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Influence of snow cover on food hoarding in Pygmy Owls *Glaucidium passerinum*

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Voles are the most preferred prey of Pygmy Owls (*Glaucidium passerinum*) in Northern Europe, where the extensive snow cover may decrease the availability of voles. Snow cover may thus cause changes in the diet from what is expected on the basis of prey abundance alone. Food hoarding behaviour of Pygmy Owls was examined in relation to snow cover. Pygmy Owls hoard small birds and mammals in tree holes and nest boxes on their autumn and winter territories. During five winters, we examined hoarded prey items from artificial hoarding boxes provided to Pygmy Owls in central Finland. The most intensive food hoarding periods occurred before the fall of snow, during which 73% of prey items were hoarded. Presence or absence of snow cover did not affect the number of hoarded birds, but snow cover dramatically lowered the number of hoarded voles. Pygmy Owls began to exploit caches before the beginning of the snowy season and stopped exploitation in spring. According to the high utilization degree of the hoarded prey, especially during the period with permanent snow cover, we suggest that the Pygmy Owl's food hoarding behaviour acts as a buffer for seasonal variation in food supply.

1. Introduction

Many species of mammals and birds hoard food when it is abundant and retrieve it later (Haftorn 1956, Sherry 1989, Källander & Smith 1990, Vander Wall 1990, Brodin & Ekman 1994). The fundamental advantage of food hoarding, which affects all food hoarding animals to some degree, is that food stores can supplement the diet during a period of food scarcity. The adaptive advantages of food hoarding may be considered with respect to the time span between hoarding and retrieval (Nilsson *et al.* 1993). Hoarding food is commonly observed in species living in the holartic area (Roberts 1979, Andersson 1985, Smith & Reichman 1984, Korpimäki 1987, Brodin *et al.* 1994, Suhonen *et al.* 2007).

The extent of food hoarding may change depending on many variables, e.g. the photoperiod (Shettleworth *et al*. 1995), and the type of food available (Vander Wall 1990). In order for food hoarding to be beneficial, long-term food hoarders should save their stores for a period of increased food requirement and/or low food availability. Cold snowy winters lead to increased food requirement and lower food availability. Alterations in the environment and consequential decrease in the availability of preferred food during the hoarding period has an immediate impact on the hoarding behaviour. The few studies of predation in relation to snow cover (Olsson 1984, Sonerud 1986, Canova 1989, Lindström & Hörnfeldt 1994, Karlsson 2002) suggest that the relative proportion of alternative prey in the diet of a predator increased with an increasing snow depth. Significance of the alternative prey could be less important to the predator if it has hoarded enough food.

In this study we describe the food hoarding and retrieving behaviour of Pygmy Owl (*Glaucidium passerinum*) before and after permanent snow cover. The Pygmy Owl is the smallest avian predator in the boreal coniferous forests in Europe (Mikkola 1983, Strøm & Sonerud 2001). It is an ideal predator to study the food hoarding behaviour and the usage of caches because it hoards prey in cavities and nest boxes during late autumn and winter (Kellomäki 1966, 1977, Solheim 1984, Mappes *et al.* 1993, Suhonen 1993, Suhonen *et al.* 2007) and the contents of caches are thus easy to examine. The main prey items are small mammals, mainly voles, during the winter; the most common alternative prey are birds and shrews (Kellomäki 1966, Solheim 1984, Suhonen 1993, but see Ekman 1986, Kullberg 1995).

Food hoarding seems to reach the maximum intensity when prey species are most abundant or conspicuously vulnerable. The cyclicity of the main prey does not have a large effect upon the numbers of stored prey, but instead it has a clear effect on the composition of prey species stored (Suhonen 1993). During years with high vole densities, Pygmy Owls hoard mostly voles and they shift to passerine birds during years of low vole densities (Suhonen 1993). During the hoarding period they bring several prey items to a cache per day (Järvi 1986). The number of prey items per cache varies from 1 to 200 per store (Kellomäki 1966, Solheim 1984). Here, we study four aspects. (1), When do Pygmy Owls hoard food? (2), When do they retrieve the hoarded food? (3), How does the start of permanent snow cover influence the amount of hoarded food? (4), How does the start of permanent snow cover influence the prey species composition of the hoarded food?

