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Caching behaviour, prey choice and surplus killing by Pygmy Owls Glaucidium passerinum during winter, a functional response of a generalist predator

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Nestboxes with different-sized entrance holes were put out to study caching behaviour and prey choice of Pygmy Owls in southeastern Norway in the winters 1971/72 to 1976/77. Pygmy Owls preferred nestboxes with entrance holes less than 55 mm for caching, while nestboxes with larger holes were primarily used as sheltered feeding sites. Caching took place from October to April, with a peak in November to January. Single caches contained up to 97 prey items, and regular surplus killing by individual Pygmy Owls may explain the sudden filling up of caches. Of the 1321 prey items identified, 1173 were small mammals. The bank vole *Clethrionomys glareolus* was the most frequent prey species. Birds were taken in the highest proportions in years of low vole abundance.

Choice of caching sites is discussed as an adaptation to avoid cache-robbing from other species. Caching may itself be an adaptation to fluctuating prey availability during winter. The flocking of tits during winter is discussed as a possible anti-predatory behaviour pattern to reduce the predation risk from Pygmy Owls.

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1. Introduction

Prey caching has been reported among Falcons *Falco* spp., especially during the breeding season (Cramp & Simmons 1980, Vaughan 1961, Stendell & Waian 1968, Oliphant & Thompson 1976, Fox 1979). Usually caching takes place when the female or young are satiated and left over prey is hidden by the male for later use. In Accipitridae prey remains are often left on the nest (Collett 1921), while falcons may retrieve the prey and store it away from the nest (Stendell & Waian 1968, Oliphant & Thompson 1976). Eleonora's Falcons *Falco eleonora* establish caches of up to 20 prey items per cache during breeding (Vaughan 1961), while exploiting increased prey resources of autumn migrant Passerines.

Prey caching is also recorded in winter by the Merlin *Falco columbarius richardsonii* (Pitcher et al. 1979) and American Kestrel *F. sparverius* (Collopy 1977), indicating that caching in falcons may be an ordinary phenomenon whenever prey species are abundant.

Fox (1979) argues that prey caching may have a higher adaptive value for owls than for other raptors, since owls lack a crop in which to store surplus food. Prey caching has been noted in caged owls (Collins 1976). Several owl species cache prey leftover in the nest (Collett 1921, Haftorn 1971, own obs.), and Hawk Owls *Surnia ulula* (Ritchie 1980) and Snowy Owls *Nyctea scandiaca* (H. Vide-Bang pers. comm.) carry prey items away from the nest before caching them.

The Pygmy Owl has long been known to establish large caches of prey items in winter (Collett 1921). Caches of 150 (G.A. Sonerud pers. comm.) and 200 (Solheim 1973) prey items have been recorded. Regularly surplus killing and caching seem to be an important part of this species' behaviour and not merely a casual event as in many carnivores (Kruuk 1972). The large caches established by this species outside the breeding season seem to be quite unique among raptors. So far little has been done to study this activity, apart from registering prey species and cache sizes.

2. Material and methods

Pygmy Owl caching behaviour was studied during the winters 1971/72 to 1976/77. Artificial nestboxes were placed in six localities in southeastern Norway (Fig. 1), all close to agricultural fields within the boreonemoral zone (Anon. 1977). The nestboxes were mostly hollow tree stumps as described by Sonerud et al. (1972). Nestboxes with entrance ≤55 m were denoted Pygmy Owl (PO) nestboxes, and those with entrance >80 mm Tengmalms' Owl (TO) nestboxes. New nestboxes were provided during the study period and old ones were sometimes moved due to clearcut logging. The number of available nestboxes was not constant.

The nestboxes were checked 1-6 times during winter. Checking of winter caches might lead to replacement of prey animals by the Pygmy Owls (cf. Sect. 4.2), so the nestboxes were not checked more often than once a month. Whole prey items were identified and left undisturbed if fresh. Bird feathers were identified but not quantified, giving minimum numbers of prey items of each species. Owl pellets were not collected but served as an indication of the occupant species in the TO nestboxes. PO nestboxes had entrance holes too small to be used by owls other than Pygmy Owls. Feathers, pellets and other prey remains were always removed from the nestboxes and so new remains were detectable at the next visit.

In April old, decaying prey items were removed from the nestboxes to allow breeding of hole-nesting species other than the Pygmy Owl. Fresh prey were left undisturbed.

