Sex-dependent risk taking in the collared flycatcher, *Ficedula albicollis*, when exposed to a predator at the nestling stage

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An increased mortality rate is a cost of parental care, and can be high during the provisioning phase of altricial nestlings. When a parent stops feeding the nestlings temporarily after seeing a predator, it can reduce its own predation risk, but the suspension of parental care may also reduce its offspring's chances of surviving. We modelled this situation by exposing a stuffed sparrowhawk near collared flycatcher nests and removing it when both parents had seen it. We measured the time (return time) between the removal and when each parent entered the nestbox. The parents' risk taking and the return time are assumed to be inversely related. We studied which brood variables the parents take into account when deciding how much risk they are willing to take during the provisioning period. Males took more risk for older and better-quality nestlings and earlier broods. The females' behaviour was opposite to that of the males: they took significantly less risk for older and better-quality offspring and visited the nestbox later for earlier broods. The males' behaviour supported the reproductive value hypothesis, that risk taking is related to brood value and survival chances, whereas the females' behaviour supported the harm to offspring hypothesis, that risk taking is related to the broods' vulnerability.

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Because of their restriction to a nest site, the majority of bird species are exposed to a high level of predation pressure during the breeding season. Nest predation is especially high amongst altricial species (Ricklefs 1969) and, in addition, the mortality rate of adults increases in proportion to their parental investment (Slagsvold et al. 1995; Slagsvold & Dale 1996).

Parent birds attempt to optimize the trade-off between their own reproductive value and the predation risk endangering them and their nestlings; however, the cost of such behaviour can be high. There are at least four trade-off situations where the risk from predation can be optimized.

(1) Some bird species seem to control the duration of the nestling period according to the degree of predation pressure. In those areas where the density of bald eagles, *Haliaëtus leucocephalus,* is high, the young of the rhinoceros auklet, *Cerorhinca monocerata,* leave the nesting burrow earlier than in areas where it is low. In this case there is a trade-off between the condition of offspring at fledging and the survival of the parents themselves (Ydenberg 1994; Harfenist & Ydenberg 1995).

(2) Those species where parents cannot control the duration of the nestling period (e.g. 13 days in the

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collared flycatcher) usually react only to the appearance of predators near their nest, regardless of predator density in the area. When a predator is present the parents may attack or mob it (Montgomerie & Weatherhead 1988; Forbes et al. 1994). Thus, there is a trade-off between injury to, or the death of, both parents, and the lower probability of current nest predation.

(3) Once the predator has left, the parents usually suspend parental care for a while. We call this behaviour danger-dependent suspended parental care. Dale et al. (1996) investigated this behaviour in both sexes of the pied flycatcher, *Ficedula hypoleuca*, and Bures & Pavel (1997) studied it in female meadow pipits, *Anthus pratensis*. The cost of risk taking in danger-dependent suspended parental care can depend on the type of predator (Dale et al. 1996). When the predator (e.g. snakes, dormice, mustelids, woodpeckers) poses a danger to the nest, the cost of this behaviour is significant damage to the clutch or brood (cooling of eggs or starvation of offspring), while the benefit is that the predator cannot discover the nest site by using the parent birds as visual cues. Thus, a trade-off exists between the extent of damage to, and predation of, the eggs or nestlings.

(4) On the other hand, those raptors (sparrowhawks, *Accipiter nisus*, goshawks, *A. gentilis*) that specialize in capturing small passerines can be considered dangerous solely to parent birds. In this case the cost of suspended

parental care is similar to that of nest predation: clutches and broods suffer if parental care is suspended. The benefit is that parents themselves avoid injury or death. Thus, a trade-off exists between the extent of harm caused to broods and the survival of the parents (Dale et al. 1996).

In the present study we focused upon the danger-dependent suspended parental care behaviour of the collared flycatcher, using a model that imitated a predator threatening adult birds. We assumed there are no intrinsic differences between the sexes that affects the probability of escaping from a predator. Male collared flycatchers are more conspicuous than females, but a study on a sibling species of similar colour (the pied flycatcher) did not suggest that the black-and-white males suffered a higher risk of predation than the duller brown females (Götmark 1992). At least four hypotheses may explain the consequences for the parents' fitness of temporarily ceasing parental care.

