1986	1985 – 1986	1986 – 1987
Treatment	<i>df</i>	1:6	1:6	1:6	2:12
	<i>F</i>	0.38	0.95	0.97	105.2
	<i>P</i>	0.56	0.37	0.36	<0.001
Seed type	<i>df</i>	3:18	3:18	3:18	3:18
	<i>F</i>	5.66	3.90	2.65	5.87
	<i>P</i>	0.007	0.026	0.080	0.006
Patch size	<i>df</i>	1:6	1:6	1:6	1:6
	<i>F</i>	0.001	70.9	0.004	4.62
	<i>P</i>	0.98	<0.001	0.95	0.08
Treat. * Seed t.	<i>df</i>	3:18	3:18	3:18	6:36
	<i>F</i>	2.01	0.51	0.29	17.1
	<i>P</i>	0.15	0.68	0.83	<0.001
Treat. * Patch s.	<i>df</i>	1:6	1:6	1:6	2:12
	<i>F</i>	0.28	0.15	1.48	4.73
	<i>P</i>	0.61	0.71	0.27	0.031
Seed t. * Patch s.	<i>df</i>	3:18	3:18	3:18	3:18
	<i>F</i>	3.30	5.71	1.67	0.73
	<i>P</i>	0.044	0.006	0.21	0.54
Treat. * S.t. * P.s.	<i>df</i>	3:17	3:18	3:18	6:36
	<i>F</i>	0.33	0.43	0.20	1.30
	<i>P</i>	0.80	0.73	0.90	0.28

The tree way interaction (given *in italics*) was not significant and removed before the final analyses of other effects.

highest predation was on hawthorn nuts, irrespective of treatment.

## 2.2 Patch size effects: small woodlots vs. large woods

In the first year, predation rates were similar in small woodlots and large woods (Figs.2a and b, Table 1). Also, there was no significant interaction between habitat type and treatment. In the second year, predation rates after one week were higher in small woodlots than in large woods (Figs.2c). Also over winter predation rates were higher in the small woodlots, though this effect was numerically less strong (effect size 0.064 vs. 0.30) in this long run (Fig.2d) and the effect not quite significant (Table 1). Only in the second winter was there an interaction between habitat type and treatment (Fig.2). This was because in small woodlots there was a clear division between fully covered treatments and those open and partly covered; predation rates being higher

in the latter. In large woods, however, predation rates also in some open and partly covered treatments were lower and in the range of those fully covered. This interaction was not seen in the first year nor after one week in the second year. There were no three way interactions between seed species, treatment and habitat type (Table 1).

