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Strategy of the Pygmy Owl while hunting avian and mammalian prey

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The hunting behaviour of pygmy owls was studied by following radio-tagged individuals. There was a seasonal change in their hunting strategy, which involved a switch between hunting mammals in summer and birds in winter. When hunting mammals owls acted as sit-and-wait predators, remaining perched for long periods and quite close to the ground. Hunting for avian prey was characterised by shorter perching times on higher perches in the trees. Pygmy owls attack from above, and predation risk for avian prey appears to be greater in the exterior and lower parts of a tree. This relative predation risk within the tree is of importance in interspecific competition for foraging sites in tits. Interspecific niche separation is likely to affect not only the access to food but the exposure to predation as well. The exposure gradient may be of importance for adaptations balancing the risk of predation and starvation.

1. Introduction

No other individual failure, such as being unsuccessful in finding food or in obtaining matings, has as great an influence on individual fitness as the failure to avoid a predator (Lima and Dill 1990). Since survival is the most important component affecting fitness (Clutton-Brock 1988), predation may be an important agent shaping behaviour and niche use in the coexisting boreal tits (genus *Parus*). During winter these birds live in mixed-species flocks and feed upon non-renewable food resources such as insects, spiders and hoarded seeds (Haftorn 1956; Jansson 1982). The species use different microhabitat niches in the tree. Coal tits *(Parus ater)* and goldcrests *(Regulus regulus)* forage in the outer parts of the branches, crested tits *(P. cristatus)* in the middle of the branches, willow tits *(P. montanus)* close to the trunk, and treecreepers *(Certhia familiaris)* on the trunk (Haftorn 1956; Hogstad 1978; Alatalo et al. 1985; Alatalo et al. 1987). The species show different morphological adaptations for an efficient use of their foraging niches in body size, beak shape and foot and leg structure (Palmgren 1932; Snow 1954, Haftorn 1956; Lack 1971; Partridge 1976; Norberg 1979; Herrera 1981). Flocking allows the tits to economise vigilance time (Ekman 1987; Hogstad 1988), suggesting that a trade-off between foraging and predation is important in determining winter habitat use and survival (Pulliam & Caraco 1984). As the food resources become depleted, the birds have to spend more time searching for food. This reduces the time left for predator vigilance (Caraco et al. 1980; Ekman 1987), leading to a

high mortality through predation during winter (Jansson et al. 1981). Whereas there are several behavioural studies of boreal tits, there are few studies on their predators' hunting behaviour.

In winter the pygmy owl *(Glaucidium passerinum)* is the main predator on tits of the coniferous forest. The owl preys to a larger extent on species that forage on the outer parts of the branches such as coal tits and goldcrests, than on birds like crested tits and willow tits that forage closer to the trunk, sheltered by branches (Ekman 1986; Suhonen et al. 1993). Since body size influences social dominance relations, larger species (crested tit and willow tit) can probably preclude smaller species (coal tit and goldcrest) from the microhabitats where they are least vulnerable to predators (Alatalo & Moreno 1987). The lower food abundance in the inner parts of the trees where the dominant species forage (Suhonen et al. 1992), suggests that dominant species trade food abundance and predation risk, while subordinate species have to forage in habitat niches more exposed to predation.

The pygmy owl is a diurnal sit-and-wait predator that attacks its prey from ambush (Mikkola 1983; Solheim 1984), and it feeds to a large extent on small avian prey in winter (Jansson 1964; Ahlbom 1970; Mikkola 1970; Kellomäki 1977; Solheim 1984; Ekman 1986; Moeckler & Anger 1992; Suhonen 1993). However, little is known about its behaviour and hunting strategy. In this paper, I present descriptive data on the hunting behaviour and seasonal variation in the prey choice of pygmy owls. This leads to a more comprehensive understanding of the relative predation risk within the tree for its potential avian prey, and makes possible an estimation of the actual predation risk of the prey birds during winter.

2. Methods

The study was conducted in the area around Tovetorp Zoological Research Station, in southeast Sweden (58°56'N 17°08'E). The area is dominated by coniferous forests of spruce *(Picea abies)* and pine *(Pinus sylvestris)*, including some deciduous trees like birch *(Betula pendula)* and aspen *(Populus tremula)*. Eight pygmy owls were equipped with radio transmitters during 1991–1994; four individuals in winter (October–March) and four in summer (April-September). In spring the owls were trapped by use of play-back and mist-nets, and in winter they were caught in nest boxes used for hoarding. Radio transmitters weighed 2.5–3.0 grams (4–5% of the weight of a pygmy owl) and were mounted as back-packs. In pygmy owls, females are larger than males (Cramp 1985), thus owls were sexed using weight and wing length measures.