The population of small mammals was evaluated by snap-trap lines and observations of rodent activity in the field (G.A. Sonerud pers. comm. and own obs.). The localities were situated in similar habitats in the boreonemoral region (Anon. 1977), and the rodent fluctuations seemed not to show any detectable asynchrony within the study region. Bird populations were not censused.

3. Results

3.1. Nestbox choice

The number of available PO and TO nestboxes per winter is given in Table 1. About 50% of both PO and TO nestboxes were used as caching and/or foraging cavities and Pygmy Owls showed no preference for either

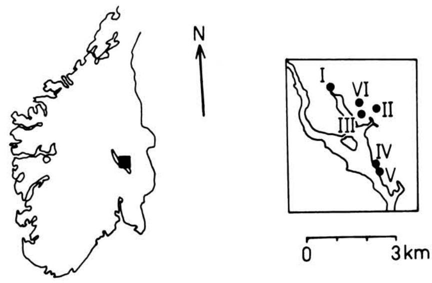

Fig. 1. Location of the six areas where Pygmy Owl caching behaviour was studied in 1971-1977.

type ($\chi^2 = 0.13$, $P > 0.5$). As Tengmalm's Owls *Aegolius funereus* have been found to cache prey during winter in Finland (Korpimäki 1980), I cannot totally exclude this species as an occupant of the TO nestboxes. However, as all pellets indicated that the actual users were Pygmy Owls, I have treated all TO nestboxes as used by this species only.

The TO nestboxes never contained more than one whole prey item at a time, while PO nestboxes contained up to 97 prey items. The Pygmy Owls thus showed clear preferences for PO nestboxes when caching ($\chi^2 = 10.6$, $P < 0.01$).

3.2. Caching behaviour

Although nestboxes were checked in September, prey items were never found in this month and rarely before the end of October. Caching activity seemed to start when the daily maximum temperature dropped below 0° C. The cache sizes found each month and year are given in Table 2. Small caches were most frequent. Prey caching reached a maximum in November to January with a mean of 26.3 prey items per cache at the end of this period. Caching then levelled off to only 3.4 prey items per cache in April (Table 2).

Table 1. Available and used nestboxes per year. All caches in nestboxes with entrance ≥80 mm contained only one prey item per cache.

		1971/72	1972/73	1973/74	1974/75	1975/76	1976/77	Total
Entrance	Available	3	15	37	31	34	25	145
≤ 55 mm	Used for caching	3	4	25	12	16	8	68
	Used for caching and/or foraging	3	4	26	13	18	8	72
Entrance	Available	2	7	13	4	3	3	32
> 80 mm	Used for caching	0	0	4	0	0	1	5
	Used for caching and/or foraging	2	2	8	1	3	1	17

Table 2. Number of whole prey items per cache per month per year. ★ = no nestboxes checked. - = nestboxes checked, but no prey items recorded.

	Oct.	Nov.	Dec.	Jan.	Febr.	March	April
1971/72	4	1,1,2,2,5	5	★	★	★	★
1972/73	1,1,2,2,4,5	2	-	★	★	★	★
1973/74	1,1,4,24,37	1,1,3,3,14, 17,17,60,61, 63,69,71,94	13,14,15,17, 28,41,62	10,68,68,73	1,3,16,45, 46,47	1,1,4,9,18, 20,50	1
1974/75	7	1,2,4,4,5,33	★	2,3,21	1,2,3,38	3	3
1975/76	-	2,11,16,30,33	18	1,1,3,9,10,14, 19,20,48,56	1,4,6,8,15, 24,29,43	★	2,3,8
1976/77	★	1,24	-	1,1,97	★	1,1,2	★
Total	93	653	213	525	332	110	17
Mean/month	7.1	20.4	23.7	26.3	18.4	10	3.4
Median	4	5	17	12	12	3	3

Table 3. Prey groups found in Pygmy Owl caches in the winters 1971-1977. — Wood tits = *Parus* sp. excluding *P. major* and *P. caeruleus*, but including *Relgulus regulus* and *Certhia familiaris*. — Seed specialists = *Acanthis flammea, Carduelis spinus, Pinicola enucleator* and *Loxia* sp. — Agricultural species = *Parus major, P. caeruleus, Sitta europea, Passer domesticus* and *P. montanus*.

