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Provisioning response to manipulation of apparent predation danger by parental Pied Flycatchers

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We tested whether nest visitation rate of parent Pied Flycatchers (*Ficedula hypoleuca*) is decreased by an experimentally increased predation risk. We simulated predation risk by placing a stuffed Pygmy Owl (*Glaucidium passerinum*) in the nest vicinity and by playback of pygmy owl's whistling. We used Blackbird (*Turdus merula*) treatment as a control. Surprisingly, the parental nest visitation rate was about 25% higher in the treatment than in the control group. The treatments were reversed on the same day. Pairs of the "control treatment" in the first phase increased their nest visitation rate by 16% as a response to the "owl treatment". Four possible explanations exist. Parents may increase delivery in order (1) to silence the begging of the nestlings, who might otherwise betray the nest location to the owl, or (2) to increase the growth rate of the nestlings so that they fledge sooner, probably disperse better and so elude the danger. Alternatively, (3) the parents may view a predator as a threat to themselves, and remain in the vicinity of the nest where they are most familiar and therefore safest. In addition, (4) increased nest visitation might form part of nest defense behaviour against the owl.

1. Introduction

In raising offspring, parents must often undertake risks that endanger future reproduction (Lima & Dill 1990, Magnhagen 1991). Parents of altricial nestlings face danger both while provisioning and in defending the nest against predators. A number of studies have investigated nest defence and found that the intensity of defence varies in accordance with life history predictions based on factors such as the reproductive value of the brood (e.g. Curio *et al.* 1985), the hunger of the brood (e.g. Listøen *et al.* 2000), or the proximity to predator nests (e.g. Rytkönen & Soppela 1995), but few studies have examined whether parents change provisioning in response to predation danger.

Generally, one might expect parents to reduce provisioning under predation danger (e.g. Clark & Ydenberg 1990). Parent Atlantic Puffins (*Fratercula arctica*)for example, reduce the time spent at the breeding colony in response to the danger posed by greater Black-backed Gulls *Larus marinus*, and the young fledge at a lower mass (Harris 1980). Rhinoceros Auklets *Cerorhinca monocerata* in colony areas where Bald Eagles *Haliaeetus leucocephalus* endanger parents fledge younger and smaller than in low predation risk areas (Harfenist & Ydenberg 1995). However

Martindale (1982) suggested that provisioners should increase the nest visitation rate and reduce load size. Though his analysis applied specifically to defense against conspecific nest-usurpers, the model could be applied more generally (Martin 1992).

Here we report a field experiment on Pied Flycatchers (*Ficedula hypoleuca*), in which we simulated the presence of a Pygmy Owl (*Glaucidium passerinum*) near the nest, and measured the subsequent rate of nest visitation. Along with Sparrowhawks (*Accipiter nisus*), Pygmy Owls are the main diurnal predators of small birds in northern European forests (Mikkola 1970, 1983, Kellomäki 1977, Korpimäki 1985, Marti *et al.* 1993), and pose a danger to both parental and nestling Pied Flycatchers. Parent flycatchers deliver prey (dipterans, caterpillars and spiders; see Lundberg & Alatalo 1992) to the nest, and defend against predators.

2. Material and methods

We conducted the study in summer 1998 on the island of Seili (60°14´N, 21°58´E), Nauvo, in the vicinity of Turku, south-western Finland, where some 300 nest boxes suitable for Pied Flycatchers (10 × 10 × 25 cm, entrance hole diameter 32 mm, placed 170–200 cm high) are available in 160 ha of mixed woodland. On the study site, there are 50 nest boxes suitable for Pygmy Owls (entrance hole diameter 45–50 mm). At least two were active, as we found Field Voles *Microtus agrestis* cached during preceding winter and early spring.