(1) The cost of renesting hypothesis states that the sex with the higher renesting cost will take greater risks than its mate (Barash 1975; Martin 1987; Rytkönen et al. 1993). In the collared flycatcher, the female builds the nest and incubates the eggs alone so a repeated breeding attempt means a larger cost for her than for the male. The predictions of this hypothesis for the collared flycatcher are: (a) early in the breeding cycle when the renesting potential is high, females take greater risks than their mates; and (b) early females take greater risks than late females in the same phase of breeding.

(2) The obligate parental duty hypothesis states that those birds whose investment cannot be compensated by their mate take fewer risks than their mates as their deaths would lower the survival of the offspring. In those species where the female broods the young alone, for example, she takes less risk than her mate, at least until the brooding period has ended (Regelmann & Curio 1986).

(3) According to the reproductive value of offspring hypothesis the risk taken by a parent bird is directly related to the brood size and/or probability of survival of the offspring. This hypothesis predicts that there will be an increase in risk taking (a) in consecutive stages in the breeding cycle (eggs, young nestlings, older nestlings), (b) with larger clutches and/or broods and/or better-quality offspring, and (c) in earlier broods (Andersson et al. 1980; Clutton-Brock 1991).

(4) The harm to offspring hypothesis (Dale et al. 1996) states that the more sensitive the offspring are to the disadvantage resulting from the suspension of parental care, the greater the risk the parent is willing to take. Predictions deriving from this are: (a) risk taking by a parent decreases through the various breeding stages of eggs, young nestlings, older nestlings, in accordance with the related changes in vulnerability; and (b) less risk is taken for nestlings in good than in poor conditions.

In testing these predictions we determined whether there is a difference between the decision-making strategies of the two sexes, and how much risk parent birds are willing to take to continue caring for their offspring when exposed to a predator during three phases of the nestling period (exothermic, early endothermic, late endothermic). We also examined whether the condition of nestlings and the timing of breeding influenced risk taking by the two sexes.

METHODS

Study Area and Species

We conducted the study from early May to mid-June 1997 on an artificial nestbox plot in a continuous oak woodland near Budapest, Hungary, where the dominant tree species is *Quercus petraea*. We placed boxes in a grid system 20–30 m from each other. They were fixed on trees about 1.5 m above the ground. The collared flycatcher is a small, single-brooded, long-distance migratory, insectivorous passerine. Sexes are dichromatic. Males arrive in Hungary in late April, a few days before females. There is a significant bias in parental care, with only females incubating and brooding the nestlings, whilst both sexes feed the offspring. According to our observations courtship feeding is very rare. During the egg laying and incubation phases, males seek extrapair copulations and attempt to become polygynous. As polygyny can affect risk-taking behaviour of both sexes, we studied monogamous pairs only.

Experiment

We used a stuffed adult female sparrowhawk to simulate the presence of a predator that preys on adult flycatchers. A stuffed mistle-thrush, *Turdus viscivorus*, was used as a control. We recorded the reaction of nest owners to these models between 0800 and 1200 hours. The models were placed ca. 2 m from the front of a box and ca. 1 m above the ground. In each trial a model was left in place until both parents had detected it and gave alarm calls. The observer then covered the model and carried it away to the hide, then recorded the time until the first entry into the nestbox by each parent (return time). Since collared flycatchers are very cautious, we made observations from a hide at least 40 m away. The disturbance caused by the removal had little impact on the outcome of the experiments as all birds were subjected to the same experimental procedure, and thus one would not expect systematic differences between groups (Dale et al. 1996). In analyses we used the return time which is the reciprocal value of risk taking. A trial was completed when each parent had entered the nestbox. We conducted 39 and 23 trials with the sparrowhawk and mistle-thrush, respectively. The data were omitted if only one parent was present during a trial or other bird species disturbed the experiment. The first bird to visit the nestbox was deemed the risk taker, the second the follower. All observations were independent as each pair was tested only once. The experiment was carried out under licence from Pilis Park Forestry.

