

## Abundance of owls and Bramblings *Fringilla montifringilla* in relation to mast seeding in south-eastern Sweden

STEFAN LITHNER & K. INGEMAR JÖNSSON

---

### Abstract

We investigated the relationship between mast seeding in beech *Fagus sylvaticus* and oak *Quercus spp.*, and the occurrence of the rodent-dependent predators Tengmalm's Owl *Aegolius funereus*, Long-eared Owl *Asio otus* and Tawny Owl *Strix aluco* in south-eastern Sweden (Blekinge) 1992–2000. We also compared available data on seed production with data on winter flocks of Brambling *Fringilla montifringilla*, mainly depending on beech seeds as winter food. Years of good beech mast production were followed by years of high frequency of Tengmalm's Owl and Long-eared Owl, indicating a rapid numerical response to improved food conditions. The Tawny Owl did not respond in the same way, but tended to reach high densities two years after mast seeding. These results suggest that mast seed production may influence the populations of rodent-

feeding predators, and that the numerical response may be very rapid in potentially nomadic specialist predators. This was indicated particularly for the Tengmalm's Owls arriving in Blekinge rather late in spring of 1999. Winters following good beech mast production normally held large numbers of Bramblings. However Bramblings were absent in Blekinge during the winter of 1992/93 despite the very good year for beechnut production in 1992. Thus, low number of Bramblings was no reliable indication for low numbers of owls the following spring.

*Stefan Lithner, Vinkelgatan 26B, 374 38 Karlshamn. E-mail: s.lithner@delta.telenordia.se*  
*K. Ingemar Jönsson, Department of Theoretical Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden.*

---

Received 15 June 2001, Accepted 22 March 2002, Editor: T. Pärt

### Introduction

Population densities and breeding parameters in owls feeding on rodents are well known to vary depending on their prey densities (Hörnfeldt 1978, Korpimäki 1984, Korpimäki & Nordahl 1989). In northern Fennoscandia (north of 61°), rodent populations commonly show cyclicity, with peaks every 3–5 years, resulting in corresponding cyclicity in predator populations (Hansson & Henttonen 1985). In a transition zone from latitude 61°, cyclicity gradually diminishes towards the south. South of latitude 59° rodent populations are known to be non-cyclic (Hansson 1984, 1999). The causal factors behind these patterns remain controversial (e.g. Stenseth & Ims 1993, Korpimäki & Krebs 1996).

In southern and south-western Europe populations of small mammals are more stable than in northern Europe (Hansson & Henttonen 1985). However, outbreaks among small rodents occur and are known

to follow high seed productions of European beech and oak (Jensen 1982, Hörnfeldt et al. 1986, Hansson et al. 2000). Forests dominated by oak in central Europe show clear peaks in rodent populations every 6–9 years following massive seed production (e.g. Hansson et al. 2000). Jensen (1982) showed that outbreaks among forest rodents in eastern Jutland, Denmark, occurred only after mast seeding in beech. Following large mast seeding in late summer and autumn, forest rodents breed more or less continuously until late summer the following year, in contrast to the normal breeding season from April through September (e.g. Jensen 1982). These forest rodent populations reached very high densities in the next autumn, followed by a pronounced decline in the following winter (e.g. Hansson et al. 2000). Two factors that probably play important roles for this decline are predators and shortage of food (e.g. Hansson et al. 2000). According to Erlinge et al.

(1983) predators have a high capacity to reduce the densities in non-cyclic populations of small rodents in southern Sweden. Interestingly, in southern Scandinavia, fluctuations in small mammal population densities co-vary only during mast seeding (Hansson & Henttonen 1985), indicating a strong general effect on small mammal populations by mast seeding.

Availability of seeds seem to be extremely difficult to forecast from one year to another and may vary from 5000 kg per hectare to no seeds at all (see review in Jedrzejewski & Jedrzejewska 1996). If by chance oak and beech get heavy mast seeding two years in a row the increase in numbers of forest rodents continues (Hansson et al. 2000). Years with abundant beech seed crops occur at two to ten year intervals (Matthews 1955, Drozd 1966, Zemanek 1972, Jensen 1982, Nilsson 1985), but they rarely coincide with those of oak (Bergstedt 1965, Nilsson 1985).

By affecting the populations of small mammals, mast seeding should also have an indirect effect on the population dynamics of rodent feeding owls, but few data on this are available. In years of mast seeding, seed eating birds such as the Brambling may occur in large numbers during winters in southern Sweden. Since seed eating birds may compete with forest living rodents for seeds, presence of large numbers of such birds may reduce the effect that mast seeding has upon rodent populations and their predators.

In this paper, we analyse the relationships between three species of owls, wintering Bramblings *Fringilla montifringilla*, and mast seeding, in southern Sweden. The owls studied were Tengmalm's Owl *Aegolius funerus*, Long-eared Owl *Asio otus* and Tawny Owl *Strix aluco*, all more or less dependent on availability of small rodents. Tengmalm's Owl and Long-eared Owl are regarded as nomadic or migratory vole specialist predators, while Tawny owl is considered a resident generalist predator (Korpimäki 1992).

## Methods

### Study area

Among five topographical zones in Blekinge distinguished by Björnsson (1946) our study includes observations in the Forest Zone, the Median Zone, and to some extent also the Coastal Zone. Our main study area in the Forest Zone (~65% forest) is situated in the north-central part of the province Blekinge, south-eastern Sweden (56° 20' N, 14° 50' E). The forest was dominated by 49% spruce (*Picea*) and

21% pine (*Pinus*), but with interspersions of about four per cent of beech and oak distributed in patches (W. Olsson, Board of Forestry, Blekinge, pers. comm.). Close to 60% of the trees in the forested area in the district were over 50 years old and 13 % were over 90 years old (Skogsvårdsstyrelsen 1995).

The Median Zone has a more even distribution of arable fields, deciduous forest and coniferous forest (about 30% each). The Coastal Zone has a relatively open landscape, but varies considerably. The Bräkne-Hoby transect, situated about five km from the coast, consists of 17% arable fields, 51% coniferous forests and 18% deciduous forest (8% beech forest, 5% oak and 5% other deciduous forest) (data from local property assessments).