2. Material and methods

2.1. Study area and study species

We studied the food hoarding behaviour of Pygmy Owls throughout autumn and winter at two different study areas in Finland, in Konnevesi (62°37’N, 26°20’E), central Finland, and in Kortesjärvi (63°18’N, 23°10’E and 63°10’N, 23°10’E), in the province of South Ostrobothnia, western Finland. In both areas, the landscape is dominated by mixed coniferous forest interspersed with patches of birches (*Betula* spp.). The ground is snow-covered from the end of November to early April. In the Konnevesi area we have data from five winters 1988–1992 and 1993–1994, and in the Kortesjärvi area from two winters 1990–1992 (for more details, see Suhonen et al. 2007). In addition, we used published data on the contents of Pygmy Owl caches in Kälviä (63°54’N, 23°20’E) in Mid Ostrobothnia, western Finland (Järvi 1984, 1986) (Table 1).

2.2. Data collection and analysis

Hoarding-boxes were provided for Pygmy Owls in all study areas (Table 1). The boxes had an entrance hole of 45 mm, small enough not to be used by other owls (Solheim 1984). We did not trap any owls from our study area. Prey items cached by Pygmy Owl in the hoarding-boxes were checked two to three times per month from late October to late March. Stored prey items were identified to the species level and their sex and age were examined. Each prey item was marked individually, birds by colour rings and small mammals by toe clipping.

Because voles are the main prey species of Pygmy Owls, small mammal abundance was estimated by snap-trapping in late September or early October in two to four sample plots in all study ar-

Table 1. Locations of the study areas, studied year, number of boxes with larders, number of hoarded prey items before and during the permanent snow cover and dates of permanent snow cover in different study areas. Density of voles per 100 trap night, All data were collected by us, except data from Kälviä 1983–84 and 1985–86 collected by Järvi (1984, 1986).

Study		Winter	Number of boxes with larders	Number of prey items		Density of voles per 100 trap nights	Date of permanent snow cover
				before	during		
Konnevesi	6237'N 2620'E	1988–89	20	88	27	32.0	19.Nov
		1989–90	15	59	31	0.2	5. Dec
		1990–91	40	228	103	9.3	19. Nov
		1991–92	23	132	83	23.1	9. Dec
		1993–94	17	206	35	2.4	26. Dec
Kälviä	6354'N 2320'E	1983–84	11	38	39	>18.0[1]	15.Nov
		1985–86	8	103	26	>1.0[1]	24. Nov
Kortesjärvi	6318'N 2310'E	1990–91	5	99	75	9.9[2]	16.Nov
		1991–92	10	192	5	21.9[2]	21. Dec

Source of vole density: 1 = Korpimäki *et al.* 2002, estimated from their Figure 1, 2 = Suhonen *et al.* 2007

eas. Sample plots were in each of the main habitat types (a cultivated field, an abandoned field, a clear-cut area, spruce forest and a pine forest) in all study areas except the Kälviä area. At each plot, 50–420 Finnish metal snap-traps were set 10 m apart in small mammal runs and were checked once a day. The density index derived from the trapping results was the number of animals caught per 100 trap nights. Density of *Microtus* voles in Kälviä was estimated from figure 1 in Korpimäki *et al.* (2002).

To ensure sufficient replication each winter we used different areas as independent observations for statistical testing. Altogether, we had nine independent observations. The exception was for the analysis of the use of hoarded prey, for which we used eight winters, because observations about the use of hoarded food were not included in the published data from Kälviä in 1985 (Järvi 1986). We report the mean and the standard deviation of prey hoarded during a ten-day period. We used paired t-test (two-tailed) for testing the data before and during permanent snow cover periods.