The experiments lasted 8–24 min. Parents visit broods every 5–15 min in this species (our unpublished data) so the broods with six nestlings in our study missed only

Table 1. Mean times±SD that collared flycatcher females and males took to return to the nest after presentation of a sparrowhawk or mistle thrush during three physiological phases of the nestling period

	Female	N	Male	N
Sparrowhawk				
Ectotermic	5.1±2.75	12	19.0±2.09	12
Early endothermic	9.6±2.27	11	14.4±3.44	11
Late endothermic	9.4±6.34	16	10.2±4.73	16
Mistle thrush				
Ectotermic	1.8±0.99	8	1.6±0.82	10
Early endothermic	2.1±0.90	6	2.2±0.82	6
Late endothermic	1.9±0.96	7	2.3±1.39	7

one or two feeds per nestling during the whole nestling phase (13 days) because of our experiments. There was no difference in fledging success between experimental ($\bar{X}=0.88$, $N=62$) and nonexperimental broods ($\bar{X}=0.82$, $N=78$; Mann–Whitney U test: $Z=0.9$, NS).

We measured the risk-taking behaviour of parents at three nestling stages: exothermic (3–4-day-old nestlings, 12 broods), early endothermic (6–7-day-old nestlings, 11 broods) and late endothermic (10–11-day-old nestlings, 16 broods). After a trial in the late endothermic phase, each of the nestlings in a brood was immediately weighed with a Pesola spring balance (0.1 g accuracy). Broods were categorized as poor-quality broods (average nestling body mass equal or lighter than the median) and good-quality broods (nestlings heavier than the median).

We divided the data of broods in the late endothermic phase into two categories: early broods (first egg laid on or before median laying date) and late broods (first egg laid after the median laying date). For statistical tests we used Statistica for Windows (Statsoft 1994). All tests were two tailed.

RESULTS

Sparrowhawk and Mistle-thrush Models

To analyse the effects of the two types of stimulus birds and the three nestling phases on behaviour we performed a repeated measures ANOVA where phase and stimulus bird were the independent variables and return time of the two sexes the repeated factor. In all three phases of the nestling period, the return time was significantly greater when the sparrowhawk, rather than the mistle-thrush, was placed nearby (Tables 1, 2). When the birds were presented with the control, there were no differences in behaviour between the nestling phases (Tables 1, 2; Duncan test for interactions: NS). Although there was a significant interaction of stimulus bird × sex, this was caused by the difference in response given by the two sexes to the sparrowhawk model. With the mistle-thrush there was no difference between the sexes in any phase (Tables 1, 2; Duncan test for interactions: NS). In the presence of the sparrowhawk, parents never entered the box, whilst when the mistle-thrush was used, in three of 22 trials one or both parents visited the nestlings.

Table 2. Repeated measures ANOVA for the effect of stimulus bird (sparrowhawk and mistle thrush) and nestling stage (ectothermic, early and late endothermic) on behaviour of parents measured as return time of the two sexes as the repeated measures variable

Source	df	Mean square	F	P
Stimulus bird (1)	1	2279.73	249.85	<0.001
Breeding phase (2)	2	13.32	1.46	0.24
Sex (3)	1	297.64	20.50	<0.001
Interactions				
1, 2	2	18.09	1.99	0.14
1, 3	1	270.22	18.61	<0.001
2, 3	2	104.03	7.16	<0.002
1, 2, 3	2	115.29	7.94	<0.001

Return time is the time a parent took to return to the nest after the presentation of the sparrowhawk or mistle thrush.

Comparison of Breeding Phases

Females returned to the nestbox most quickly in the ectothermic phase (Fig. 1, Tables 1, 2; Duncan test for ectothermic–early endothermic: $P=0.02$; for ectothermic–late endothermic: $P=0.019$). This suggests that females take greater risks when nestlings are younger, which is in line with the harm to offspring hypothesis, but is inconsistent with the reproductive value hypothesis.

Males, however, showed an opposite trend: their return times decreased during the nestling period (Fig. 1, Tables 1, 2; Duncan test for ectothermic–early endothermic: $P=0.013$; for early endothermic–late endothermic: $P<0.001$). The behaviour of males supports the reproductive value hypothesis and not the harm to offspring hypothesis.