### Data on owl occurrence

Data on owl occurrence were collected from five point transects ("Main Transects"), situated along small roads in the Forest Zone in the years 1993–1997. In one of these transects, monitoring was continued during 1998–2000. Each transect included 13–24 points at 2 km intervals, and all transects a total of 94 census points. Transect recordings were carried out twice each year about one month apart during late winter and early spring (13 February–1 May) with the majority (83%) in the period between 8 and 31 March. At each point, all owls heard during exactly 3 minutes were noted (see Holmberg 1979). Advertising calls as well as pair-formation calls and different types of contact calls were registered.

Transect censuses were carried out under good weather conditions (light winds, no precipitation) between 22.00 and 03.00 hrs. Each point was considered to be an independent unit. Thus at a particular point all owls were counted regardless of whether some individual owls may have been recorded previously. Due to differences in transect length an index of owl density was calculated by dividing the total number of recorded owls along a transect by the number of points in the transect.

In addition to the Main Transects, we obtained data on owl occurrence from two other areas. During 1998–2000 owls were counted along a 27 km long transect (18 points, inter-point distance ~1.5 km, monitored 2–5 times annually in central Blekinge, east and south of the village Bräkne-Hoby ("Bräkne-Hoby Transect") in the Coastal Zone.

Also, from 1994 through 2000, Long-eared Owls were censused in the beginning of June using the same method as described above along a 9.5 km long transect, with stops every 0.5 km, in the Median

Zone north of Karlshamn ("Median Transect"; J. Wolgast, pers. comm.) Since breeding of Long-eared Owl seems to increase from north to south in Blekinge (Blekinge Ornitologiska Förening 1993, Monthly reports from The Ornithological Society of Western Blekinge (VBOF) 1991–2000) we also used information on reported breedings of Long-eared Owls in our study area presented in the monthly reports by VBOF. These data were based on voluntary reports by local ornithologists. Comparisons in variation between years in the number of reported breeding Long-eared Owls should therefore be made with some caution.

#### *Production of beech mast and acorns*

Quantitative data on beech mast production during 1992–1999 were collected from seven sites in the Ryssberget area in the north-easternmost part of the province of Scania adjacent to Blekinge, between five and 90 km from our transects, by P.-M. Ekö, Swedish University of Agricultural Sciences in Alnarp, pers. comm.). No quantitative data were found for acorns, but some subjective data were obtained from Denmark and Blekinge.

#### *Brambling occurrence and rodent species*

Information about occurrence of larger numbers of Bramblings in Blekinge during the winters (November–March) 1991/92–1999/2000 were obtained from the annual reports of the Blekinge Ornithological Society (BOF), monthly reports from VBOF, and from own field observations (S. Lithner). We did not count rodents, but the forest rodents present in our study area were *Clethrionomus glareolus*, *Microtus agrestis*, *Apodemus sylvaticus* and *Apodemus flavicollis*.

## Results

#### *Owl abundance*

In the Main transects, the number of Tengmalm's Owls varied considerably among years and transects, but the yearly patterns were fairly consistent among different transects, although no pairs of transects were significantly correlated among years ( $P > 0.10$  in all years, two-tailed test). Altogether, the best years for Tengmalm's Owl were 1993, 1996 and 1999 (Figure 1). Years with high abundance at the first inventory also showed high abundance in the

Table 1. Average number of recorded individuals per point for Tengmalm's Owl, Tawny Owl and Long-eared Owl on the Main Transect (Main) and the Bräkne-Hoby Transect (B–H) during the years 1993–2000.

*Medeltal registrerade individer per punkt av pärluggla, kattuggla, och hornuggla för huvudområdet (Main) och för Bräkne-Hobyområdet (B–H) under åren 1993–2000. Early = tidig. Late = sen.*

Year År	Census Inventering	No. points Ant. punkter		Tengmalm's Owl Pärluggla		Tawny Owl Kattuggla		Long-eared Owl Hornuggla	
		Main	B–H	Main	B–H	Main	B–H	Main	B–H
1993	Early	94	–	0.54	–	0.20	–	0	–
1993	Late	79	–	0.51	–	0.14	–	0.025	–
1994	Early	94	–	0.096	–	0.32	–	0.021	–
1994	Late	70	–	0.11	–	0.29	–	0.014	–
1995	Early	94	–	0.011	–	0.26	–	0	–
1995	Late	66	–	0	–	0.045	–	0	–
1996	Early	94	–	0.28	–	0.18	–	0.032	–
1996	Late	94	–	0.30	–	0.085	–	0	–
1997	Early	94	–	0.085	–	0.053	–	0	–
1997	Late	94	–	0.043	–	0.096	–	0	–
1998	Early	66	18	0.091	0	0.015	0.22	0	0
1998	Late	22	18	0	0	0.23	0.056	0	0
1999	Early	22	18	0.18	0.056	0.46	1.22	0.32	0.61
1999	Late	22	18	0.73	0.56	0.46	0.56	0.18	0.22
2000	Early	22	18	0.045	0	0.59	0	0	0
2000	Late	22	18	0	0.056	0.14	0.17	0	0

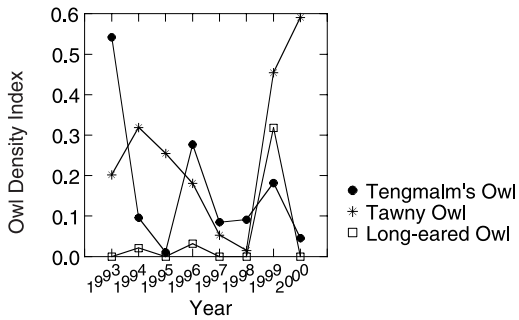


Figure 1. Density indices (mean recorded individuals/point) for Tengmalm's Owl, Tawny Owl and Long-eared Owl in different transects of the "Main" study area at early inventories 1993–2000.

*Täthetsindex (medelantal/antal punkter) för pärluggla, kattuggla och hornuggla i olika transekter i huvudområdet under den tidiga inventeringsomgången 1993–2000.*

second inventory (all transects pooled;  $r_s=0.85$ ,  $P<0.02$ , two-tailed test,  $n=8$ , Table 1). In 1999, much more owls were observed in the second inventory than in the first (Table 1).

In the Bräkne-Hoby transect, no Tengmalm's Owls were heard in 1998, whereas in 1999 seven birds were registered. Six of those apparently arrived in the area in late spring. During inventories in April up

to 15 April, no Tengmalm's Owls were found in the area, whereas six birds were present on 1–2 May. In 2000 one Tengmalm's Owl was heard on the Bräkne-Hoby transect.