3. Results

3.1. Food hoarding

The most intensive food hoarding behaviour of Pygmy Owls was during the snowless period in October and early November (Table 2). The difference in the total number of cached prey items before the permanent snow cover period was mainly a result of the large number of cached voles and shrews. The proportion of hoarded voles and shrews was 87% before the permanent snow cover period, but dropped to 60% during the permanent snow cover period (Table 2). Presence or absence of the permanent snow cover did not affect the number of hoarded birds and mice (Table 2). The mean number of hoarded prey items per 10 days per nest-box was higher before permanent snow cover than during it (t_8 = 2.51, P = 0.037; Fig 1a).

The total number of hoarded prey species was higher before the permanent snow cover than during it (Table 2). This difference was due to differences in the number of mammalian species hoarded, because the number of avian species was equal and was not affected by the snow cover period (Table 2). On average, more mammals were hoarded per day per box in each study area before (3.1 ± 3.7 hoarded prey items during a 10 day period) than during permanent snow cover (0.7 ± 0.9; t_8 = 2.34, P = 0.048). However, the numbers of hoarded birds during a 10 day period per next-box was almost the same (before permanent snow cover: 0.3 ± 0.3, during permanent snow cover: 0.1 ± 0.1; t_8= 2.15, P = 0.064).

Table 2. Mean (SD) number of hoarded prey items per study year (n = 9) before the permanent snow cover and during the permanent snow cover. Note that some bird species have been omitted because sample sizes were small. Test statistic refers to a paired t-test with d.f. = 8.

Prey	Before snow cover	During snow cover	t	P
Microtus spp.	49.3 ± 53.0	12.7 ± 21.4	2.38	0.045
Clethrionomus glareolus	24.2 ± 21.2	6.7 ± 8.9	2.97	0.018
Sorex spp	35.7 ± 48.6	8.9 ± 14.7	2.40	0.059
Micromys minutus	6.2 ± 8.0	5.4 ± 13.2	0.19	0.857
Tot n of mammals	116.3 ± 73.2	36.0 ± 30.3	3.58	0.007
Tot n of mammal spp	4.3 ± 0.9	3.0 ± 1.1	4.00	0.004
Parus major	1.6 ± 1.6	2.4 ± 2.4	–1.06	0.321
P. montanus	3.7 ± 5.5	1.0 ± 1.4	1.79	0.111
Regulus regulus	1.7 ± 2.8	3.8 ± 5.8	–1.73	0.121
Tot n of birds	10.0 ± 9.1	11.2 ± 13.0	–0.45	0.662
Tot n of bird spp	4.0 ± 2.5	3.6 ± 3.1	0.84	0.426
Tot n of prey	126.3 ± 68.3	47.1 ± 32.2	3.52	0.008
Tot n of spp	8.3 ± 2.7	6.4 ± 3.8	2.39	0.044

Table 3. Mean number (SD) of consumed prey items per study year (n=8) before and during the permanent snow cover. Note that some bird species have been omitted because sample sizes were small. Test statistics refer to a paired t-test with d.f. = 7.

Prey	Before snow cover	During snow cover	t	p
Microtus spp.	2.5 ± 2.5	33.9 ± 30.2	–3.11	0.017
Clethrionomus glareolus	3.1 ± 4.7	14.0 ± 16.8	–1.83	0.109
Sorex spp	3.3 ± 7.6	25.4 ± 36.5	–2.03	0.082
Micromys minutus	0.9 ± 2.1	10.5 ± 18.4	–1.44	0.192
Tot n of mammals	9.5 ± 14.0	83.1 ± 65.7	–3.19	0.015
Tot n of mammal spp	2.4 ± 1.6	3.3 ± 1.3	–1.51	0.176
Parus major	0.8 ± 1.0	2.3 ± 2.1	–2.51	0.040
P. montanus	0.5 ± 0.9	2.5 ± 3.1	–1.67	0.138
Regulus regulus	0.5 ± 1.4	3.8 ± 4.9	–2.30	0.055
Tot n of birds	2.1 ± 4.1	12.9 ± 14.3	–2.49	0.042
Tot n of bird spp	1.0 ± 1.3	4.3 ± 2.6	–3.26	0.014
Tot n of prey	11.6 ± 14.9	93.9 ± 65.1	–3.47	0.010
Tot n of spp	3.6 ± 2.9	8.0 ± 3.1	–3.61	0.009