	1971/72	1972/73	1973/74	1974/75	1975/76	1976/77	Total
Clethrionomys glareolus	1	2	505	14	154	100	776
Microtus agrestis	0	5	132	16	24	20	197
Sorex sp.	2	0	52	23	110	4	191
Apodemus sp.	3	0	3	1	0	2	9
Mammals, total	6	7	692	54	288	126	1173
Wood tits	7	0	13	15	17	3	55
Seed specialists	0	1	8	42	4	3	58
Agricultural species	3	1	6	0	6	2	18
Other birds	1	0	6	9	1	0	17
Birds, total	11	2	33	66	28	8	148
Prey items per year	17	9	725	120	316	134	1321
Mammals/birds	0.6	3.5	21.0	0.8	10.3	15.8	7.9
Vole population	low	high	high	low	high	high	

3.3. Prey choice and surplus killing

A total of 1321 prey items were identified during the study period, of which 1173 were small mammals (Table 3). The Bank Vole *Clethrionomys glareolus* was the main prey species. Field Voles *Microtus agrestis* and Shrews *Sorex* spp. made up almost equal parts of the diet, but numbers varied markedly between seasons. The Wood Mice *Apodemus* spp. were only found on nine occasions and must be considered a casual prey species. In the winters 1971/72 and 1974/75, when rodent populations were low, birds dominated as prey. The bird prey have been grouped in Table 3 according to winter habitat and behaviour. The groups wood tits and seed specialists made up the main bird prey, with almost equal amounts represented. The group other birds involved some large species such as the Great Spotted Woodpecker *Dendrocopos major* and Redwing *Turdus iliacus*.

It is difficult to measure how a raptor assesses availability of different prey species, and I have therefore tested for differences in choice of small mammals versus birds as prey only. Significant differences in prey choice between different years predominate and are correlated with the abundances of voles (Table 3). I have also compared prey choice of Pygmy Owls in different localities within seasons (Table 4). There were no significant differences except in 1973/74 when prey choice in area III differed significantly from that in others. This may, however, be biased by two TO nestboxes. As showed earlier (Sect. 3.1), those nestboxes were avoided for caching activities and birds may be overrepresented as

Table 5. Choice of prey in Pygmy Owl caches with ≥25 prey items. Figures are selected from the maximum cache sizes recorded during winter. Roman numerals refer to the areas in Fig. 1.

Vole population:	1973/74 high							1974/75 low		1975/76 high					1976/77 high
	I			II		IV	V	I		I	II			IV	II
Clethrionomys glareolus	33	65	36	38	33	52	63	8		12	25	31	33	2	70
Microtus agrestis	18	24	22	21	3	11	1	8		9	2		2		19
Sorex araneus	8	4	11	1	1	3	4	17	1	8	21	1	20	21	4
S. minutus	2		1			1									
Apodemus sylvaticus			1	1											2
Carduelis spinus									4						
Acanthis flammea									31						
Loxia curvirostra															1
Regulus regulus									2					1	
Certhia familiaris														1	
Parus ater	1												1		
P. montanus	1	1										1			
P. caeruleus				1						1					
P. major														1	
Passer domesticus						1									
Turdus iliacus						1		1							
Cache sizes	63	94	71	62	37	69	68	34	38	30	48	33	56	26	97

pers. comm.). American Kestrels flew directly to a caching site after making a kill, thus indicating that the caching site was selected before the bird took off with the prey (Collopy 1977). Also Marsh Tits *Parus palustris* showed preferences for certain storing places (Shettleworth 1983).

4.2. Caching behaviour

A Pygmy Owl seems to cache prey items in several nest cavities in autumn (Sect. 3.2). By establishing more than one cache the risk of loosing food to other individuals is lowered. Prey animals are placed with the belly down in a regular pattern inside the nestboxes. This handling pattern is also found in other raptors when caching prey items (Collins 1976, Collopy 1977). Any disturbances caused by other cacherobbing predators may thus be discovered by the Pygmy Owls, and replacement of prey may take place. Replacement behaviour in Pygmy Owl was recorded using individually marked prey animals (Ahlbom & Carlsson 1972).

As Pygmy Owls preferred PO nestboxes for caching, food resources may be depleted only by conspecifics. However, Pygmy Owls show strong territorial behaviour through winter and intruders are usually attacked and driven away (Lindberg 1966, Solheim unpubl.).

The median value of prey items per cache increased greatly relative to mean values from November to December (Table 2), i.e. no caches contained disproportionately more prey items than others. If a Pygmy Owl exploits its earliest caches first as do Marsh Tits (Cowie et al. 1981), the small caches would be emptied first (see Sect. 3.2). This could explain the observed increase in median values of prey items per cache. The result would, however, also be the same if prey items were replaced from big caches to small ones.