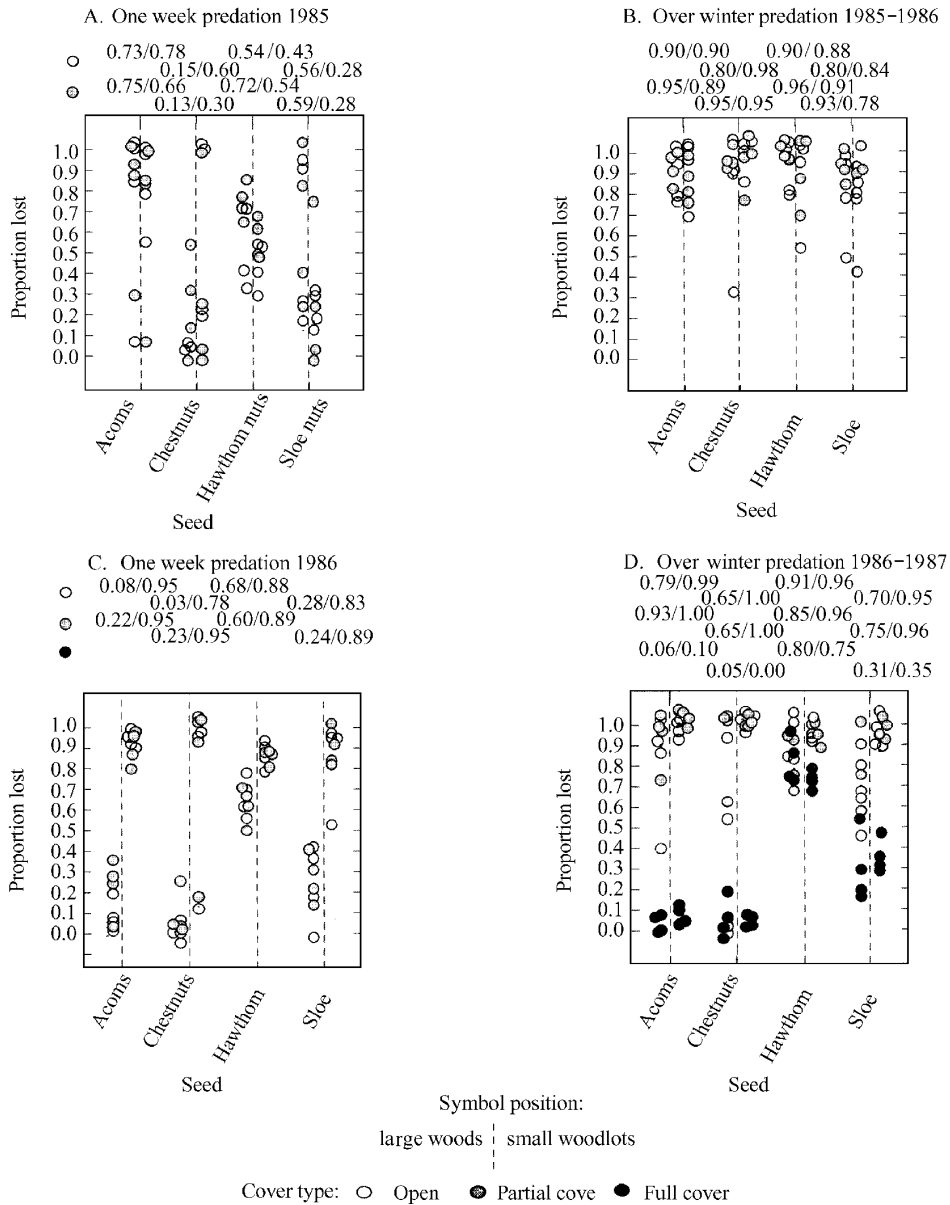
## 3 Discussion

### 3.1 The experiment

Two of the study seeds (sloe and hawthorne) are fleshy-fruit seeds. The study investigates the fate of these seeds after possible consumption of the fruits by fruit-eating birds. These fruits are readily consumed by birds and the seeds are passed, usually with little loss of germination potential (Guitian and Fuentes 1992, Masaki et al., 1994; Meyer and Witmer, 1998; Vander Wall et al., 2004). Thus, the effects of the many birds that may exploit these fruits are not part of the present study. On the other hand, what is scored probably to a large extent represents true predation in the sense that the seeds are lost from the plant population. This is true for consumption by birds that are able to exploit the seeds rather than fruit pulp (Guitian and Fuentes, 1992), in the case of sloe and hawthorne nuts, e. g., Hawfinches *Coccothraustes coccothraustes* (Biljsma, 1998). This is also true for those seeds that are removed by rodents. Those that are not directly consumed by the rodents are scatter-or larderhoarded. Although the significance of those few that germinate in these situations may be high for the plant population, most are probably permanently lost (Iida, 1996; Hulme and Borelli, 1999).

The absolute density of seeds could, by local enhancement, affect predation rates. The stress in this study is not on actual predation rates but relative rates among treatments, as a clue to identify groups of predators. However, local enhancement may still be factor of some importance. This is so if different groups of predators react differently to seed density variation. In the present case, the total density of large tree and shrub seeds was 140/m<sup>2</sup>. Sun et al. (2004) report a density of 130 acorns/m<sup>2</sup> in a Chinese oak forest and Maeto and Ozaki (2003) densities up to 120 acorns/m<sup>2</sup> in mast years. Gardner (1977) recorded, in the best of 5 years, up to 1 000 ash seeds/m<sup>2</sup> in each of two areas. Because ash seed fall is spread out over a full year, less seeds were probably present simultaneously. However, typically, 25% fell in November. Locally, the present experimental setup should thus represent a natural but high seed density, typically found right under a parent tree or in a mast year.

### 3.2 Interpretation



**Fig. 2 Comparing predation effects between large woods and small woodlots**

The set of symbols to the left of the dashed lines, for each seed species, show results for sites in large woods and those to the right results for small woodlots. Data points refer to different sites (8 in each year) and treatments. Symbols have been slightly relocated y-wise. Mean values, for large/small woods and each cover type separately are given above each set of symbols.