Owls were located and then followed within 30 meters. Human presence was not considered a significant disturbance, because the owls often moved towards me and sometimes killed prey close by. I estimated perch height in meters and recorded perch time in the trees and observed hunting behaviour (one owl studied during winter was excluded from the analyses because of fewer than 10 perch observations). Observations were made in daylight hours, 0300 to 2200 in summer and 0600 to 1 800 in winter. Individuals were studied from 10 days up to four months and they were observed for a total of 118 hours in summer and 66 hours in winter (Table 1). In summer, automatic cameras were mounted at five pygmy owl nests to record activity and prey items brought to the nest. When recording activity during winter, I followed the owl to the roost in the evening and returned immediately before daybreak to record activity in the morning. Besides direct observations of hunting events, prey choice in winter were also recorded by identifying cached prey items in nest boxes and natural cavities. Snow cover was poor during the first two winters (1991/92 and 1992/93), whilst there was up to 30 centimeters of snow during the last winter (1993/94).

3. Results

3.1. Seasonal change in prey choice

The pygmy owls showed a seasonal shift in diet from eating mostly rodents during summer to mostly small passerine birds during winter. In summer, more than 55% of the prey items brought to the owl nests consisted of small mammals, mainly voles *(Microtus agrestis* and *Clethrionomys glareolus),* but also mice *(Apodemus* sp.)

and shrews (*Sorex* sp.). However, a substantial portion of the summer diet was composed of birds (43%, both adults, nestlings and fledglings). In addition, one of the breeding males brought some lizards to the nest (Table 2). In winter, the owls preyed on birds to a larger extent than in summer ($p = 0.012$, chi-square = 6.35, df = 1; Table 3). This comparison is based only on observed hunting events and cached prey items, which is the only data I have from winter. If prey items recorded by automatic cameras at the nests in summer are added (Table 2), my conclusions are substantially reinforced ($p = 0.0001$, chi-square = 16.86, df = 1).

3.2. Hunting behaviour

In summer the activity of breeding owls peaked at dawn and dusk. The only time when I recorded no activity at the nest was during one hour in the middle of the night (Fig. 1). During winter an owl alternated between, on average, four night-roosting holes. The owls entered their roost at dusk and left it at dawn and were never seen to use the same roost two nights in a row. The owls I followed to their night roost were all found in that same hole the following morning (observed four times for each of the three owls during winter). Thus, both in summer and winter the owls were diurnal.

Table 1. Sex, home range area, total number of observation hours, total number of perch observations and study period for each pygmy owl. Home range areas of the pygmy owls were calculated with minimum convex polygon (Harris et al. 1990) based on all locations of the owls during the study.

Sex	Home range area (ha)	Observation hours	Perch observations	Study period
female	95	14	8	1/12–11/12–91
male	217	50	121	11/4–13/5–92
male	245	50	111	11/5–13/7–92
male	*1	8	25	20/5–30/5–92
male	*2	10	20	27/5–30/6–92
male	232	10	14	25/9–10/12–92
male	230	26	81	14/11–92–30/3–93
female	40	16	32	10/1–25/1–94

*1 This floater stayed in the study area for 10 days before it left the study area.
*2 This floater moved about 12.000 meters in one month before it disappeared.

Table 2. Number of different prey types recorded by automatic cameras at five pygmy owl nests.

Nest -year	Prey type Mammals	Juvenile birds	Adult birds	Lizards
N –92	18	14	8	0
K –93	38	2	9	4
F –93	105	29	45	0
S –94	8	10	5	0
F –94	36	25	13	0
total	205	80	80	4

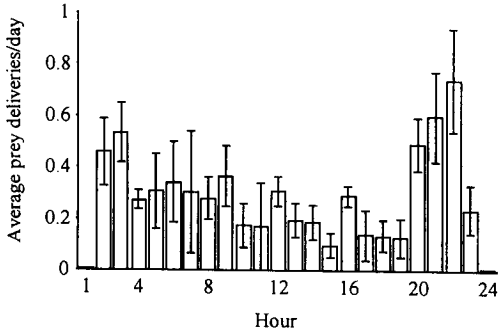

Fig. 1. Average number of food deliveries per hour (with standard error) by pygmy owls to their nest. Data from a total of 56 days of camera recording at five nests, n = 5.

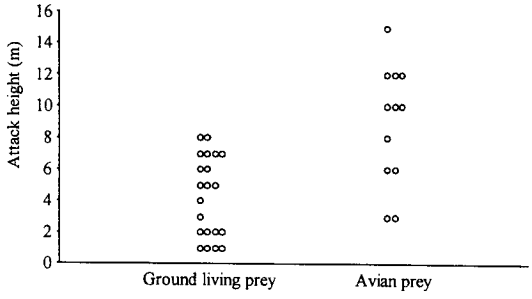

Fig. 2. Observed attack heights for different prey types.