Risk Takers and Followers

In the ectothermic and the early endothermic phases, when nestlings were most vulnerable, females were the risk takers in all trials ($N=23$). On days 10 and 11 there was no difference in the visiting order of the sexes: females were the risk takers in nine trials and males in seven trials (Wilcoxon signed-ranks test: $Z=0.4137$, $N=16$ pairs, $P=0.679$). The sharing of roles (risk taker/follower) between the sexes equalized with increasing reproductive value and the simultaneously decreasing vulnerability of
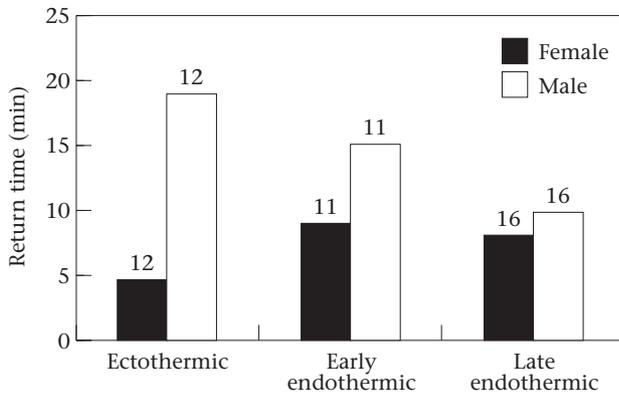
Figure 1. Median time collared flycatcher females and males took to return to the nest after presentation of a predator in relation to three physiological phases of the nestling period. Sample sizes are given above the bars.

the offspring. In the late endothermic phase females with light broods were the risk takers in eight trials and males in one trial (Wilcoxon signed-ranks test: $Z=2.547$, $N=9$ pairs, $P=0.011$). With heavy broods there was an opposite but not significant trend: in six out of seven trials the male was the risk taker (Wilcoxon signed-ranks test: $Z=1.775$, $N=7$ pairs, $P=0.076$).

Effect of Brood Quality

We used return time of the two sexes as the repeated measures variable and average brood weight as the independent variable in an ANOVA. The interaction term showed that the behaviour of both sexes depended on the body mass of nestlings (Fig. 2a; $F_{1,14}=32.496$, $P<0.001$). Females with heavy nestlings entered the box later than those with light ones. Males showed an opposite trend, returning sooner when nestlings were heavier. Males thus made decisions according to the reproductive value of the brood, and females according to its vulnerability.

Early and Late Broods

We compared parental behaviour of the sexes when the nestlings were 10–11 days old, applying a repeated measures ANOVA where the independent variable was the laying date and return time of the two sexes the repeated measures variable. The interaction between sex and laying date illustrates the sexual differences: males that bred early returned sooner than those that bred late, while late females returned sooner than early females ($F_{1,14}=6.962$, $P=0.019$; Fig. 2b). The behaviour of males was again consistent with the reproductive value hypothesis and contradicted the harm to offspring hypothesis. The behaviour of females supported the harm to offspring hypothesis.

DISCUSSION

Rytkönen et al. (1993), in a study of the nest defence behaviour of the willow tit, *Parus montanus*, found
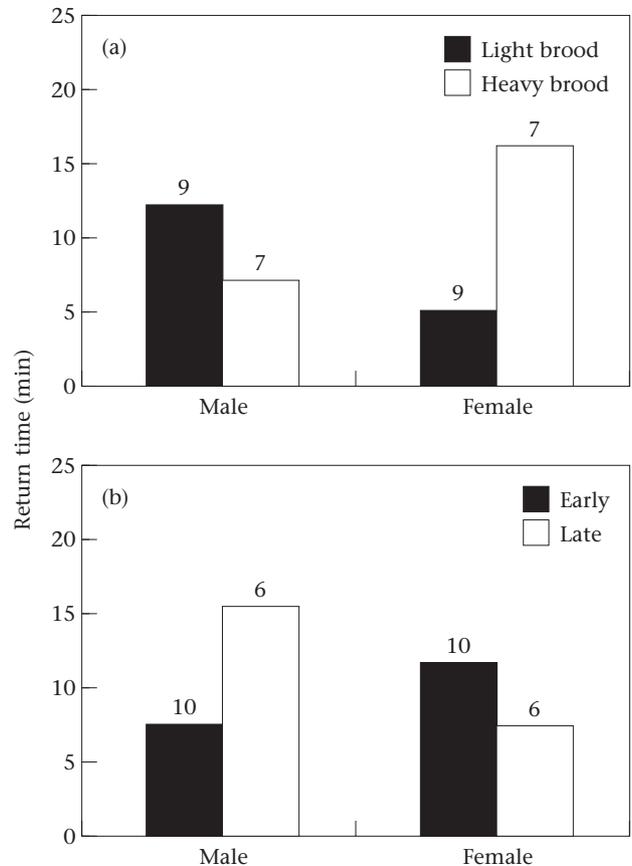