In all plots, except the experiment with full cover that was made in the second season, signs of rodent presence were common. Small rodent species common in this area are *Apodemus flavicollis*, *A. sylvaticus* (rare in large forests) and *Clethrionomys glareolus* (Loman, 1991a, b; pers. obs.). These all feed on seeds of various sizes (Watts, 1968; Hoffmeyer, 1976; Jensen, 1984). Potentially seed eating birds in these forests were tits (especially *Parus caeruleus* and *P. major*), jay *Garrulus glandarius*, nuthatches *Sitta europea* (mainly in the large woods) and various finches, in particular groups of bramblings *Fringilla montifringilla*. Compared to the rodents, these are unlikely to venture under a

net close to the ground to feed, except possibly under exceptional circumstances (Bodil Enoksson, pers. comm; Åke Lindström, pers. comm.). Such exceptional circumstances could be a rich artificial source of seeds in a winter period when alternative food is covered by snow. However, the present seeds were distributed in approximately natural densities and were not at all available to small birds in case of snow cover (that would block the entry to the seeds). I therefore interpret the fact that a partial net cover did not decrease seed predation as evidence that the dominating source of predation was that from small rodents.

The fact that hawthorn nuts, that were the smallest seeds in this study, were almost as much

predated under the fully covered treatment as in the other treatments in the second over winter experiment suggests however that much predation on these seeds was from insects or possibly slugs (that could enter the fully covered sets as easily as those sets partially or not at all covered).

### 3.3 Perspective

Also other studies have attempted to identify seed predators by means of experiments. This has usually involved comparing different methods of presentation, including enclosures, or comparing day and night removal. In forest and shrub habitat on large and medium seeds, small mammals emerge, like the case is in the present study, as the dominating group of predators (Santos and Telleria, 1994; Hulme, 1997; Hulme and Hunt, 1999; Hulme and Borelli, 1999; Plucinski and Hunter, 2001; Donoso et al., 2003; DeMatta et al., 2004). However, in one study (Kjellson, 1985) insects were important, as is suggested for over winter predation on hawthorn nuts in one year of this study. Other similar studies in forest and shrub habitats mention large mammals (DeMatta et al., 2004) and birds as the most important seed predators. The latter was the case in Zimbabwe shrubland (Linzey and Washok, 2000) and in forest fragments in Spain (Santos and Telleria, 1994) and Brazil (Pizo and Viera, 2004). Birds probably had at least some impact in Spain (Hulme, 1997) and England (Hulme and Borelli, 1999).

### 3.4 Landscape structure

At least in the second year of the study, there was an effect of landscape structure on total predation; short term predation was heavier in the small woods. This suggests higher rodent densities or less alternative food in these woods. Indeed, an inverse relation between woodland size and mouse *P. leucopus* density has been found by Nupp and Swihart (1996). A similar pattern exists for *A. sylvaticus* and *C. glareolus* in the present study area (pers. obs.). Donoso et al. (2003) also found higher seed predation in small habitat fragments. Furthermore, they found that this effect was strongest for large seeds. I also found an interaction between seed species and patch size for the one week predation. In contrast, this was because predation rates on the smallest seeds (hawthorn) in 1986 was almost similar in small and large woods, while for the other three, predation was highest in the small woodlots. In another seed predator study in the same area, no effect of patch size was found in any of three study years (pers. obs.).

If only open and partially covered treatments were analysed, there was no interaction between habitat type (small woodlot/large wood) and treatment. This suggests that birds were invariably rare as

seed predators in this study. Including the fully covered treatment that was used in the second winter, an interaction was found. This suggests a variation in the relative importance of rodents and invertebrates; possibly because rodents were, at least in this year relatively more important in small than in large forests.

In contrast, Santos and Telleria (1994) found mice to be the dominating *Juniperus* post seed fall seed predators in large forest fragments (150 – 270 ha) but in contrast, thrushes dominated as seed predators in smaller (0.2 – 16 ha) fragments. Similarly, birds were more important than rodent in small forest fragments in Brazil while the opposite was considered the norm in large, unfragmented forests (Pizo and Viera, 2004).

Summarizing, patch size effects are potentially affecting seed predation rates but there is much variation among sites, seed species and years. This is probably related to what predator species are actually present, something that is subject to much spatial and temporal variation.