The owls seemed to locate flocks of birds by their contact calls, then move closer and roam along the fringe of the bird flock until an opportunity to attack from ambush appeared. The general movements of pygmy owls can be characterised by short gliding flights (about 5 to 50 meters) between perches in trees. The pygmy owls used a hunting strategy where they attacked with a height advantage. When hunting mammals the owls acted as sit-and-wait predators, staying perched quite close to the ground for long periods before attacking or moving on. To gain a height advantage when hunting birds, the owls moved upwards in a tree close to the prey to be attacked, and thus attacked from a higher perch when hunting avian prey than when attacking prey on the ground (Mann-Whitney U-test; $p = 0.001$, $z = -3.23$, based on a total of 12 observations from two owls attacking avian prey, and on a total of 21 observations from three owls attacking ground living prey; Fig. 2). In accordance to the "height advantage strategy" the owl attacked birds significantly more often downwards than upwards (observed number of attacks upwards = 0, observed number of attacks downwards = 8; two-tailed binomial test: $p = 0.008$). Furthermore, when birds passed within one meter above the owls, the owls were never observed to attack (n = 4).

In accordance with the observed difference in prey choice between seasons the owls used different hunting strategies in winter and summer. In winter when mainly hunting birds, owls perched for shorter times compared to summer (Mann-Whitney U-test, $p = 0.03$, $Z = -2.12$, based on a total of 263 observations from four owls in summer (n = 4) and on a total of 102 observations from three owls in winter (n = 3); Fig. 3). Moreover, the combination of a "height advantage" and hunting for avian prey entailed that the owls perched higher in the trees in winter compared to summer (Mann-Whitney U-test, $p = 0.05$, $Z = -1.94$, based on a total of 277 observations from four owls in summer (n = 4) and on a total of 127 observations from three owls in winter (n = 3); Fig. 4).

Only for the most studied owl individual during winter was there enough observations to calculate attack frequency and hunting success. This owl moved, on average, 432.5 meters/hour; SE = 54.2; n = 15 (measured by adding the interperch distances the owl covered within an hour), had an average attack frequency of 0.42 times per hour (SE = 0.11, n = 15) and was successful in 3 out of 11 attacks (27%). All these attacks were towards birds.

Table 3. Number of prey observed killed and found cached by pygmy owls in winter and summer.

	Mammals	Adult birds
Winter	7	12
Summer	17	4

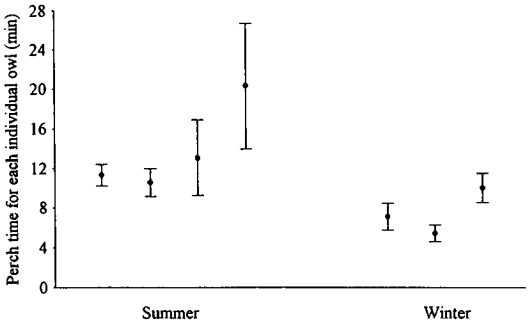

Fig. 3. Average perch time in minutes with standard error for the individual owls in summer and winter.

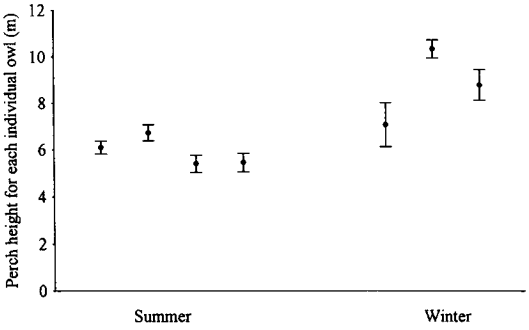

Fig. 4. Average perch height in meters with standard error for the individual owls in summer and winter.