Figure 2. Median time collared flycatcher females and males took to return to the nest after presentation of a predator in relation to (a) body mass of nestlings in the late endothermic phase and (b) whether the brood was early (first egg was laid on or before median laying date) or late (started after the median laying date). Sample sizes are given above the bars.

evidence for the cost of renesting hypothesis. The female willow tit took higher risks and defended her nest more aggressively than the male in the first part of the breeding season. Later, the male became more active. We found similar results for the collared flycatcher. However, in our case this hypothesis was not supported. When we started our investigation during the nestling period, even though we found several abandoned nests, egg laying had apparently ceased in our study plots. Therefore the renesting potential of the species could be considered very low in our study. The collared flycatcher is a long-distance migrant that arrives in Hungary in mid-April and leaves in the second half of July. In the year of our study collared flycatchers arrived at our study plots 2 weeks later than in previous years. In addition, they had to moult before the autumn migration. These time constraints could have resulted in a late onset and an early termination of the breeding season with little, if any, chance of renesting. Decisions made in the nestling phase were thus not likely to be related to renesting.

If the incubating or brooding female flycatcher dies, the male will also abandon the nest, which means the end of that particular nesting attempt. According to the obligate parental care hypothesis, brood survival

could be increased if the female took fewer risks during the incubation or brooding period than later when a single male could rear the nestlings on his own. Since we found that the female took significantly greater risks during the brooding stage than for older nestlings, the obligate parental care hypothesis can be discarded.

We examined three variables (age and weight of nestlings and timing of breeding) that could be decisive in testing the reproductive value and the harm to offspring hypotheses. The probability of nestlings fledging improves with age but the parents' cost of replacing the lost nestlings would also increase. Older nestlings thus represent a greater reproductive value to their parents than young ones. Nestlings of the same age can be of different reproductive value; a number of studies have shown that heavier chicks and early fledglings are more likely to survive, so their reproductive value is higher (Clutton-Brock 1988; Daan & Tinbergen 1997). Because the renesting potential at the time of our study was low, the confounding effect of this factor was probably negligible.

Altricial nestlings deprived of parental care at different stages of development will be affected to different extents. Ectothermic nestlings are harmed most: owing to a lack of proper plumage and high body surface/mass ratio, they lose their body heat fast. Their metabolic rate drops, they are more difficult to feed and their digestion is slower. Returning chilled nestlings to normal condition takes much parental effort and prolonged brooding (O'Connor 1984). Less harm is done to the early endothermic nestlings, as they are able to control their body temperature and thus in general do not need brooding. At the same time, because of the increase in weight and growing feathers, they are more sensitive to the withdrawal of feeding than late endothermic nestlings, which have a slow growth rate and fully developed plumage (Brooke & Birkhead 1991). Among nestlings of the same age, larger ones are less vulnerable because they can conserve energy better and store more fat than those in poorer condition.

According to the harm to offspring hypothesis, the more vulnerable nestlings suffer more from the withdrawal of parental care than the less vulnerable ones, and so parents take higher risks for younger and weaker chicks. Consequently, the predictions of the reproductive value and the harm to offspring hypotheses are contradictory with regard to age and quality of broods.