The experiment was conducted between 18 June and 6 July, 1998, when flycatcher nestlings were about 7 d of age. Nestlings fledge at 14–16 d. We selected 15 pairs of Pied Flycatcher nests, matched for brood size and age. One nest was randomly assigned to the 'owl first' treatment group, in which we placed a stuffed Pygmy Owl in the front of the nest (2–3 m) for one minute. After removal of the owl, we played-back the whistling call of a Pygmy Owl at a distance of 20 m for 4 h. The other nest was assigned to the 'Blackbird first' group (control), in which we placed a stuffed Blackbird *Turdus merula* 2–3 m from the nest for one minute, and thereafter played-back blackbird song at a distance of 20 m for 4 h. At the end of this 05.00–09.00 period we reversed the treatments and repeated the procedure (09.30–13.30) to examine whether exposure to a predator had long-lasting effects (e.g. nest visitation rates in the Blackbird control group may differ due to preceding exposure to the Pygmy owl). Thus each nest was successively exposed to both presentations on the same day, in balanced order. Each pair of nests was tested only once.

We measured the nest visitation rates of parents over the 8 h trial using an automatic recorder mounted on the entrance hole of the nest-box, and connected to a data-logger. We placed the recorder on the nest on the day before the experiment to habituate parent birds to the equipment. The apparatus used a light beam and recorded in each 30 s period how many seconds the entrance hole was closed (light beam interrupted). We assumed that each 30 s period with any interruption corresponds to one nest visit, regardless of how many seconds the entrance hole was closed. In four nests directly observed for 6 h (3 h in both Blackbird control and treatment groups; a total of 363 feeding trips were observed), the visually-observed feeding frequency of parents did not differ from that recorded by the data loggers (mean 0.49/min SE = 0.11; and 0.52/min SE = 0.06, respectively; Mann-Whitney U-test, U = 11.00, P = 0.31), confirming that the method gave accurate measures.

At the same time, we also confirmed that both female and male parents were feeding young "normally" at each nest, by entering the nest-box in a similar way both in the Blackbird and Pygmy Owl groups. Although based on a small sample size, we did not observe any behavioral differences in feeding trips at the nest between the Blackbird and Pygmy Owl periods (e.g. no differences in alarm call rates or unsuccessful feeding trips etc.). Unfortunately, due to poor visibility on bushy territories, we were unable to quantify the behavioral responses between control and experimental periods accurately with a larger sample size (e.g. sex related differences during the experiment).

The entrance hole of the flycatcher nest-boxes was too small to allow Pygmy Owls to enter, and so nestlings in the boxes were safe from owls. Parents, however, may not discriminate whether small entrance hole is accessible to Pygmy Owls, especially because in old natural cavities owls may enlarge entrance holes making it accessible to them. Therefore, we predict that during the experiment both parents and nestlings were exposed to predation danger. This is also supported by the fact that parents responded to the owl mount very effectively with alarm calls, and movements around the mount (see Listøen *et al.* 2000).

Statistical analyses were performed using SAS 6.10 statistical package (SAS Institute Inc. 1990). All tests were two-tailed. We report group means and standard errors (mean ± SE) below. Sample sizes differ slightly in some analyses because in three cases the playback unit failed for short periods while broadcasting the call of Pygmy Owl.

3. Results

The treatment groups were well-matched. There was no difference in the number of nestlings between 'owl first' and 'Blackbird first' nests (5.73 ± 0.25 vs. 5.73 ± 0.25; paired t-test, t_{28} = 0,00, P = 1.00). Neither were there differences in the wing length or body mass of the nestlings (wing length, 20.96 ± 1.54 mm vs. 20.71 ± 1.34 mm; body mass 10.34 ± 0.44 g vs. 10.31 ± 0.36 g, respectively; all comparisons by paired t-test, df = 28, all P > 0.90).

Despite that parents responded very effectively to the owl mount, the beginning of visitation rates between the treatment and control groups did not differ. It took on average 5.33 min (± 1.27, range 2–18 min, n = 15) to visit the nest after exposure to the owl, and 5.40 min (± 0.87, range 2–14.5 min, n = 15) to do so after exposure to the Blackbird, a non-significant difference (independent t-test, t_{28} = 0.04, P = 0.967). To get accurate and unbiased estimates on feeding rate, the model presentation was not included in the nest visitation rates. Therefore, we excluded the first five minutes after the mount presentation from the analyses below.