**Acknowledgements** I appreciate Kerstin Persson for her help in the field.

### References

- Andresen E, 2002. Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* 34: 261 – 272.
- Bijlsman RG, 1998. Breeding biology and population trend of Hawfinches *Coccothraustes coccothraustes* in Flevoland. *Limosa* 71: 137 – 148.
- Bosch F, 1997. The utilization of habitat by roe deer (*Capreolus capreolus* Linne, 1758) and fallow deer (*Cervus dama* Linne, 1758) in the recreation area Kottenforst near Bonn. *Z. Jagdwissenschaft* 43: 15 – 23.
- Bossemma I, 1969. Jays and oaks: and eco-ethological study of a symbiosis. *Behaviour* 70: 1 – 117.
- Clarke PJ, Kerrigan RA, 2002. The effects of seed predators on the recruitment of mangroves. *J. Ecol.* 90: 728 – 736.
- Courtney SP, Manzur MI, 1985. Fruiting and fitness in *Crataegus monogyna*: the effects of frugivores and seed predators. *Oikos* 44: 398 – 406.
- DeMatta EA, Curran LM, Rathcke BJ, 2004. Effects of small rodents and large mammals on neotropical seeds. *Ecology* 85: 2 161 – 2 170.
- DeSousa N, Griffiths JT, Swanton CJ, 2003. Predispersal seed predation of redroot pigweed *Amaranthus retroflexus*. *Weed Sci.* 51: 60 – 68.
- Diaz M, Gonzales E, Munoz PR, Naveso MA, 1993. Effects of food abundance and habitat structure on seed-eating rodents in Spain wintering in man-made habitats. *Z. Säugetierk.* 58: 302 – 311.
- Donoso DS, Grez AA, Simonetti JA, 2003. Effects of forest fragmentation on the granivory of different sized seeds. *Biol. Conserv.* 115: 63 – 70.
- Enoksson B, 1988. Age- and sex-related differences in dominance and foraging behaviour of nuthatches *Sitta europaea*. *Anim. Behav.* 36: 231 – 238.
- Enoksson B, 1990. Autumn territories and population regulation in the nuthatch *Sitta europaea*: an experimental study. *J. Anim. Ecol.* 59: 1 047 – 1 062.
- Focardi S, Capizzi D, Monetti D, 2000. Competition for acorns among wild boar *Sus scrofa* and small mammals in a Mediterranean wood-