Pygmy Owls occasionally kill prey bigger than themselves, such as water voles *Arvicola terrestris* (Kellomäki 1977) and Great Spotted Woodpeckers (Likachev 1971, Heggelund 1975, Kellomäki 1977, this study). Such big prey items were only recorded at the end of the breeding season in Finland, indicating that only females could manage them (Kellomäki 1977). Pygmy Owls may carry Great Spotted Woodpeckers whole to the caching place, working the prey up to the nestbox bit by bit (Heggelund 1975). However, big prey items were usually cut up before being carried to the caches, and sometimes also dispersed in several caches (Ahlbom 1970, own obs.).

4.3. Prey choice

Pygmy Owls have been reported to prey upon 26 mammal and 72 bird species (Glutz von Blotzheim 1980). As a generalist predator the Pygmy Owl may be expected to exploit the most easily caught prey species. In this study, Bank Voles dominated the winter diet. This was also found by Arnekleiv (1978) and Korpimäki (1980). Also the choice of birds seems to be similar to that found by Arnekleiv (1978) and birds only dominated in years of low vole populations (Table 3).

Kellomäki (1977) found that Pygmy Owls also preyed upon animals other than voles in years of high vole populations. He explained this as an adaptation to breeding in low-productive woodlands. Thus Pygmy Owls could not be food specialists. My own results, however, indicate that the boreonemoral areas of high productivity have the highest frequencies of Pygmy Owl wintercaching (unpubl. data) and breeding (Solheim 1984) in years of low and intermediate vole abundance. The food choice of Pygmy Owls may better be explained as a functional response, i.e. Pygmy Owls hunt for and kill all prey species that happen to be available at the moment. This is also in accordance with the diversity of hunting techniques used by Pygmy Owls (Scherzinger 1974). If Pygmy Owls in general show functionalresponse hunting, great individual differences in prey choice should not be expected. My results seem to fit this prediction (Sect. 3.3), with Pygmy Owls showing greater similarities of food choice between localities within years than between years.

Kellomäki (1977) found hole-nesting birds to be more preyed upon by Pygmy Owls than expected from their availability. This may be caused by the greater vulnerability of incubating birds or young in the nest, which have no possible way of discovering a Pygmy Owl before it appears in the entrance hole. Prestrud (1975) watched a Pygmy Owl entering a nestbox with two adult starlings *Sturnus vulgaris* inside. One of them escaped, but the other was killed inside and later retrieved. Also Great Spotted Woodpeckers (Likachev 1971, Heggelund 1975, own obs.) found dead in nestboxes may have been surprised and killed on the spot. Prey species such as the Swift *Apus apus* (Lundberg 1947, Mikkola 1970, Kellomäki 1977) and Bats *Chiroptera* spp. (Kellomäki 1977) must also have been killed inside nestholes. Likachev (1971) reported that Pygmy Owls during breeding time regularly raided nestholes of Pied Flycatchers *Ficedula hypoleuca* and Great Tits *Parus major*.

4.4. Surplus killing

Surplus killing by Carnivores is often thought to be a rare event only occuring when certain conditions prevail (Kruuk 1972). This behaviour may be triggered when large numbers of prey are unable to escape the predator or if severe climatological conditions inhibit the normal antipredatory behaviour of the prey (Kruuk 1972). The surplus killing by Pygmy Owls seem to follow a different pattern from that of carnivores. The species composition of the biggest caches established by Pygmy Owls indicates that surplus killing takes place when one species or group of prey animals become more vulnerable than usual (Sect. 3.3). In 88.4 % of all observed caching incidents of American Kestrels, the raptor continued hunting after caching a prey item and once four frogs were observed to be cached during five hours (Collopy 1977). Observations from 1977/78 (Solheim unpubl.) showed that a Pygmy Owl cached 67 small mammals in 16 days, thus at least four prey items must have been cached during one day; the maximum number probably being much higher.

When discovering groups of accessible prey animals, Pygmy Owls will return to prey on the resource until it becomes totally exploited or nonprofitable. During breeding time a Pygmy Owl was observed to kill the last of ten young Wrynecks *Jynx torquilla* in their nest. The other young were already preyed upon (Sonerud et al. 1972). The same behaviour is observed in Little Owls *Athene noctua* (Burton 1983) and New Zealand Falcons *Falco novaeseelandiae* which returned to nests until all young were taken (Fox 1979). Thus it does not seem necessary for a Pygmy Owl to be in continually close contact with large numbers of prey unable to escape if they are to make surplus kills. To kill more prey than immediately needed seems to be a well defined part of Pygmy Owl behaviour, and it will take place in winter whenever there are prey to catch and nestholes to cache in.