The main results are summarized in Table 1. In the initial 4h phase, the parental nest visitation rate of the 'owl first' treatment group was significantly higher than that of the 'Blackbird first' group (0.55 ± 0.10 visits per min, n = 12 vs. 0.41 ± 0.11, n = 15, independent t-test, t_{25}= 3.40, P= 0.002). After the treatments were reversed, parents initially exposed to the Blackbird increased their provisioning rate from 0.41 (±0.11) visits per min to 0.49 (±0.17; n = 15, paired t-test, t_{28} = 2.67, P = 0.02) in response to the Pygmy Owl treatment. In contrast, parents first exposed to the owl did not change their nest visitation rate after exposure to the Blackbird (0.55 ± 0.10 visits per 1 min vs. 0.55 ± 0.13, n = 12, paired t-test, t_{22} = 0.40, P = 0.70). The nest visitation rate re-

Table 1. Nest visitation (visits per min) of parent Pied Flycatchers after simulated owl and blackbird presence near their nest-boxes. The overall rate is the visitation rate over the entire 4h phase, and we also report the rates in each hour of each phase.

		Overall	Hour 1	Hour 2	Hour 3	Hour 4
OWL FIRST TREATMENT						
Phase I (owl)	mean	0.55	0.53	0.55	0.53	0.55
	SE	0.10	0.16	0.13	0.14	0.09
	n	12	14	13	13	13
Phase II (blackbird)	mean	0.55	0.55	0.54	0.56	0.55
	SE	0.13	0.12	0.13	0.17	0.15
	n	13	13	13	13	13
BLACKBIRD FIRST TREATMENT						
Phase I (blackbird)	mean	0.41	0.43	0.40	0.41	0.43
	SE	0.11	0.13	0.13	0.12	0.14
	n	15	15	15	15	15
Phase II (owl)	mean	0.49	0.50	0.48	0.51	0.49
	SE	0.17	0.19	0.17	0.19	0.22
	n	15	15	15	15	14

mained rather steady during each treatment period (see Table 1), so the differences cannot be due to the parent flycatchers staying away from their nests for different periods after initial exposure to the owl or Blackbird (cf. Listøen *et al.* 2000), and then resuming normal activity.

4. Discussion

The results show that the provisioning behavior of Pied Flycatcher parents responded differently to the experimental simulation of Pygmy Owl presence than to the experimental simulation of Blackbird presence. The results suggest that nest visitation increased after exposure to the owl: this was apparent between treatment groups ('owl first' and 'Blackbird first') in the initial 4h period, as well as within nests between the two 4h periods in the 'Blackbird first' treatment. In contrast, the 'owl first' treatment group did not reduce the nest visitation rate after exposure to the Blackbird treatment.

The flycatcher parents did not necessarily increase their nest provisioning, however. Johnson and Swihart (1989) recorded the trip length and load size delivered by parental American Robins (*Turdus migratorius*) close to and far away from an American Kestrel (*Falco sparverius*) nest and observed that the pair (one of three) near the kestrel nest made longer provisioning trips (i.e. lower nest visit rate — opposite to what we recorded), but delivered larger loads. We did not measure the amount of food delivered. Parents may or may not have changed their selection of prey for delivery in our experiment, and the increase in nest visitation rate may have increased the delivery rate; or it may have been unable to offset completely the reduction in delivery rate caused by altered prey selection. Nest visitation is not a good estimate of delivery in parids, for example (e.g. Royama 1966, Bengtsson & Ryden 1983, Blondel *et al.* 1991) or other birds (e.g. Tolonen & Korpimäki 1994). Also, Pied Flycatchers may visit nests without food (e.g. von Haartman 1954), though the proportion of nest visits without food in the Pied Flycatcher is low in southern Finland. For example, a total of 934 video-recorded nest visits during the nestling phase revealed only 56 nest visits without food, i.e. 6.0% (T. Eeva; unpubl. data). Our direct field observations suggested that parental feeding behaviour was similar between the treatment groups, but a modest change in the rate of non-provisioning visits may have not been detected by our method.

