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Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher

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Abstract According to life-history theory, there will often be a conflict between investment in current versus future reproduction. If a predator appears during breeding, parents must make a compromise between ensuring the growth and survival of offspring (nest defence, feeding and brooding of young), and reducing the risk of predation to ensure their own survival. We model three hypotheses for the outcome of this conflict which are particularly relevant for altricial birds. They are not mutually exclusive, but focus on different costs and benefits. (1) Parental investment is determined by the parents' own risk of predation. This hypothesis predicts that a lone parent should take smaller risks than a parent that has a mate. (2) Parental investment is related to the reproductive value of the offspring: Parents are predicted to take greater risks for larger broods, larger-sized or older offspring. (3) Finally, we present the new hypothesis that parental investment is related to the harm that offspring would suffer during a period of no parental care (incubation, brooding, feeding). This hypothesis predicts that parents should take greater risks for younger offspring, or for offspring in poorer condition, because the marginal benefit of parental care is largest in such cases. Hence, one may also expect that lone parents should take greater risks than two parents because their offspring are more in need of care. We tested these hypotheses on the pied flycatcher (*Ficedula hypoleuca*) by presenting a stuffed predator of the parents (a sparrowhawk, *Accipiter nisus*) close to the nest when parents were feeding the young. Risk taking was measured as the time that elapsed until the first visit to the nest. Most support was found for the "harm to offspring" hypothesis. Previous studies have usually measured the intensity of nest defence against typical nest predators, and have found evidence for the "reproductive value of offspring" hypothesis. However, our model predicts that the importance of the reproductive value of the offspring should decrease relative to the harm that offspring would suffer if they were not cared for when the predator type changes from a nest predator to a predator of adults, and when conditions for breeding turn from good to bad.

Key words Parental care · Predation risk · Risk taking · Reproductive value · *Ficedula hypoleuca*

Introduction

A central issue in life-history theory is the tradeoff between investment in current versus future reproduction (Trivers 1972; Clutton-Brock 1991; Stearns 1992). Predation risk for parents and offspring is one factor that has major effects on decisions of investment (Montgomerie and Weatherhead 1988; Lima and Dill 1990). In species where parents have to provide food for the offspring and offspring are unable to escape predators themselves, such as in altricial birds, there is a parental tradeoff between feeding of young or nest defence, and risk of predation on the parents. Hence, when predators are present, the parents face the problem of whether to continue feeding or defending the nest to ensure the growth and survival of the young, or to stop these activities to ensure their own survival.

In birds, a number of studies have addressed the question of how intensively parents should defend their nest when it is approached by a nest predator. The results of most studies support the hypothesis that the intensity of nest defence behavior such as alarm calling, distraction displays, mobbing and even attacks on the predator, increases with the reproductive value of

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the brood (reviews by Montgomerie and Weatherhead 1988; Clutton-Brock 1991). Thus, parents apparently take greater risks with increasing brood size, age and condition of the young. The direct costs of nest defence to the parents have not been well documented, but predation risk for adults may be particularly high during the breeding season in general (Perrins and Geer 1980; Newton 1986; Haartman 1988), and predation may occur during nest defence (Buitron 1983). Costs to parents will be highest when predators of adult birds are present close to the nest. Parents should then stop feeding for a period of time to avoid being killed, and one might expect that feeding would resume more rapidly the greater the reproductive value of the brood.

Previous studies have usually only considered the effect of nest defence on the probability that the brood will be predated or survive. However, defence of the brood against a nest predator, or interruption of feeding due to a predator of adult birds will also affect the condition of the nestlings. Nestlings of altricial birds are entirely dependent on their parents for survival, and may suffer if they are not fed or brooded for a period of time. If parental behaviour is adjusted to the harm that nestlings would suffer if they were not cared for, one would expect parents to take greater risks when nestlings are in poor condition (see below for details), which is the opposite of what would be expected if parents responded according to the reproductive value of the nestlings (Clutton-Brock 1991).