- land. *J. Zool.* 250: 329–334.
- Fuentes M, 2000. Frugivory, seed dispersal and plant community ecology. *Trends Ecol. Evol.* 15: 487–488.
- Gardner G, 1977. The reproductive capacity of *Fraxinus excelsior* on the Derbyshire limestone. *J. Ecol.* 65: 107–118.
- Guitian J, Fuentes M, 1992. Reproductive biology of *Crataegus monogyna* in northwestern Spain. *Acta Oecol.* 13: 3–11.
- Gurnell J, 1993. Tree seed production and food conditions for rodents in an oak wood in southern England. *Forestry* 66: 291–315.
- Hay ME, Fuller PJ, 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology* 62: 1395–1399.
- Herrera CM, 1995. Plant-vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary and historical determinants. *Ann. Rev. Ecol. Syst.* 26: 705–727.
- Hoffmeyer I, 1976. Experiments on the selection of food and foraging site by the mice *Apodemus sylvaticus* (Linné, 1758) and *A. flavicollis* (Melchior, 1834). *Säugetierk. Mitt.* 24: 12–124.
- Hulme PE, 1997. Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia* 111: 91–98.
- Hulme PE, Borelli T, 1999. Variability in post-dispersal predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* 145: 149–156.
- Hulme PE, Hunt MK, 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *J. Anim. Ecol.* 68: 417–428.
- Hulme PE, Kollmann J, 2005. Seed predator guilds, spatial variation in post-dispersal seed predation and potential effects on plant demography: a temperate perspective. In: Forget PM, JE Lambert, PE Hulme, Vander Wall SB ed. *Seed fate. Predation, Dispersal and Seedling Establishment*. Wallingford, UK: CABI Publishing, 9–30.
- Ida H, Hotta M, Ezaki Y, 2004. Predispersal predation by rodents to beechnuts (*Fagus crenata* Blume). *Ecol. Res.* 19: 503–509.
- Iida S, 1996. Quantitative analysis of acorn transportation by rodents using magnetic locator. *Vegetatio* 124: 39–43.
- Janzen DH, 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2: 465–492.
- Jensen TS, 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. *Oecologia* 54: 184–192.
- Jensen TS, 1984. Seed-seed predator interactions of European beech *Fagus sylvatica* and forest rodents *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* 44: 149–156.
- Kelbel P, 1996. Damage to acorns by insects in Slovakia. *Biologia (Bratislava)* 51: 575–582.
- Kjellsson G, 1985. Seed fate in a population of *Carex pilulifera* L. II. Seed predation and its consequences for dispersal and seed bank. *Oecologia* 67: 424–429.
- Kollmann J, Coomes DA, White SM, 1998. Consistency in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Funct. Ecol.* 12: 683–690.
- Linzey AV, Washok KA, 2000. Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. *Afr. Zool.* 35: 295–299.
- Loman J, 1991a. Small mammal and raptor densities in habitat islands area effects in a south swedish agricultural landscape. *Landscape Ecol.* 5: 183–189.
- Loman J, 1991b. The small mammal fauna in an agricultural landscape in southern Sweden with special reference to the wood mouse *Apodemus sylvaticus*. *Mammalia* 55: 91–96.
- Maeto K, Ozaki K, 2003. Prolonged diapause of specialist seed-feeders makes predator satiation unstable in masting *Quercus crispula*. *Oecologia* 137: 392–398.
- Manson RH, Ostfeld RS, Canham CD, 2001. Long-term effects of rodent herbivory on tree invasion dynamics along forest-field edges. *Ecology* 82: 3320–3329.
- Masaki T, Kominami Y, Nakashizuka T, 1994. Spatial and seasonal patterns of seed dissemination of *Cornus controversa* in a temperate forest. *Ecology* 75: 1903–1910.
- Masaki T, Tanaka H, Shibata M, Nakashizuka T, 1998. The seed bank dynamics of *Cornus controversa* and their role in regeneration. *Seed Science Research* 8: 53–63.
- McCormick JT, Meiners SJ, 2000. Season and distance from forest-old field edge affects seed predation by white-footed mice. *Northeastern Naturalist* 7: 7–16.
- Meyer GA, Witmer MC, 1998. Influence of seed processing by frugivorous birds on germination success of three north American shrubs. *Amer. Midl. Natur.* 140: 129–139.
- Nilsson SG, Wästljung U, 1987. Seed predation and cross-pollination in mast-seeding beech *Fagus sylvatica* patches. *Ecology* 68: 260–265.
- Nupp TE, Swihart RK, 1996. Effects of forest patch area on population attributes of white-footed mice *Peromyscus leucopus* in fragmented landscapes. *Can. J. Zool.* 74: 467–472.
- O'Dowd DJ, Hay ME, 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology* 61: 531–540.
- Ostfeld RS, Jones CG, Wollff JO, 1996. Of mice and mast. *BioScience* 46: 323–330.
- Ostfeld RS, Manson RH, Canham CD, 1997. Effects of rodent on survival of tree seeds and seedlings invading oldfields. *Ecology* 78: 1531–1542.
- Pizo MA, Vieira EM, 2004. Granivorous birds as potentially important post-dispersal seed predators in Brazilian forest fragments. *Biotropica* 36: 417–423.
- Plucinski KE, Hunter Jr ML, 2001. Spatial and temporal patterns of seed predation on three tree species in an oak-pine forest. *Ecography* 24: 309–317.
- Santos T, Telleria JL, 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper *Juniper thurifera*. *Biol. Conserv.* 70: 129–134.
- Stapanian MA, Smith CC, Finck EJ, 1994. Population variabilities of bird guilds in Kansas during fall and winter: weekly censuses versus Christmas bird counts. *Condor* 96: 58–69.
- Sun S, Gao X, Chen L, 2004. High acorn predation prevents the regeneration of *Quercus liaotungensis* in the Dongling mountain region of north China. *Restor. Ecol.* 12: 335–342.
- Ulfstrand S, 1963. Ecological aspects of irruptive bird migration in northwestern Europe. *Proc. XIII Internat. Ornith. Congr.* 780–794.
- Vander Wall SB, Kuhn KM, Gworek JR, 2004. Two-phase seed dispersal: the link between frugivorous birds and seed-caching rodents. *Ecol. Soc. Amer. Ann. Meeting Abstracts* 89: 519–520.
- Walther BA, Gosler AG, 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (*Aves: Parus*). *Oecologia* 129: 312–320.
- Watts CHS, 1968. The foods eaten by woodmice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus* in Wytham Woods, Berkshire. *J. Anim. Ecol.* 37: 24–41.
- Wästljung U, 1989. Effects of crop size and stand size on seed removal by vertebrates in hazel *Corylus avellana*. *Oikos* 54: 178–184.