The collared flycatcher males took more risks for older and better-quality chicks or earlier broods, which supports the reproductive value hypothesis and contradicts the harm to offspring hypothesis. Evidence for the reproductive value hypothesis has been found in the majority of nest defence studies (Montgomerie & Weatherhead 1988; Clutton-Brock 1991), but not in a study of pied flycatchers where the danger-dependent suspended parental care was examined. The male pied flycatcher's behaviour did not depend on the body mass of the nestlings and the time of season; moreover, risk taking decreased as the nestlings grow older, which contradicts the predictions of the reproductive value hypothesis (Dale et al. 1996).

It is not clear why the behaviour of the two flycatcher species differs so markedly, as they are closely related and sometimes even hybridize (Lundberg & Alatalo 1992). They have a mixed mating system: the pairs are predominantly monogamous (80–90%) but some males live in polyterritorial polygyny. Foraging, migratory behaviour and breeding biology are very similar as well. As our study was designed and carried out in the same way as Dale et al.'s (1996), the different results did not originate from different methodology. The reason could be that in the collared flycatcher there is a trade-off between parental effort and future sexual attractiveness (Gustafsson et al. 1995). So males invest more (provisioning more and/or taking more risks) in nestlings having better future survival prospects. This implies that the males would take risks according to the reproductive value of the offspring. In pied flycatchers, although they are a well-studied species, no evidence has been found for such a relationship. If there is no trade-off situation, the constraint that could limit the male's parental effort is lacking. This could explain the difference between the male's behaviour of the two sibling species.

The collared flycatcher females' behaviour was opposite to that of the males. They took significantly less risk for older and better-quality nestlings and tended to visit the nestbox later with earlier broods. Moreover, in pairwise comparisons of pair members they were the risk takers in the ectothermic and early endothermic phases in all cases, although in the late endothermic phase the sexes did not differ with respect to the sequence of nest visits. However, with lighter broods, females returned to the nest before males significantly more frequently. These results exclude the reproductive value hypothesis, but they support the harm to offspring hypothesis. Similarly, pied flycatcher females took fewer risks for older nestlings (Dale et al. 1996). Bures & Pavel (1997) also found that female meadow pipits took higher risks for more vulnerable (lower cloaca temperature) nestlings.

In females, we found a significant change in behaviour at the ectothermic–endothermic transition. In the early endothermic phase females were the risk takers in all cases, which suggests that there is no good-quality brood that exceeds the reproductive value threshold where males would become the risk takers. So it is likely that the influence of nestling age on reproductive value is more significant than the effect of brood condition in this phase.

Why do males make decisions according to the reproductive value, while a female's priority is vulnerability? As in the early phase of breeding (incubation, brooding), it is mainly the female that looks after the brood; she invests more than the male in the nestlings. The death of the nestlings would be more costly to her than to the male, so when their probability of death is high (i.e. in the ectothermic phase or with poor-quality nestlings) the female takes greater risks than her mate. Gotlander's (1987) finding, that pied flycatcher females invest more in lighter nestlings than in the heavier ones in a brood, strengthen our results. Moreover, the female can improve her reproductive success only by increasing her parental

effort, which aims at ensuring that all the nestlings fledge.

Males can increase their reproductive success not only by attending one brood but also from extrapair paternity and/or polygynous status. A further explanation for the difference in the sexes may be that the female is more sure of the nestlings' maternity (there is no evidence for intraspecific brood parasitism in this species) than the male is of his paternity, which again implies the female should take more risks. The males' current reproductive efforts show a negative correlation with the size of the forehead patch in the following year (Gustafsson et al. 1995). The forehead patch, as a badge, plays an important part in male-male competition for nestboxes (Pärt & Qvarnström 1997), in female choice and attaining polygynous status (Gustafsson et al. 1995). To decide on the level of risk taking (a form of parental effort), the males thus consider the reproductive value of the current brood, that is, in the case of poor-quality fledglings the benefit of risk taking is small, yet the future reproductive cost is high.

To conclude, in the collared flycatcher the two sexes follow different risk-taking strategies: males consider the reproductive value of the broods, females their vulnerability when making decisions. However, it is not clear what kind of cues are used to assess reproductive value and vulnerability of offspring.

Acknowledgments

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