Here we attempt a thorough analysis of the factors affecting risk taking by parents, as measured by intensity of nest defence or how soon feeding is resumed after predator exposure. There are three hypotheses that are not mutually exclusive, but which focus on different costs and benefits, namely that risk taking is related (1) to the risk to the parents of being taken by the predator, (2) to the reproductive value of offspring, or (3) to the harm that nestlings would suffer if they were not fed or brooded. We derive predictions from the hypotheses, and we present a field test using the pied flycatcher, *Ficedula hypoleuca*. The hypotheses and predictions apply in particular to altricial birds.

Hypotheses and predictions

In contrast to previous studies which have mostly considered how intensively parents should defend their nest in response to a nest predator, we attempt to expand our analysis to a wider range of situations which are basically similar. We consider how parents should react to any kind of predator in order to increase the chances that the nest or brood will escape predation, and/or in order to be able to continue caring for the offspring (incubating, brooding, or feeding) as quickly as possible. Parental behaviour will be considered to be constrained mainly by their own risk of predation; we disregard energetic aspects of different behavioral decisions. In case of nest predators, parental risk of predation will typically be low whereas nest predation risk will be high; in case of predators of adult birds such as hawks (*Accipiter* spp.) predation risk will be high for parents and low for nests. However, we emphasize that these are two ends of a continuum because many predators pose a threat to both parents and offspring. Parental risk of predation is assumed to increase both with increasing intensity of nest defence and with a more rapid onset of feeding after exposure to a predator of adult birds, and these are therefore collectively termed risk-taking behaviours.

The benefits of risk taking are also in part the same both when nest predators and predators of adult birds are present. Increased risk taking increases the probability that the nest or brood will not be preyed upon, and it also reduces the time elapsing before incubation, brooding or feeding can resume. Thus, we assume that increased nest defence both reduces the chance that the predator will successfully locate and kill offspring (Andersson et al. 1980; Greig-Smith 1980; Blancher and Robertson 1982; Wiklund 1990), and reduces the time elapsing before the predator leaves the vicinity of the nest.

The risk to parents hypothesis

The "risk to parents" hypothesis focuses on the cost of risk taking. The hypothesis predicts that parental behaviour is determined by their own risk of being taken by the predator irrespective of the reproductive value or condition of the offspring. An obvious prediction is that risk-taking behaviour by parents should decrease the more dangerous the predator is to them, so that the cost remains the same. Another prediction is that risk taking will be affected by the number of individuals providing care to the offspring. If there is biparental care, each parent benefits from the vigilance of the other. Thus, parents can take greater risks without incurring greater costs in such a situation compared to a situation of uniparental care.

The reproductive value of offspring hypothesis

Models of parental care have reached the general conclusion that parents should increase their investment in relation to the reproductive value of the offspring (Andersson et al. 1980; Lazarus and Inglis 1986; Winkler 1987; Montgomerie and Weatherhead 1988; Clutton-Brock 1991). This means that parents with larger broods, larger-sized or older offspring should take greater risks than those with smaller broods, smaller-sized or younger offspring. Further, early breeders would be expected to take greater risks than late breeders. This is because the survival prospects of the offspring may be better for those reared early than for those reared late in the breeding season (Wallin 1987; Wiklund 1990). Note that this prediction may change if renesting potential is taken into account (Montgomerie and Weatherhead 1988).

The harm to offspring hypothesis

The "harm to offspring" hypothesis focuses on the effect that a period of no parental care (incubation, brooding, or feeding) has on the offspring. The marginal benefit of investment will in general be highest for offspring in poor condition or offspring that are unable to manage on their own. The idea that the physiological vulnerability of the offspring can affect parental behaviour such as nest defence was originally proposed by Montgomerie and Weatherhead (1988). Here we expand this idea and we derive specific predictions that can help separate it from the two hypotheses presented above. Since the reproductive value of offspring hypothesis has found support in many previous studies, we also consider when the harm to offspring hypothesis may be expected to be more important than the risk to parents and the reproductive value of offspring hypotheses. We stress that the idea that parents take risks in relation to the harm to the offspring of a period of no parental care should be considered a distinct hypothesis which deserves proper testing.