The Tawny Owl data showed a less consistent pattern among transects as compared to Tengmalm's Owl ( $P>0.10$  for all pairwise correlations, two-tailed tests). Year 1994 was a good year, while the high records from 1999 and 2000 are more uncertain since they are based on only one transect (Figure 1). Unlike for the Tengmalm's Owl data, there was no year in which densities were low in all transects. Furthermore, there was no correlation between the early and late inventory (all transects pooled;  $r_s=0.26$ ,  $P>0.50$ , two-tailed test,  $n=8$ )

Long-Eared Owls were recorded only in 1993, 1994, 1996 and 1999 in the Main Transects (Table 1, Figure 1), with the highest number recorded in 1999. Registrations from early and late inventories were not correlated (all transects pooled;  $r_s=0.50$ ,  $P>0.20$ , two-tailed test,  $n=8$ ).

Recordings were too few to allow comparisons among transects in yearly recordings. Although only one Long-eared Owl was observed in our Main Transect, the monthly VBOF reports indicate that 1993 was actually a good year for Long-eared Owl, with 27 families located. Also 1996 and 1999 stand out as good years for breeding Long-eared Owls in western Blekinge (Table 2). These breedings,

Table 2. Number of Long-eared Owls registered in the Median Transect (MT), registered breeders of Long-eared Owl in western Blekinge (Br.), and production estimates of beech and oak mast in the Ryssberget area (Scania) and in Denmark. The acorn data are subjective estimates.

*Antal hornugglor registrerade i "Inre Dallandskapet" (MT), rapporterade häckningar av hornuggla i Västblekinge (Br.) samt uppgifter om bok- och ekollonproduktion på Ryssberget och i Danmark. Uppgifterna om ekollon är subjektiva uppskattningar.*

Year	MT	Br.	Beech Bok Ryssberget (no./m <sup>2</sup> )	Beech Bok Denmark (Kg/ha)	Acorns Ekollon Denmark	Acorns Ekollon W Blekinge
År						
1991	–	4	–	–	–	–
1992	–	1	679	1000	Good year	No notes
1993	–	27	163	–	–	–
1994	0	3	0	–	–	–
1995	0	3	766	1000	Good year	> Average
1996	3	9	0	–	–	–
1997	0	0	0	–	–	Very good
1998	0	0	154	1000	Good year in S Dk	–
1999	3	41	0	–	–	–
2000	0	0	–	3–500, 800 in Sjælland	Good year	Very good

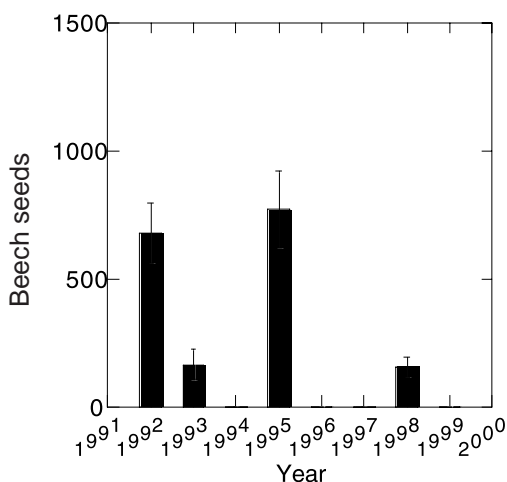


Figure 2. Beech seed production ( $\pm$ SE) in the Ryssberget area, north eastern Scania, in 1992–1999 based on estimates from seven different sites. Data from the Swedish University of Agricultural Sciences in Alnarp.

*Bokollonproduktion (medelvärde $\pm$ SE) i området Ryssberget i nordöstra Skåne (uppskattingar från 7 lokaler). Data från Sveriges Lantbruksuniversitet, Alnarp.*

however, were mainly located south of our Main Transects. In the Median Zone Transect, Long-eared Owls were observed in 1996 and 1999 (Table 2). Fifteen Long-eared Owls were registered in the Bräkne-Hoby Transect in 1999.

Pooling the various sources of information on owls in western Blekinge, our study suggests that 1993, 1996 and 1999 were the peak years of Tengmalm's Owl and Long-eared Owl, while Tawny Owl showed peaks in 1994 and 1999. However, we obtained no significant correlations in the yearly pattern among the three owl species ( $P > 0.20$  in all three comparisons, two-tailed tests).

#### *Production of beech mast and acorns*

The beechnut production was registered at twelve different sites in the provinces of Scania and Halland in southern and south-western Sweden. These collections show that production of beechnuts varied considerably among sites also in years generally regarded as good years for beechnut production (Gemell & Övergaard 1995). Hence figures from 1995 vary between 2.36 and 17.09 million seeds per hectare (R. Övergaard, pers. comm.). Data from the seven sites on Ryssberget in north-eastern Scania during 1992–1999 show that 1992 and 1995 were years with “very good” beech mast production (1992:

mean=679 /m<sup>2</sup>;1995: mean=766 /m<sup>2</sup>), while 1993 and 1998 were “good” years (1993: mean=163 /m<sup>2</sup>, 1998: mean=154 /m<sup>2</sup>). In the other years no seed production was observed (Figure 2).

In Denmark, the years 1992 and 1995 stand out as good years for beechnut production, and 1992, 1995 and 2000 were good years for acorn production all over Denmark, while 1998 was a good year only on the islands of Lolland and Falster (Henrik Knudsen, State Forest Research Centre for Reproduction of Plants, pers. comm). Information on acorn production in the eastern part of Blekinge was obtained from Flakulla Provinience (Cecilia Rooth, pers. comm.). Since the mid-1990s, 1997 and 2000 stand out as very good years, while 1995 was “better than normal.” Also, “a good year in the early 1990s” was reported, which may correspond to 1992.

The information from Denmark and Blekinge shows some correspondence, pointing out 1992 (possibly), 1995 and 2000 as good or very good years for acorn production. Interestingly, 1992 and 1995 were good years for both beechnuts and acorns in Denmark, and possibly also in southern Sweden.