3.2. Exploitation of hoarded food

The Pygmy Owls consumed a large proportion (61%) of cached food items during winter. The proportions of consumed prey items in two different prey groups, small mammals and birds, were 61% and 71%, respectively. The Pygmy Owls began to consume hoarded food a little before the snowy season, but the larger proportion of hoarded food (89%) was consumed during the permanent snow cover period (Table 3). The number of consumed prey items per 10 days per nest-box in each study area did not differ between the before and during permanent snow cover periods ($t_8 = -0.95$, $P = 0.37$; Fig 1b).

4. Discussion

We find that the snow cover is one of the main factors behind the food hoarding behaviour of Pygmy Owls. Snow causes a large change in the owls' environment and therefore has a great influence on food hoarding and retrieval. Pygmy Owls hoard

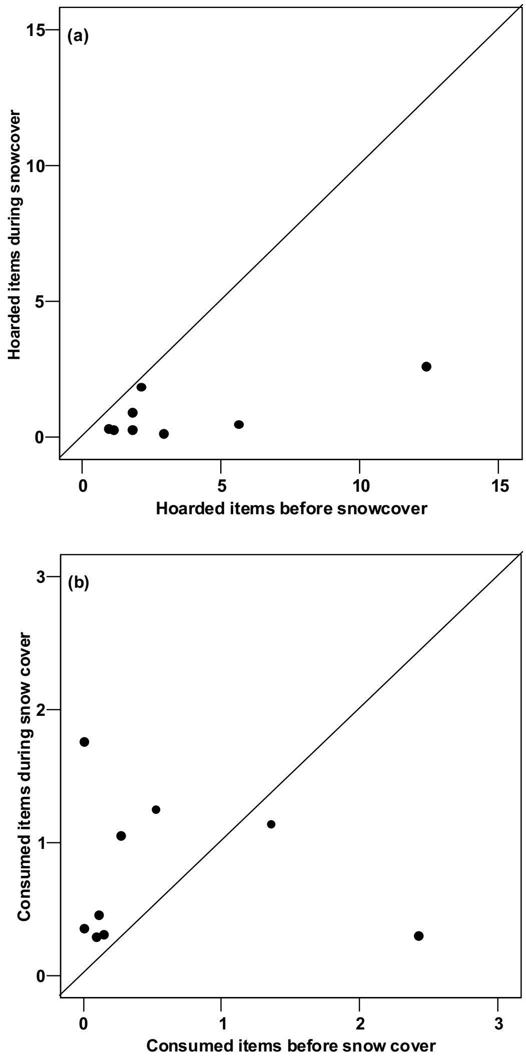

Fig. 1. (a) Number of hoarded prey items during a 10 day period per nest-box before and during permanent snow cover in each study area (see Table 1). (b) Number of consumed prey items during a 10 day period per nest-box before and during permanent snow cover in each study area (see Table 1). The diagonal line shows the expected relationship in case the number of hoarded and consumed prey were equal before and during permanent snow cover.

most of their prey items before the snowy season, and consume the prey items during it. Therefore, we suggest that food hoarding would be adaptive against lower hunting success and scarcity of food during the period of permanent snow cover. The proportion of the most preferred prey (small mammals) in the hoarded prey decreased dramatically after the snow had fallen. The only exception were harvest mice, which were hoarded in approximately the same numbers before and during the snowy season. Harvest mice feed and move above the snow cover and therefore are more vulnerable to predation than voles and shrews (Kaikusalo 1972). Pygmy Owls have symmetrical ears and cannot localise prey items by sound alone (Nordberg 1977). Hence, they combine vision and hearing when searching for prey and are thus able to locate prey under the snow cover, but they are too light (male 47–62 g, female 55–70 g) (Mikkola 1983; Strøm & Sonerud 2001) to penetrate the snow cover when hunting small mammals.