Consider first the effect of offspring age on parental behavior. Older nestlings have higher body masses and can therefore conserve energy more efficiently. In addition, older nestlings have a more developed plumage which further enhances energy conservation. In contrast, younger nestlings lose relatively more energy because of low body masses and poorly developed plumage. This means that the marginal benefit of parental care (B_m), such as feeding and brooding, is greatest for the youngest offspring [$B_m(Y) > B_m(O)$]. Thus, parents should take greater risks for younger offspring than for older offspring [$R(Y) > R(O)$; Fig. 1], which is the opposite of the prediction on risk taking from the reproductive value of offspring hypothesis. Similarly, the harm to offspring hypothesis predicts that parents should take greater risks for offspring in poor condition (low body masses) than for offspring in good condition (high body masses). In birds, the post-fledging survival is positively related to offspring condition in such a way that the marginal benefit gained by feeding offspring in poor condition is usually greater than that gained by feeding offspring in good condition (Magrath 1991; Slagsvold et al. 1995a).

The harm to offspring hypothesis does not give a clear prediction regarding brood size, unlike the reproductive value of offspring hypothesis. Larger broods means that delivered food is allocated to more nestlings thus reducing the per capita food delivery (Clutton-Brock 1991). On the other hand, larger broods may conserve energy better than smaller broods, larger broods are often reared by higher quality parents which are able to provide more food, or larger broods are reared when food is more plentiful. In sum, brood size *per se* does not necessarily affect nestling condition, and it is the condition of the young that is expected to affect parental risk taking under this hypothesis. Time of season can neither be expected to have a direct effect on the marginal benefit of parental care. Late broods are generally small, are often reared by low-quality parents, and at a time when food has become scarce. These factors suggest that offspring will be in poor condition. On the other hand, late broods are reared during warmer weather, and the food is divided between fewer nestlings. Thus, the marginal benefit of feeding and brooding late broods may not necessarily be different from the marginal benefit of feeding and brooding early broods.

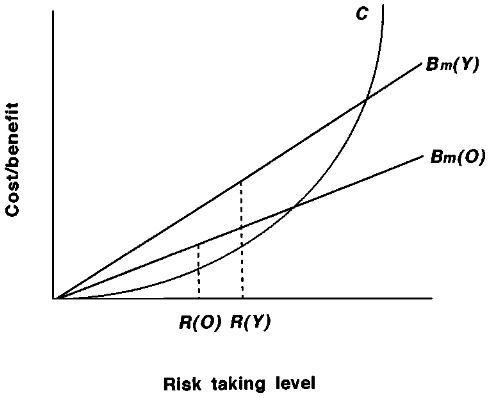

Fig. 1 Influence of the harm that nestlings would suffer if they were not fed (or otherwise cared for) on risk taking of parents. Two benefit curves which indicate the marginal benefit of being fed are indicated; $B_m(O)$ old offspring, $B_m(Y)$ young offspring. The optimal level of risk taking (R) occurs where the net benefit ($B_m - C$) is highest (C is the cost to the parents). Since $B_m(Y) > B_m(O)$ it follows that $R(Y) > R(O)$. Hence, parents should take greater risks if they care for younger nestlings since the marginal benefit of feeding is greater for young offspring

From the harm to offspring hypothesis it can be predicted that single parents should take greater risks than parents in pairs. This is because nestlings of secondary females of polygynous males, or widowed females, usually have offspring of poorer condition than paired females (Bart and Tornes 1989; Slagsvold and Lifjeld 1994). Thus, the marginal benefit of parental care is larger for offspring of single parents than for offspring with two parents. However, single parents can be expected to greater risks than parents in pairs even in the absence of clear differences in offspring condition. Single parents often compensate for the loss of assistance by having a generally increased feeding rate (Alatalo et al. 1982). Thus, single parents probably have a more limited ability to catch up with the increased food requirements of the offspring after a period of no feeding, compared to nests with two parents.