#### *Brambling abundance*

Bramblings occurred in large numbers during the winters of 1993/94 (29,670), 1995/96 (4.4 millions) and 1998/99 (15,150) in Blekinge. These figures correspond well with the high beechnut production in 1993, 1995 and 1998. In the remaining winters, from 1991/92 through 1999/2000, no flock as large as 100 Bramblings were observed in Blekinge, not even during the winter of 1992/93 despite the very good year for beechnut production in 1992. In January and February 1993, a very large flock containing roughly two million birds was observed in the north-western part of the province of Scania (Kjellén & Lindström 1993, Lithner 1995).

#### *Relationships between beech mast production and owls*

We found a significant correlation between high numbers of beech mast and recordings of Tengmalm's Owls in the following spring ( $r_s = 0.89$ ,  $P < 0.005$ , one-tailed test,  $n = 8$ ). In the Long-eared and Tawny Owl, no such correlation was found in our Main Transect area ( $r_s = 0.26$ ,  $P > 0.50$ , one-tailed test,  $n = 8$ ). However, high numbers of beech mast was positively correlated to observations of breeding Long-eared Owls in the following spring ( $r_s = 0.69$ ,  $P < 0.025$ , one-tailed test,  $n = 8$ ).

In 1992 and 1995 the beech mast production was very high and rather similar. In 1993 the number of Tengmalm's Owl per point was 93% higher than in 1996 (first inventory) and the number of reported breedings of Long-eared Owls was three times higher in 1993 than in 1996. The lower abundance of owls in 1996, hence, coincides with the high numbers of Bramblings observed during the winter 1995/96.

## Discussion

### *Numeric response in owls following mast seeding*

We found a good correspondence between a high production of beechnuts in one year and the abundance of Tengmalm's and Long-eared Owls in the following year, suggesting a positive numerical response by small forest rodents to beechnut production, and a corresponding numerical response in the owl populations. The Tawny Owl did not follow the same pattern of fluctuation because the clearest peak occurred 1994, one year after the peak in Tengmalm's Owls. This difference among owl species is consistent with the view that the response of resident predators lags behind increases in prey densities, while nomadic predators respond without time lag (Korpimäki & Krebs 1996). The increase in Tawny Owls in the years following good years for Tengmalm's and Long-eared Owls may represent juveniles recruited to free territories while rodent availability in the autumn was still relatively good. For example, a report by Philipsson (2001) suggests a high production of Tawny Owl fledglings in years following summers of high beech mast production.

The origin of the individuals causing the rapid increase of the Tengmalm's Owl population in peak years is difficult to evaluate at present. Both Tengmalm's Owl and Long-eared Owl are known to be partially nomadic or migrating vole specialists in northern Fennoscandia (Korpimäki 1992), rapidly tracking local or regional abundance of prey populations. In central Europe, however, populations of these predators tend to be more resident. In Tengmalm's Owl, Korpimäki & Hongell (1986) identified a transition from resident generalist predator populations in central Europe to nomadic microtine specialist predator populations in northern Sweden and Norway. Western Finland was identified as a transition area, where males are resident while females and juveniles are nomadic. In northern Sweden, populations of Tengmalm's Owl respond strongly already in the beginning of a summer increase in vole populations (Hörnfeldt et al. 1990),

and leave the area already at the beginning of a decrease in vole abundance (Löfgren et al. 1986). Our study area is situated between the nomadic or partially nomadic northern populations and the more stable central European populations, and the existence of nomadism in our population of Tengmalm's Owls has not been established earlier. In addition to the large annual variation recorded in Tengmalm's Owls, immigration by nomadic individuals was suggested by the appearance of high owl numbers during late April 1999 in both the Main Transect and the Bräkne-Hoby Transect. Hence, it is clear that the dramatic changes in the Tengmalm's and Long-eared Owls populations cannot be explained by local recruitment of juveniles. Thus, either the owls recorded in peak years were present but silent also in the years when few birds were heard (see Lundberg 1979), or nomadic birds had moved in. Alternatively, some of the birds were present but mainly silent during poor years while the majority of the owls moved into the area during peak years as suggested by Korpimäki & Hongell (1986). Our findings in Tengmalm's Owls seem to support the latter hypothesis. Further efforts to verify the numbers of resident non-breeders, and the existence of long-distance recruitment (i.e. by recovery of ringed birds), are required to shed some light on this question.

During the first two years following the years of very good production of beechnuts (1993 and 1996) very few Long-eared Owls were found in the Main Transects, running mainly through the Forest Zone. However, the number of calling Long-eared Owls was relatively high in the Median Zone in these years. Also, the number of families found in the Coastal Zone following years with very good beech mast production were ten to twenty times higher than average during years not preceded by any beech mast production. In 1999 the number of Long-eared Owls was high also in the Main Transect. Possibly, the fact that several areas were clear-cut along this transect could have contributed to this effect. Clear-cutting favours *M. agrestis*, which at least in southernmost Sweden (Scania) is the most important prey for Long-eared Owl (Nilsson 1981).

### *Numeric responses of small mammals to mast seeding*

Jensen (1982) showed a strong positive correlation between mass production of beechnuts and rodent density the following year in forests dominated by beech. It is also known (e.g. Pucek et al 1993, Hansson et al. 2000) that heavy mast seeding in oak

causes outbreaks among forest rodents followed by peaks in population densities during the autumn the following year.

Coinciding years of high beechnut and acorn production are known to be rare (Bergstedt 1965, Nilsson 1985), but this seems to have occurred in southern Sweden in both 1992 and 1995. In terms of recorded owls, however, 1993 was a considerably better year than 1996, particularly for the Tengmalm's Owl. This suggests that other factors than seed production may have been involved in determining the abundance of owls.

Although 1997 is not mentioned as a good year for acorns in the Danish report, the production was very good in eastern Blekinge, while the production of beechnuts seems to have failed. 1998 was a moderate year for the Tengmalm's and Tawny Owls, and a poor year for the Long-eared Owl. Therefore, the high production of acorns in eastern Blekinge seems not to have affected the presence of owls in 1998. Perhaps the number of oak trees is too small to produce enough acorns to play an important role compared to beechnuts in the areas monitored, or the large production of acorns in eastern Blekinge was a local event without effects on the central and western parts of the province.

#### *Competition for seeds from Bramblings*

Does the presence of large numbers of Bramblings influence the numeric response of small mammals to mast seeding in beech and oak? Kjellén & Lindström (1993) calculated the need of energy for Bramblings based on an estimated basal metabolism of 40 kJ per bird and day (Aschoff & Pol 1970), and a field metabolism in winter (Dolnik 1982) to be at least 120 kJ per bird and day. Nilsson (1979) calculated the need of energy by a different method and arrived at a slightly higher need of energy (171.7 kJ). Furthermore, Bramblings are able to obtain at the most 83% of the energy in a seed (Dolnik 1982).

