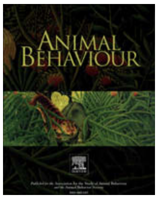
Animal Behaviour 77 (2009) 43–47

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe



Is parental risk taking negatively related to the level of brood reduction? An experiment with pied flycatchers

Vallo Tilgar*, Kairi Kikas

Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu

ARTICLE INFO

Article history:
Received 19 March 2008
Initial acceptance 10 June 2008
Final acceptance 25 August 2008
Published online 30 October 2008
MS. number: 08-00195R

Keywords:
brood reduction
Ficedula hypoleuca
mortality
pied flycatcher
predation risk
reproductive value hypothesis

Predation risk is an important factor affecting investment decisions in wild birds. The parental risk-taking response is assumed to depend on the value of the current brood, but to date empirical studies have yielded equivocal results. We tested the 'reproductive value of the offspring' (RV) hypothesis by assuming that parents perceive the probability of offspring survival as a significant component of RV. We predicted that survival of offspring as perceived by parents would be inversely related to the level of brood reduction. Accordingly, parents with the same number of offspring may take fewer risks if they have lost offspring than if they have not. We experimentally reduced brood size in a small passerine, the pied flycatcher, *Ficedula hypoleuca*, and exposed parents to a stuffed sparrowhawk, *Accipiter nisus*, a predator of adults. For a given brood size, the time elapsed until parents first entered the nestbox after removal of the predator was positively correlated with the level of brood reduction. Parental risk-taking behaviour was not affected by brood size per se when adjusted for the level of brood reduction. No sex-related differences in antipredator responses were found. To our knowledge, this is the first experimental evidence that birds are capable of perceiving brood reduction and of adjusting their antipredator behaviour to the changed value of their offspring.

Theoretical models of life history evolution predict that the resolution to the parents' dilemma of whether to place themselves or their offspring at greater risk of mortality when threatened with predation will depend on the reproductive value of the offspring (RV) and their own probability of survival. Empirical studies on fishes (Carlisle 1985) and various species of birds (raptors: Wallin 1987; Wiklund 1990; penguins: Amat 1996; passerines: Montgomerie & Weatherhead 1988; Dale et al. 1996; Lambrechts et al. 2000; Rytkönen 2002) have supported this concept by finding positive relationships between parental risk taking and different measures of 'reproductive value' such as brood size, offspring age and condition.

In birds, the reproductive value of the brood can also depend on nest predation risk which might affect offspring survival. For example, early breeders would be expected to take greater risks than late breeders because the probability of breeding failure increases as the breeding season progresses (Wallin 1987; Wiklund 1990). The level of brood reduction per se can also change the expected fitness value of the offspring, but the evidence for this is poor. Chinstrap penguins, *Pygoscelis antarctica*, and great tits, *Parus major*, reduced nest defence intensity after losing one or more eggs (Curio 1987; Amat 1996; but see Wallin 1987 for tawny owls, *Strix aluco*). However, these studies were not specifically designed to investigate the impact of brood reduction on parental risk-taking behaviour while accounting for differences in current offspring number and quality.

Furthermore, the RV hypothesis based on brood reduction can also provide an alternative explanation to largely accepted traditional ones. For example, given that the number of living offspring is usually negatively related to the number of dead offspring, we can speculate that parents do not count their offspring but that they perceive the reduction of brood size per se as a danger or threat to the surviving offspring. Hence, parents with the same number of offspring may take fewer risks if they have lost offspring than if they have not.

Brood reduction is common in many bird species (Stenning 1996; Gebhardt-Henrich & Richner 1998). Partial brood loss is mainly caused by starvation of the smallest chicks from food shortage or harsh weather conditions (e.g. Sheldon et al. 1998; Rytkönen & Orell 2001), but parasites (Merino & Potti 1995) and nest predators (Watt 1980; Halupka 1998; Walankiewicz 2002; Thompson & Burhans 2003; Zanette et al. 2006) can also be the cause. It can be assumed that the mechanisms of nestling mortality can influence parental risk-taking decisions. Sudden disappearance or death of nest-bound offspring can be perceived by parents as an indicator of a risky environment and a potential threat to living nestlings, whereas starvation leading to the death of the runt of the brood may have only a slight effect on parental behaviour.

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* Correspondence: V. Tilgar, Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, Tartu 51014, Estonia.
E-mail address: vallo.tilgar@ut.ee (V. Tilgar).

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doi:10.1016/j.anbehav.2008.08.027

Our aim in this study was to test experimentally whether brood reduction per se may affect parental risk-taking behaviour in a small passerine bird, the pied flycatcher, *Ficedula hypoleuca*. This species has frequently been used as a model species in antipredator studies (e.g. Dale et al. 1996; Listøen et al. 2000; Michl et al. 2000). Pied flycatchers have reasonably large brood sizes (6–7 nestlings) and about 13% of broods in our study area suffer some brood reduction with average nestling mortality about 15% (Mänd & Tilgar 2003). Although we have little information about the causes of nestling mortality in pied flycatchers, partial brood loss in this species is predominantly caused by starvation of the runts, and to a lesser extent by nest predators such as woodpeckers (personal observations). Natural tree cavities are more accessible to nest predators than are nestboxes (Lundberg & Alatalo 1992). Hence, the frequency of partial nest predation may be even higher in those populations breeding in natural cavities than predicted on the basis of our population breeding in nestboxes. To address the question raised above, we imitated partial brood loss and recorded parental risk-taking behaviour against a model of a sparrowhawk, *Accipiter nisus*. Specifically, we predicted that (1) for a given number of offspring, parental risk taking is negatively correlated with the level of brood reduction and (2) for a given level of brood reduction parental risk taking is positively related to the number of offspring. In testing these predictions, we determined whether there is a difference between the decision-making strategies of the two sexes. Previous studies on different passerines have found that males take significantly more risk for offspring in the late nestling phase than females (Onnebrink & Curio 1991; Michl et al. 2000; Hogstad 2005).