Hoarded food is assumed to be important in dampening seasonal fluctuations in food availability, especially in geographic areas with pronounced seasonality (Roberts 1979, Smith & Reichman 1984). Pygmy Owls hoard more prey items in a snowless autumn. Pygmy Owls consume most of the hoarded prey items during snowy winters. The exploitation rate of cached prey items was high (61%) during the snowy months, when the energy expenditure was supposedly high and the availability of prey was low. This kind of food hoarding behaviour seems to be profitable, because it supplements the diet during the period of food scarcity and decreases seasonal fluctuations in food abundance.

When conditions become favourable for the escape strategy of a prey type, costs of capture should rise drastically, making the net energy value of live prey low (possibly negative). Consequently, the predator should have little to lose and much to gain from surplus killing and prey caching when the costs of making a kill are at their lowest (Oksanen *et al*. 1985). Pygmy Owls hunt all kind of prey to some degree, but prefer prey what happens to be most available at the moment. This is also in accordance with the diversity of hunting techniques used by Pygmy Owls (Kullberg 1995). The decreased availability of preferred prey, caused by extensive snow cover, does not cause a clear shift to alternative prey. The functional response to this decrease was exploitation of caches.

Winter is energetically the most stressful period in the northern latitudes. Increased energy requirements, because of low temperatures, shorter days and extensive snow cover, makes the survival over winter difficult for diurnal animals. Voles move mostly under the snow cover and therefore the hunting is very difficult for Pygmy Owls, because they can not penetrate the snow cover. Food hoarding before the snowy season would be the most reasonable pattern of behaviour and Pygmy Owls did behave in this prudent way. The most intensive hoarding period was before the fall of the extensive snow cover (Fig. 1), when the density (Korpimäki et al. 2002) and availability of preferred prey is high. Furthermore, the large proportion (61%) of cached food was consumed during the severe period. Daily consumption of hoarded food was similar between snowless and snowy periods, because the snowy period is almost twice as long as the snowless hoarding period. Food hoarding plays an important role in dampening fluctuations in availability of food and seems to be an adaptive response to variations in the environment. Most likely this behaviour is profitable and therefore increases the probability of surviving a severe period (see Stacey & Bock 1978, Wauters *et al.* 1995), but the relation of food hoarding to the survival of Pygmy Owls is not addressed in the present study.

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Pysyvän lumipeitteen vaikutus varpuspöllön *Glaucidium passerinum* ravinnon varastointiin

Tutkimme pysyvän lumipeitteen tulon vaikutuksia varpuspöllön *Glaucidium passerinum* syksyiseen ravinnon koostumukseen ja varastointiin. Metsä- (*Clethrionomys glareolus*) ja peltomyyrä (*Microtus agrestis*) ovat suosituimpia saaliskohteita Suomessa. Talviaikainen pysyvä lumipeite vähentää huomattavasti myyrien saatavuutta ja täten aiheuttaa muutoksia varpuspöllön ravinnon varastoimis- ja saalistuskäyttäytymisessä.

Varpuspöllö varastoi varpuslintuja ja pikkunisäkkäitä puiden koloihin ja linnunpönttöihin syys- ja talvireviireillään. Kiihkein jakso ravinnonvarastoinissa osuu ajalle juuri ennen pysyvän lumipeitteen tuloa, loka– marraskuulle. Suurin osa varastoiduista saaliseläimistä (73 %) varastoidaan ennen lumipeitteen tuloa. Kuitenkin varastoitujen lintujen määrissä ennen ja jälkeen lumipeitteen ei ole eroa.

Varpuspöllöt aloittavat hyödyntämään varastojaan hieman pysyvän lumipeitteen tulon jälkeen ja jatkavat varastoitujen eläinten käyttöä kevättalvelle saakka. Varastoiduista eläimistä yli 60 % käytetään talven aikana, joten ravintovarastoilla on todennäköisesti suuri merkitys varpuspöllöjen selvitymiselle talven yli.

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