Weights of Beechnuts in Scania and Blekinge vary considerably between rich non-acid soils and meagre acid soils, and also a great deal from one year to another on the same soil (0.142–0.213 g). In western Blekinge the average weight of a beechnut in 1984 was 0.163 g and that of a single seed 0.0864 g (I. Stjernquist, Department of Plant Ecology, Lund University, pers. comm). According to Grodzinsky & Sawicka-Kapusta (1970) one seed contains 2.53 kJ. Thus, to cover its energy need during one day in western Blekinge a Brambling should consume between 58 (according to Kjellén & Lindström 1993)

and 82 (using Nilsson's (1979) figure) seeds.

Hence two million Bramblings can potentially consume between 17.4 and 24.8 tons/day, i.e. between 1550 and 2250 tons of beechnuts in three winter months. Consequently, large amounts of wintering Bramblings should have a substantial effect on the numerical response of small mammals depending on beech mast production, and thus on numerical response of rodent-dependent owls. High numbers of Brambling seem to follow most years of good beechnut production, but not every winter following summers with high production of beech mast. The higher abundance of Tengmalm's Owl in 1993 compared to 1996, despite similar levels of beech mast in 1992 and 1995 is consistent with the hypothesis that Bramblings (absent in 1992/93 while abundant in 1995/96) modified the potential food source of small mammals.

Calculations of energy transformation show that the Brambling's strategy during winter, to roost in large dense flocks, is superior to those of other passerines (Jenni, & Jenni-Eierman 1987). Also during summer Brambling densities can be very high even at breeding sites when food is abundant (Mikkonen 1985). Thus the Bramblings seem to prefer wintering in flocks as large as the food supply permits. This may explain why a flock of about two million Bramblings were wintering in north-western Scania, while practically no Bramblings were found in Blekinge during the winter of 1992/93 despite the very good year for beech mast in 1992.

#### **Acknowledgements**

We are grateful to Mats Olsson for participating in the planning and censusing of owl transects, and to Jörgen Westergren for help in censusing. Thanks also to Johan Wolgast for providing data on Long-eared Owls, to Per-Magnus Ekö and Rolf Övergaard, Swedish University of Agricultural Sciences in Alnarp for kindly allowing us to use their data on beechnut production, to Willy Olsson, Forestry Department in Western Blekinge (Skogsvårdsstyrelsen i västra Blekinge) for providing information on distribution of beech- and oak forests, to Johan Wolgast and Fredrik Lennartsson for assistance with data from older bird reports in Blekinge and to Ingrid Stjernquist, Department of Plant Ecology, University of Lund, for providing data on beechnuts weights from our study area. We are also indebted to Lennart Hansson, Swedish University of Agricultural Sciences in Uppsala, and Birger Hörnfeldt and Bengt-Göran Carlsson, University of Umeå, for help with

illuminating literature. Finally we thank Erik and Ebba Larssons/Thure Rignell's Foundation for financial support (to KIJ), and the County Council of Blekinge and Knut Hahn School Nature Resource Use Program in Bräkne-Hoby for financial support (to SL).

## References

- Aschoff, J. & Pohl, H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 113: 38–47.
- Bergstedt B. 1965. Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior), and *Apodemus sylvaticus* (Linné) in southern Sweden. *Oikos* 16: 132–160.
- Björnsson, S. 1946. *Blekinge: en studie av det blekingska kulturlandskapet*. Gleerups, Lund.
- Blekinges Ornitologiska Förening. 1993. *Blekinges Fåglar. Fåglar i Blekinge* Suppl. 1, Lund.
- Dolnik, V. R. 1982. Population of Ecology of the Chaffinch. *Proc. Zool. Inst.* Vol 90, Nauka, Leningrad.
- Drozd, A. 1966. Food habits and food supply of rodents in the beech forest. *Acta theriol.* 11: 363–384.
- Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., v Schantz, T. & Sylvé, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* 40: 36–52.
- Gemmel, P. & Övergaard, R. 1995. Kalkning vid naturlig förnyring av bok. Arbetsrapport nr 9, SLU, Alnarp.
- Grodzinsky, W. & Sawicka-Kapusta, K. 1970. Energy value of tree-seeds eaten by small mammals. *Oikos* 21: 52–58.
- Hansson L. 1984. Composition of cyclic and non-cyclic vole populations: on the cause of variation in individual quality among *Clethrionomys glareolus* in southern Sweden. *Oecologia* 63: 199–206.
- Hansson, L. & Henttonen, H. 1985. Gradients in density in variation: the importance of latitude and snow cover. *Oecologia* 67: 394–402.
- Hansson L. 1999. Intraspecific variation in dynamics: small rodents between food and predation in changing landscapes. *Oikos* 85:159–169.
- Hansson, L., Jedrzejewska, B. & Jedrzejewski, W. 2000. Regional differences in dynamics of Bank Vole populations in Europe. *Polish J. Ecol.* 48 (Suppl.): 163–177.
- Holmberg, T. 1979. Punkttaxering av Päruggla *Aegolius funereus* – en metodstudie. *Vår Fågelvärld* 38: 237–244 (in Swedish, with English summary).
- Hörmfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls and Thularemia in northern Sweden. *Oecologica* 32: 141–152.
- Hörmfeldt, B., Carlsson B.-G. & Löfgren, O. 1986. Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. *Oecologica* 68: 496–502.
- Hörmfeldt B., Carlsson, B.-G., Löfgren, O. & Eklund, U. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). *Can. J. Zool.* 68: 522–530.
- Jedrzejewski, W. & Jedrzejewska, B. 1996. Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta theriol.* 41: 1–34.
- Jenni, L. & Jenni-Eiermann, S. 1987. Body weight and energy reserves of Brambling in winter. *Ardea* 75 (2): 271–284.
- Jensen, T. S. 1982. Seed Production and Outbreaks of Non-Cyclic Rodent-Populations in Deciduous Forests. *Oecologia* 54: 184–192.
- Kjellén, N. & Lindström, Å. 1993. Bergfinkens övervintringsstrategier samt några iakttagelser från en skånsk sovpplats i januari–februari 1993. *Anser* 32: 187–199.
- Korpimäki, E. 1984. Population dynamics of birds of prey in relation to fluctuations in small mammal populations in western Finland. *Ann. Zool. Fenn.* 21: 287–293.
- Korpimäki, E. 1992. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. Pp. 1–10, in: Galbraith, C. A., Taylor, I. R., and Percival, S. (eds.), *The ecology and conservation of European owls*. Joint Nature Conservation Committee, Peterborough.
- Korpimäki E. & Hongell, H. 1986. Partial migration as an adaption to nest site scarcity and vole cycles in Tengmalm's Owl (*Aegolius funereus*). *Vår fågelvärld Suppl.* 11: 85–92.
- Korpimäki, E. & Krebs, C. J. 1996. Predation and population cycles of small mammals. *Bioscience* 46: 754–764.
- Korpimäki, E. & Norrdahl, K. 1989. Predation of Tengmalm's Owls: numerical responses functional responses and dampening impact on population fluctuations of microtines. *Oikos* 54: 154–164.
- Lithner S. 1995. Två miljoner bergfink. *Fåglar i Nordvästskåne*: 6–7.
- Lundberg, A. 1979. Residency, migration and a compromise: adaption to nest-site scarcity and food specialization in three fennoscandian owl species. *Oecologia* 41: 273–281.
- Löfgren, O., Hörmfeldt, B. & Carlsson, B.-G. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus*) in relation to cyclic food production. *Oecologia* 69: 321–326.
- Matthews, J. D. 1955. The influence of weather on the frequency of beech mast years in England. *Forestry* 28: 107–116.
- Mikkonen A. V. 1985. Establishment of breeding territory by the chaffinch, *Fringilla coelebs*, and brambling, *F. montifringilla*, in northern Finland. *Ann. Zool. Fenn.* 22: 137–156.
- Nilsson, I. N. 1981. Seasonal changes in food of the Long-eared owl in southern Sweden. *Ornis Scand.* 12: 216–223.
- Nilsson, S. G. 1979. Seed density, cover predation and the distribution of birds in a beech wood in southern Sweden. *Ibis* 121: 177–185.
- Nilsson, S. G. 1985. Ecological and evolutionary interactions between reproduction of beech *Fagus silvatica* and seed eating animals. *Oikos* 44: 157–164.
- Philipsson C. 2001 Kattugglor, skogsmöss, bokar, väder och växthuseffekt. *Blekinges Natur 2001*: 13–32.
- Pucek, Z., Jedrzejewski, W., Jedrzejewska, B. & Pucek, M. 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather seed crop and predation. *Acta theriol.* 38:199–232.
- Skogsvårdsstyrelsen 1995. *Blekingeskog 2000*. Karlskrona 1995.
- Stenseth, N. C. & Ims, R. A. 1993. Population dynamics of