4. Discussion

Rodents were the main prey of pygmy owls in summer, but in winter birds predominated. Similar results have been reported from several places in Europe (Germany: Moeckler & Anger 1992; Sweden: Ahlbom 1970; Ekman 1986; Norway: Solheim 1984; Finland: Mikkola 1970; Kellomäki 1977; Suhonen 1993). Other small- and medium-sized owls have larger proportions of mammals and smaller proportions of birds in their diet, and prey upon larger bird species than the pygmy owl (Mikkola 1983; Selås 1993). The switch in prey choice between seasons is probably due to several factors making birds more profitable to prey upon than rodents during winter. During short, cold winter days, small birds suffer from energy shortage (Jansson et al. 1981), and wintering tits cut back on vigilance to acquire sufficient energy so as not to starve to death during the night (Ekman 1987). Since predator vigilance impinges on the time left for foraging, birds are forced into a trade-off between vigilance and foraging. More time feeding entails lower vigilance and thus higher predation risk (Jansson et al. 1981; Ekman 1987). Energy stress may hence make birds easier prey to catch in winter than in summer (Houston & McNamara 1987). Since pygmy owls are active mainly during the light hours, the hunting period in winter is limited to the short daytime (7 hours), whilst in summer they hunt both day and night. This makes night active rodents less exposed to pygmy owls in winter compared to summer. Moreover, rodents are protected by the snow cover in winter. Pygmy owls, as well as hawk owls *(Surnia ulula),* lack the bilateral ear asymmetry that enables the larger owl species to locate prey in total darkness or subniveally (Norberg 1977; Sonerud 1986). Furthermore, their small size makes it hard to plunge deep into the snow as great grey owls *(Strix nebulosa)* do when hunting voles (Hildén & Hero 1981). Vole-hunting success of hawk owls decreased from 1.04 prey per hour on snow-free ground to 0.24 prey per hour on snow-covered ground (Sonerud 1986).

During summer the pygmy owls acted as "sit-and-wait predators", sitting motionless, low down in the trees for a long time, and waiting for voles and mice to appear. Birds are likely to be a more mobile prey than rodents, and during winter pygmy owls adopted a different hunting strategy. They followed bird flocks higher up in the tree canopy until an opportunity to attack from ambush from above appeared. By using attack frequency, hunting success and movement distances of one owl during winter I estimated the risk for a tit flock in the owl´s home range to be attacked during a day to 44%, and the risk for a tit flock to lose one member during a day to 12% (see appendix). To calculate the individual-specific risk to be killed, one has to divide 0.12 with flock size (which varies between flocks and also in time within a flock). This calculation is based on the assumption that pygmy owl territories are non-overlapping. If taking into account other avian predators in the area, including other pygmy owls, the predation risk will be even greater. Thus, even if this calculation assumes that

the pygmy owl searches thoroughly within its whole home range and there is no overlap in hunting route, avian predation can be considered an important factor affecting tit mortality during winter.

The hunting strategy of pygmy owls entails that the risk for a prey of being captured by an attacking pygmy owl depends on its position in the tree. Predation risk will be greater in the exterior and lower parts of the trees than closer to the trunk and higher up in the tree as a result of the "height advantage strategy" of attacking from above. In accordance with this, Ekman and Askenmo (1984) have shown that dominant willow tits expel subdominants from the upper and inner parts of the tree, forcing them to forage further out on the branches where they thus are more exposed to avian predators like the pygmy owl. That is probably why subordinates, despite spending more time being vigilant than the dominant willow tits (Ekman 1987), suffer from higher mortality during winter (Ekman & Askenmo 1984; Koivula & Orell 1988).

Pygmy owls prey upon a larger proportion of coal tits and goldcrests, foraging on the outer parts, than on crested tits and willow tits, foraging on the inner part of the branches (Ekman 1986; Suhonen et al. 1993). Since food abundance is lower in the inner parts of the trees (Suhonen et al. 1992), the relative difference in predation risk within the tree forces birds to do a trade-off between predation cover and food abundance. This trade-off has probably been of importance to how tit species have adapted to different microhabitats. Small tits feeding in exposed sites, where food is abundant but predation risk is high, have specialised on efficient foraging and a high predator vigilance. Larger tits, on the other hand, can, because of their size, expel smaller species from the inner parts of the branches (Alatalo & Moreno 1987). Social dominance could be at the expense of efficient foraging, as sheltered feeding sites require less predator vigilance.

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Appendix

By using data from the most intensively studied pygmy owl during winter I have tried to estimate the risk for a bird flock to be attacked by a pygmy owl. These calculations assume non-overlapping home ranges, that the owl searches thoroughly within its whole home range, and that there is no overlap in hunting routes. If the owl can hear the tits contact call from 50 meters and moves 432.5 meters per hour it would be able to search 4.3 ha during one hour. Since the winter territory of a tit flock is about 25 ha (Ekman 1979), the owl would need 5.8 hours to search a tit flock territory. The home range of the pygmy owl was 230 ha and thus covered about 9 tit territories. With a day length of 7.5 hours the risk that the owl will hunt in a specific tit territory during a given day is $(7.5/5.8)/9 = 0.14$. With an attack frequency of 0.42 per hour, the risk for one tit flock to be attacked during a day is $0.42 \times 7.5 \times 0.14 = 0.44$, and since the hunting success was 27%, the risk that a member of the flock actually gets killed will be $0.44 \times 0.27 = 0.12$.

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