Our results match the predictions of Martindale's (1982) model, in which parents shorten the duration of provisioning excursions in order to obtain a benefit from increased presence around the nest. Four specific benefits can be proposed. Parents may increase delivery in order to silence the begging of the nestlings, who might otherwise betray the nest location to the owl (e.g. Young 1996, Briskie *et al.* 1999). Increased delivery may also increase the growth rate of the nestlings so that they fledge sooner, probably disperse better and so elude the danger. Alternatively, the parents may view a predator as a threat to themselves, and remain in the vicinity of the nest where they are most familiar and therefore safest. A final possibility is that the increased nest visitation might form part of nest defense behavior against the owl. In this case we expect the parent flycatchers to have sacrificed some of the potential delivery rate in order to improve nest defense, either by restricting foraging to sites close to the nest box, by selecting smaller prey for delivery so that shorter trips are made, or by giving up some other activity. Discriminating between these hypotheses, however, will require complete measures of provisioning (frequency and size of deliveries), as well as a better understanding of how parents view the danger.

Behavioral responses of parents were not carefully examined in the present study, which should be taken into account in the future experiments on the predation risk effects on provisioning rate of birds. This could happen, for example, by including a true control without any treatment, when it is possible to compare experimentally manipulated food delivery and behavioral responses to natural non-manipulated conditions. Video recording would also ensure whether parents enter the nest-box with or without food between different treatments. To ensure this, we had observational data from four nests only, where parents seemed to show normal feeding behavior. Repeating the experiment with other predators would also be informative. For example, nestlings in cavities are safe from Sparrowhawks, while fledglings and adults are probably immune to weasels outside the nest cavity.

Parental nest visitation rate in the Blackbird control following the Pygmy Owl treatment stayed at a high and constant level. We suggest two possibilities for this. Firstly, parents continue to be affected by the predator even when it is no longer an immediate threat. Secondly, parents in the preceding Pygmy owl treatment, despite high nest visitation rate, may have decreased their provisioning *per se*, when parents may try to compensate for the increased hunger levels of their nestlings in the following Blackbird period.

The scientific literature on avian breeding, foraging behavior, and predation risk is extensive, but theory about how provisioners manage predation danger remains rudimentary, in spite of the potential implications for important topics like clutch size (e.g. Lima 1986), nest site selection, metabolic rates and others (see Ydenberg 1994). It seems that parents are likely to alter several aspects of their behaviour, and simple experiments like that described here will be most useful in helping to describe and understand their responses.

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Selostus: **Kokeellisesti lisätyn petouhan vaikutus kirjosiepon (*Ficedula hypoleuca*) pesälläkäyntien määrään**

Testasimme Turun lähistöllä vuonna 1998 vähentääkö kokeellisesti lisätty petouhka kirjosieppoemojen (*Ficedula hypoleuca*) pesälläkäyntien määrää. Petouhkana oli täytetty varpuspöllö pesän läheisyydessä ja lisätehosteena toimi varpuspöllön soidinääninauhoite. Samanlaisin järjestelyin mustarastas (*Turdus merula*) toimi kontrollina. Oletimme, että keinotekoisesti lisätyn petovaaran tulisi vähentää emojen pesälläkäyntiaktiivisuutta. Tämä vähentäisi sekä emoihin että poikasiin kohdistuvaa saaliiksijoutumisriskiä. Vastoin odotuksiamme, "petouhka" –ryhmässä emojen pesälläkäynnit lisääntyivät 25% kontrolliryhmään verrattuna. Myös samana päivänä kontrollikäsittelyn jälkeen tehty "varpuspöllö – käsittely" lisäsi emojen pesälläkäyntien määrää 16%:lla. Esitämme neljä mahdollista selitystä tuloksillemme. Emot lisäävät ruokintatehokkuutta (1) hiljentääkseen poikasten ruoankerjuuta, mikä voisi paljastaa pesän sijainnin pedolle, tai (2) ne yrittävät lisätä poikasten kasvua, jotta ne olisivat lentokykyisiä aikaisemmin ja mahdollisesti voisivat dispersoida kauaksi petoriskialueelta. (3) Emot voivat myös pysytellä pesän lähistöllä, jossa ne ovat paremmin turvassa tutussa ympäristössä pesän läheisyydessä tai (4) lisääntyneet pesälläkäynnit voivat olla osa pesänpuolustuskäyttäytymistä pöllöä vastaan. Tulos vaatii lisäselvitystä, sillä esimerkiksi pesälle tuotujen saalislastien kokoa ja määrää ei pystytty tässä tutkimuksessa selvittämään, joten on mahdollista, että emojen pesälläkäynnit petouhkaryhmässä lisääntyivät pienentyneen saaslislastikoon vuoksi.

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