lemmings: temporal and spatial variation – an introduction. Pages 61–96 in Stenseth, N. C. & Ims, R. A. (eds.), *The biology of lemmings*. The Linnean Society of London, London, UK.

Zemanek, M. 1972. Food and feeding habits of rodents in a deciduous forest. *Acta theriol.* 17: 315–325.

## Sammanfattning

### *Förekomsten av ugglor och bergfink i förhållande till ollonproduktion i sydöstra Sverige*

Under åren 1992–2000 undersökte vi sambandet mellan ollonproduktion hos bok och ek och förekomsten av pärluggla, hornuggla och kattuggla i sydöstra Sverige (Blekinge), samt förekomst av bergfink under vintrarna. År med god bokollonproduktion följdes av vårar med mycket pärl- och hornugglor. Kattugglorna följde inte samma mönster. Resultaten indikerar att ollonproduktionen kan påverka antalet gnagarberoende predatorer och att svaret i antal individer kan vara mycket snabbt hos potentiellt nomadiska predatorer. Detta tycks ha varit fallet särskilt för de pärlugglor som anlände till undersökningsområdet i Blekinge sent under våren 1999. Under vintrar som följde på somrar med stor bokollonproduktion besöktes området vanligen av stora mängder bergfink. Vintern 1992/93 infann sig dock inga bergfinkar trots att sommaren 1992 var rik på ollon. Därför är avsaknad av stora bergfinkflockar under vintern ingen säker indikation på att påföljande vår blir ugglefattig.

Det är väl känt att förekomsten av ugglor och deras häckningsresultat är knuten till tätheten hos deras bytesdjur. I norra Fennoscandia (norr om 61:a breddgraden) uppträder gnagarår cykliskt med toppar vart 3–5 år och söder om 59° anses gnagaråren vara mer stabila och icke-cykliska. I mellanliggande övergångszon minskar cykliciteten från norr till söder. Skälen härtill är ännu inte fullt klarlagda. I ekdominerade skogar i Centraleuropa inträffar gnagarår vart 6–9 år och i Danmark har gnagaråren visat sig följa ollonår för bok. Efter goda ollonår fortsätter gnagarna att föröka sig under höst och vinter och orsakar massförekomst följande vår och sommar för att drastiskt minska den därpå följande vintern. Två faktorer synes vara viktiga för denna minskning; födobrist och ökade rovdjursstammar. I södra Skandinavien följer dessa upp- och nedgångar ollonåren. Produktionen hos bok och ek är synnerligen svåra att förutsäga. Ollonår för bok inträffar vart 2–10 år och sammanfaller sällan med ollonår för ek. Eftersom ollonproduktionen påverkar förekomsten av smågnagare bör den också påverka förekomsten av de

rovdjur som är beroende av dessa, inklusive flera av ugglorna, men få data är tillgängliga. Under vintrar som följer bokollonår kan stora mängder fåglar som t.ex. bergfink visa sig i områden i södra Sverige där bokollonen är talrika och lättåtkomliga. Eftersom fåglar i vilkas diet ollon ingår konkurrerar med smågnagare om fröna skulle stora mängder ollonätande fåglar mycket väl kunna reducera ollonproduktionens effekt på populationerna av smågnagare och mindre rovdjur. I denna uppsats presenterar vi data på förekomst av skogslevande ugglor, övervintande bergfink och ollonproduktion i södra Sverige.