METHODS

Our study was conducted in coniferous forests in the surroundings of Kilingi–Nõmme (58°7′N, 25°5′E), southwest Estonia, in 2004 and 2005. The dominant tree species was Scots pine, *Pinus sylvestris*, but Norway spruce, *Picea abies*, and downy birch, *Betula pubescens*, were also present.

The pied flycatcher is a small (12–13 g), hole-nesting, short-lived, insectivorous and migratory passerine bird. The female builds the nest and incubates and broods alone, but both parents feed the chicks, which fledge within 14–16 days of hatching (Lundberg & Alatalo 1992). Pied flycatchers bred in nestboxes mounted on tree trunks at a height of about 1.5–2.0 m. The internal dimensions of nestboxes were approximately 11 × 11 cm and 30 cm high and the diameter of the entrance was 3.5–4.0 cm. Old nest material was removed each year. The distance between the nestboxes was usually 50–60 m. All nests were checked weekly to obtain data on the onset of egg laying and clutch size. We counted and weighed nestlings at day 13 posthatch (assuming hatch day = day 0). Nestlings were weighed (±0.1 g) with a Pesola spring balance. Parents were caught on their nests by using nestbox traps during the second half of the nestling period. They were also weighed and their tarsi measured. The complete data set contained 53 nests (the odd number is due to depredation of one brood before the risk-taking experiment). Both parents and chicks were ringed after measurements. As polygyny can affect risk-taking behaviour of both sexes, we studied socially monogamous pairs only.

Two stuffed specimens of sparrowhawks, *Accipiter nisus*, in a resting position were used in parallel. We chose this kind of predator to manipulate the predation risk because the sparrowhawk is a widespread bird of prey in the Baltic States (Krams 2000), including our study area (personal observation), and represents a serious threat to adult pied flycatchers (e.g. Slagsvold et al. 1995). Although the exposure of adults to a predator is dangerous only to parent birds, the interruption of parental care would decrease the condition of nestlings, potentially increasing mortality from starvation.

Risk taking as a parental restraint is influenced by many confounding variables related to environment and parental quality. Our experiment was designed to reduce the potential effect of confounding (both environmental and parental) factors by pairing the broods with regard to date of the first egg and similar clutch size (9 pairs in 2004 and 18 pairs in 2005). One brood was depredated before the risk-taking experiment and therefore we could not use a pairwise approach in the statistical analyses. For each pair, one randomly selected brood was reduced by two nestlings (on day 7 in 2004, and on day 2 in 2005), while the other brood was left unmanipulated. The nestlings' removal was imitated in control nests as well to control for the potential effect of nest disturbance in both groups. The two removed nestlings from each reduced brood were transferred to broods with the same hatching date, but not included in our analyses. In addition to experimental brood reduction, natural brood reduction occurred in three control and two manipulated broods. To describe actual brood reduction in a particular brood, we summed the nestlings that were experimentally removed from the nest (two nestlings) as well as those that died before the risk-taking experiment (0–2 nestlings). Accordingly, we use the term 'brood reduction' (the number of nestlings lost) instead of comparing the experimental group with the control group.

The parents were exposed to the predator models when the offspring were 10–11 days old. A stuffed sparrowhawk model in a sitting position was placed about 1–3 m from the nestbox, attached to the nearest tree trunk at a height of about 1.5 m. To avoid any potential effect of a specific sparrowhawk model, the presentation of models was randomized between experimental and control nests. The inclusion of the predator model as a factor in the analysis did not influence the parental risk-taking response (general linear mixed model, GLM: $F_{1,50} = 0.6$, $P = 0.5$; corrected for nest, sex and year), and therefore this predictor variable was omitted from subsequent GLM models.

The models were exposed for 20 min in 2004 and about 5–10 min in 2005 until both parents had noticed it (as indicated by their alarm calling). Parents with a sparrowhawk model present never entered the nest. As a response variable we measured the time between the moment of hawk removal and when the first parent entered the nestbox (e.g. Dale et al. 1996). Our observations confirmed that the parents enter the nestbox after predator removed to feed the nestlings. This time to resume feeding gives a direct measure of the stress imposed on nestlings by the interruption of parental care (e.g. starvation affects the nestlings' condition), whereas the intensity of alarm calling or mobbing, and the closest distance of approach to the predator are not necessarily related to nestling stress. The trial lasted 50 min after the removal of the model. Parental responses were recorded using digital video cameras. To accustom the birds to the presence of the camera we set it up 30 min before the experiment. The observers immediately left the experimental area and located themselves at least 150–200 m from the place of the experiment. The trials were spread throughout the day (0700–1700 hours) within the normal feeding time of the pied flycatcher (Lundberg & Alatalo 1992). Time of day did not influence parental response to the sparrowhawk model (GLM: $F_{1,50} = 0.03$, $P = 0.9$; corrected for nest, sex and year). The model was not exposed during rain.

Brood size manipulations did not influence parental reproductive behaviour and nestling quality. No brood was deserted after manipulation, and fledging success (Kruskal–Wallis ANOVA: $H_2 = 0.5$, $N = 80$, $P = 0.8$; calculated in relation to brood size after manipulation) and mean prefledging mass (GLM: $F_{2,78} = 1.7$, $P = 0.2$) did not differ between reduced ($\overline{X} \pm \mathrm{SE} = 13.92 \pm 0.15$ g, $N = 27$) unmanipulated (13.74 ± 0.16 g, $N = 26$) and enlarged broods