4.5. Adaptive value of winter prey caching in Pygmy Owls

Food caching may be profitable if the chances of finding the same food later is greater if cached than if left were it is discovered (Moreno et al. 1981). Prey animals may be eaten by other predators exploiting the same resources. If a prey individual is left untouched by a predator, it will most surely move to some other location and the predator will have to seek it again. Phenological changes in habitat and climate may also make a prey item less vulnerable if left for a later confrontation by the predator. For a predator then, prey leftover is worth caching whenever the costs of catching new prey is higher than the cost of carcass defence. Brown Bears *Ursus arctos* hide carcass leftover from scavengers and other bears by burying them (Elgmork 1982) but, in areas of high bear density where carcasses would demand careful guarding caching seems to be absent (Elgmork 1983). During breeding, Pygmy Owls may cache prey leftover visibly in trees in the vicinity of the nest (Thönen 1965, Sonerud et al. 1972, Waag-Nilsen 1980). Such prey items may easily be detected and demand close guarding (Thönen 1965). Prey items may be more secure if stored in nestholes, but those are often occupied by other holenesters during breeding. In winter nestholes are usually empty and provide good caching sites for the Pygmy Owl. Winter caching in the Pygmy Owl may be an adaptation to its small body size and higher relative metabolism than that of bigger raptors. Roberts (1979) argues that caching should not take place if food resources are abundant. Pygmy Owl caching, however, seems to reach maximum intensity when prey species are most abundant or conspiciously vulnerable. The appearance of voles on top of the snow ccver varies greatly through the winter (own obs.), and the food caches of Pygmy Owls may compensate for fluctuations of prey availability.

Prey caching may also secure food resources when several predator species have similar prey preferences (Oksanen 1984). In the six localities studied, Tengmalm's Owls were common and Pygmy Owl caching may thus have been a way to minimize competition from a larger raptor.

4.6. Possible anti-predatory behaviour of bird prey of Pygmy Owls

As Pygmy Owls may represent a threat to other hole-nesting species, one might expect to find some kind of anti-predatory behaviour in such birds. The Pygmy Owl is seldom active at night, and birds may lower the predation risk from Pygmy Owls by entering their night holes after dusk. Nyholm (1968) observed that woodpeckers arrived at their night nestholes half an hour after sunset. This may primarily be caused by the birds exploiting the whole timespan of short winter days for foraging, but the effect is a reduced risk of being detected by a Pygmy Owl. Woodpeckers also choose trees with several nestholes, thus reducing their chances of location by a Pygmy Owl. Wood tits and Goldcrests *Regulus regulus* formed a major part of the bird prey of Pygmy Owls during winter (Sect. 4.3). Groups of Willow Tits *Parus montanus* and Crested Tits *P. cristatus* were heavily depleted during winter (Ekman et al. 1981). Hildén (1982) argues that Goldcrests make up only a small part of Pygmy Owls' diet in Finland, and that predation plays a minor part of the winter mortality of Goldcrests. However, small flocks of both Goldcrests (Hildén 1982) and wood tits (Lehtonen 1958, Ekman et al. 1981) form winter territories and a Pygmy Owl need not kill many birds before such a flock is completely devastated.

Separate winter groups of Goldcrests and tits have different moving velocities, but up to 64 % of Goldcrests observed in November to Janyary were associated with tits (Hildén 1982). Several tit species show interspecific competition and narrowed feeding niches when foraging together in mixed-species flocks (Alatalo 1982). In spite of different moving velocities and narrowed feeding niches, Goldcrests and wood tits are often found in associated winter flocks. Treecreepers *Certhia familiaris* also often join such flocks. Both single-species and mixed-species flocks of birds have a better chance relative to single birds of discovering approaching predators (Powell 1974). Under the assumption that the predation rate by Pygmy Owls is not positively correlated with flock size, being a member of a large flock will also reduce the risk of an individual bird falling prey to an attacking Pygmy Owl. The association of wood tits, Goldcrests and Tree-creepers in winter may thus be an antipredatory behavioural pattern acting to shorten the reaction time to sudden Pygmy Owl attacks and to reduce the risk of death for a given bird.

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