### *Metoder*

Vårt huvudsakliga studieområde ("Huvudområdet") är beläget i norra och centrala delarna av landskapet Blekinge i sydöstra Sverige. Enligt Björnssons (1946) uppdelning i topografiska zoner har vi samlat information från Norra Blekinges Platåområde, Inre Dal-landskapet och i viss mån även det Kustnära Dal-landskapet. Data om uggleförekomst insamlades längs fem punktinventeringsrutter under åren 1993–1997. En av rutterna inventerades även 1998–2000. Varje rutt innehöll från 13 till 24 punkter belägna ca 2 km ifrån varandra, med ett totalantal av 94 punkter. Vid varje punkt registrerades alla ugglor som hördes, oavsett vilket läte, under tre minuter. Inventeringar utfördes två gånger per år med ungefär en månads mellanrum under senvinter till tidig vår (13 februari till 1 maj), med majoriteten utförda under tiden 8–31 mars. Inventeringarna utfördes i gott väder (lugnt, ingen nederbörd) mellan klockan 22 och 03. Varje punkt betraktades som en oberoende enhet. Således kan enstaka ugglor ha räknats på mer än en punkt. Ett index för tätheten av varje uggleart (antal hörda ugglor/antal punkter) räknades fram för varje inventeringsrutt. Detta medger en jämförelse av tätheten mellan rutterna. Vi har dessutom inhämtat uppgifter om ugglor från en inventeringsrutt utanför Bräkne-Hoby från åren 1998–2000 där 18 punkter utmed en sträcka av 27 km inventerats med samma metod som ovan. Under åren 1994–2000 inventerades också hornuggla i det Inre Dallandskapet norr om Karlshamn. Data insamlades av J. Wolgast i början av juni enligt ovan beskrivna metod. Eftersom antalet häckande hornugglor förefaller öka i antal från norr mot kusten använde vi också uppgifter om antalet lokaliserade hornugglefamiljer redovisade i Västblekinge Ornitologiska Förenings (VBOF) månadsrapporter. Dessa är inte systematiskt insamlade, vilket gör att jämförelser mellan

antal inrapporterade familjer per säsong bör ske med viss försiktighet. Trenderna är dock tydliga.

De mest betydelsefulla kvantitativa uppgifterna om bokens ollonproduktion härrör från taxering av mängd producerade bokollon på Ryssberget i nordöstligaste Skåne mellan fem och 90 km från våra rutter under åren 1992–1999 genom Sveriges lantbruksuniversitet i Alnarp (P-M Ekö). Uppgifter om större antal bergfinkar under vintrarna 1991/1992–1999/2000 erhöles ur rapporter från Blekinge Ornitologiska Förenings (BOF) årsrapport, VBOF's månadsrapporter och från personliga anteckningar (S. Lithner). Även om vi inte inventerade sorkar och möss så vet vi att det finns fyra små skogslevande gnagare av betydelse i detta sammanhang: skogs-sork, åkersork, större skogsmus och mindre skogsmus.

### Resultat

I Huvudområdet varierade antalet pärlugglor avsevärt både mellan år och rutter, men årstendensen var tämligen tydlig mellan olika rutter även om denna likhet mellan rutter ej var statistiskt signifikant. Totalt sett var de bästa pärluggleåren 1993, 1996 och 1999. År med många ugglor i första inventeringsomgången var också år med många ugglor i andra omgången (Tabell 1). Emellertid observerades många fler pärlugglor under andra inventeringen under 1999 (Tabell 1). I Bräkne-Hoby noterades ingen pärluggla 1998 medan sju ugglor registrerades under 1999. Sex av dessa hade infunnit sig efter den 15 april. En pärluggla hördes på denna rutt under 2000.

Kattugglan visade en mindre tydlig årsvariation än pärluggla (Figur 1, Tabell 1). År 1994 tycks ha varit gott, medan det är mer osäkert för 1999 och 2000. I motsats till pärluggla fann vi inget år då kattugglans täthet var låg på alla rutternas och det fanns ingen korrelation för första och andra inventeringsomgången.

I Huvudområdet noterades hornuggla endast åren 1993, 1994, 1996 och 1999 (Tabell 1, Figur 1), med högsta antalet 1999. Antalet hornugglor under första och andra inventeringsomgången var inte korrelerad. Fynden var alltför få för att tillåta en jämförelse baserad på årliga fynd. Trots att endast en hornuggla registrerades här 1993, visar VBOF's månadsrapporter att 1993 var ett gott år för hornuggla med 27 familjer funna. Även 1996 och 1999 framstår som goda häckningsår för hornuggla i västra Blekinge (Tabell 2). Nästan alla dessa var lokaliserade söder om vårt huvudområde. I Inre Dallandskapet registrerades åren 1996 och 1999 som goda hornuggleår

(Tabell 2). Femton hornugglor registrerades 1999 längs ruten utanför Bräkne-Hoby.

Sammantaget visar sig åren 1993, 1996 och 1999 vara goda år för pärluggla och hornuggla medan kattugglan visade små toppar 1994 och 1999. Vi erhöles dock inte någon signifikant korrelation på årsbasis mellan de tre ugglearterna.

Insamlade data på bok- och ekollonproduktion redovisas i Tabell 2. Beräkningar av bokollonproduktion från tolv områden i Skåne och Halland visar att produktionen varierar avsevärt mellan områden även under år som allmänt anses vara goda ollonår. Data från sju provytor på Ryssberget under åren 1992–1999 visar att 1992 och 1995 var "mycket goda" år och 1993 och 1999 var "goda år". Under övriga år iaktogs inte någon ollonproduktion (Figur 2). Enligt uppgifter från Statsskovens Plantavelsstasjon Humlebaek, Danmark (Henrik Knudsen, muntl.) var 1992 och 1995 goda bokollonår och 1992, 1995 och 2000 goda år för ekollon i Danmark medan 1998 var ett gott år bara på Lolland och Falster. Information om ekens ollonproduktion i Blekinge erhöles från Flakulla Provinience (Cecilia Rooth, muntl.). Sedan mitten av 1990-talet framstår 1997 och 2000 som goda år för ekollon, medan 1995 framstår som "bättre än normalt". C. Rooth uppger även att det fanns "ett bra år i början av 1990-talet" vilket mycket väl kan ha varit 1992. Informationen från Danmark och östra Blekinge uppvisar viss samstämmighet, och lyfter fram 1995, 2000 och (möjligen) 1992, som goda år för ekollon. Av dessa var 1992 och 1995 goda år för både bokollon och ekollon i Danmark och möjligen också i Sverige.

Bergfink uppträdde i stora flockar i Blekinge under vintrarna 1993/94 (29.670 exemplar), 1995/96 (4,4 milj.) och 1998/99 (15.150). Dessa siffror svarar väl mot den höga bokollonproduktionen som rarna 1993, 1995 och 1998. Under övriga vintrar 1991/92–1999/2000 iaktogs inga flockar med över 100 bergfinkar i Blekinge trots det mycket goda året för bokollon 1992. Under januari och februari uppehöll sig en flock med omkring två miljoner bergfinkar i nordvästra Skåne (Kjellén & Lindström 1993, Lithner 1995.)

Vi fann ett signifikant samband mellan stora antal bokollon och registrerade pärlugglor följande år. För horn- och kattuggla fann vi inte något sådant samband inom vårt huvudområde. Däremot fann vi ett positivt samband mellan stora mängder bokollon och häckande hornugglor följande vår.

Åren 1992 och 1995 var bokollonproduktionen mycket god och nästan lika stor. År 1993 var tätheten av pärlugglor nästan dubbelt så stor som 1996 och

antalet rapporterade häckningar av hornugglor tre gånger så stort som 1996.

### *Diskussion*

Vi fann ett tydligt samband mellan goda bokollonår och förekomsten av pärl- och hornuggla följande vår, vilket indikerar ett positivt samband mellan bokollon och små skogsgnagare och en påföljande numerär ökning hos dessa båda ugglor. Kattugglan visade inte ett sådant mönster. Den klara uppgången i antal under våren 1994 inföll året efter det stora antalet pärl- och hornugglor. Detta stämmer väl överens med uppfattningen att ökning i antal hos ortstroga predatorer är fördröjd i förhållande till ökningarna i tätheten bland bytesdjuren, medan nomadiska predatorer ökar utan tidsfördröjning. Det större antalet registrerade kattugglor året efter toppar av pärl- och hornugglor kan vara orsakad av att fjolårsungar etablerat sig i lediga revir medan gnartillgången under hösten fortfarande var relativt god. Studier av Philipsson (2001) bekräftar sambandet mellan goda bokollonår och stora antal flygga kattuggleungar följande år.

Vari från de pärl- och hornugglor som snabbt infann sig under goda år kom vet vi inte. I norra Fennoscandia är arterna kända som delvis nomadiska. I södra Europa är dessa i hög utsträckning stannfåglar, medan en övergångszon är känd i västra Finland, där adulta hannar av pärluggla är stannfåglar och honor och ungfåglar flyttar. Vårt undersökningsområde är beläget något söder om denna zon, och reviretablering av nomadiska fåglar har inte tidigare påvisats här. Utöver stora fluktuationer för pärluggla mellan år håller vi för troligt att särskilt den kraftiga ökningen under senare delen av april 1999 på såväl huvudrutten som Bräkne-Hobyritten kan förklaras med att nomadiska individer invandrat. Det står klart att de dramatiska förändringarna i antalet registrerade pärl- och hornugglor inte kan förklaras enbart med lokal rekrytering. Förmodligen finns alltid några individer som i huvudsak är tysta under dåliga gnagarår i området medan större antal flyttar in under goda gnagarår.

Under 1993 och 1996 påträffades mycket få hornugglor i Huvudområdet. Däremot var antalet ropande hornugglor tämligen högt i det Inre Dallandskapet och antalet lokaliserade familjer i det Kustnära Dallandskapet var 10 till 20 gånger större än under år som inte föregåtts av mycket god ollonproduktion. År 1999 var antalet stort även i Huvudområdet. Det kan bero på att flera områden

avverkats här, vilket gynnar åkersork – hornugglans viktigaste bytesdjur i sydligaste Sverige.

Jensen (1982) visade att massproduktion av bokollon följdes av massförekomst av smågnagare och Hansson et al. (2000) visade att stora ollonår för ek förorsakar massförekomst av smågnagare. År 1997 uppges ha varit ett gott ollonår för ek i östra Blekinge medan året inte nämns i rapporterna från Danmark. År 1998 var ett medelgott år för pärluggla och ett dåligt år för hornuggla i västra Blekinge. Kanske är inslaget av ek alltför litet i västra Blekinge för att spela en avgörande roll för förekomsten av smågnagare, eller kanske var den goda ekollontillgången i östra Blekinge en lokal företeelse.

Kjellén & Lindström (1993) beräknade bergfinkens energibehov under vintern till åtminstone 120 kJ medan Nilsson (1971) tog fram ett något högre värde. Dolnik (1982) visade att en bergfink kan tillgodogöra sig högst 83% av fröets innehåll. Vikter på bokollon varierar avsevärt från ett område till ett annat och dessutom avsevärt inom ett och samma område under goda ollonår. Medelvikten för en kärna norr om Karlshamn i Blekinge år 1984 var 0,0864 g och energiinnehållet har beräknats till 2,53 kJ/frö. Härur kan man få fram att en bergfink i västra Blekinge kan konsumera 58–82 frön/dag. En flock på två miljoner fåglar skulle om varje fågel intog sin dagsranson konsumera mellan 1550 och 2250 ton bokollon under tre månader. Således bör stora flockar av bergfink under vintern ha en avsevärd effekt på smågnagarnas reproduktion efter år med god bokollonproduktion och därmed också på antalet ugglor som är beroende av dessa gnagare. Förekomsten av bergfink tycks följa de flesta år av god bokollonproduktion. Det mycket stora antalet pärlugglor 1993 jämfört med 1996, trots stora mängder bokollon både 1992 och 1995, stämmer med hypotesen att bergfinken (som sakades i Blekinge 1992/93 men fanns i stort antal 1995/96) modifierar födotillgången för små däggdjur.

Bergfinkens strategi att övervintra i stora flockar är en tämligen överlägsen jämfört med andra tättingar och även under häckningen kan tätheten vara hög när näringstillgången är god. Bergfinken synes således övervintra i så stora flockar som näringstillgången medger. Detta kan möjligen förklara varför en flock med cirka två miljoner bergfinkar uppehöll sig i nordvästra Skåne medan praktiskt taget inga bergfinkar observerades i Blekinge under vintern 1992/93 trots att 1992 var ett mycket gott år för bokollon.