Relative importance of benefits

Breeding conditions

What can be said about the relative importance of the reproductive value of offspring hypothesis and the harm to offspring hypothesis? The predictions regarding offspring age and offspring condition (body mass) were in the opposite directions for the two hypotheses. Thus, the effect of the reproductive value of offspring would tend to obscure the effect of the harm to offspring of not being fed and brooded, and vice versa. However, we suggest that the general conditions during breeding may sometimes tip the balance in favour of one or the other of the factors as predictors of parental behavior.

Consider first a part of the breeding season when food is abundant and weather conditions are good (Fig. 2a). Under such conditions the marginal benefit of feeding and brooding nestlings is low for all broods. Even though the marginal benefit of caring for young nestlings is still greater than for old nestlings $[B_m(Y) > B_m(O)]$, the absolute difference is relatively small. On the other hand, the reproductive value of old offspring is greater than that of young offspring $[B_{rv}(O) > B_{rv}(Y)]$, and because the offspring are generally in very good condition and have a high probability of surviving to the next breeding season, the absolute difference is relatively large. Thus, the combined effect is that the importance of the marginal benefit of feeding and brooding offspring is low whereas the importance of the reproductive value is higher $[B_{rv}(O) - B_{rv}(Y) > Bm(Y) - B_m(O)]$. This results in the balance being in favour of reproductive value of offspring as the decisive factor for parental risk taking, and parents should take greater risks for old than for young offspring $[R(O) > R(Y)]$.

Next, consider a part of the breeding season when food is scarce and the weather is cool and wet (Fig. 2b). Under such conditions nestlings in all broods need as much food as possible, and the marginal benefit of feeding nestlings is high. The marginal benefit of feeding under bad breeding conditions does not necessarily increase relatively more for young versus old offspring compared to the case of good breeding conditions, but, at least, the absolute difference $B_m(Y) - B_m(O)$ increases. The reproductive value of the offspring decreases since they are in poor condition, and so does the absolute difference $B_{rv}(O) - B_{rv}(Y)$ between old and young nestlings. The combined effect of this is to shift the balance in favour of the harm that offspring would suffer if they were not fed (or otherwise cared for) as a decisive factor for parental risk taking $[B_m(Y) - B_m(O) > B_{rv}(O) - B_{rv}(Y)]$, and parents should take greater risks for young than for old offspring $[R(Y) > R(O)]$. In conclusion, parents should take greater risks for old versus young offspring when conditions are good, whereas the opposite should be the case when conditions are bad.

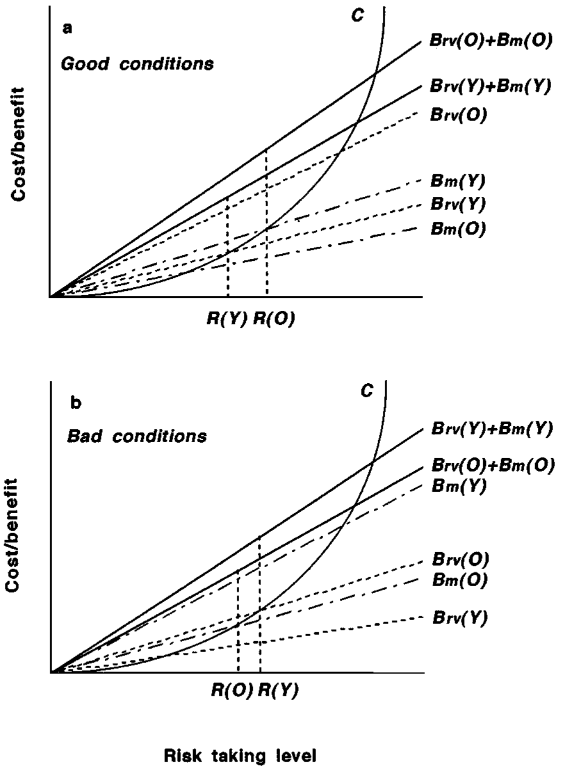

Fig. 2a, b Relative importance of two kinds of benefits for risk taking. The benefits are related to the reproductive value of offspring (B_{rv}), and the marginal benefit to the offspring of being fed (B_m). The figure illustrates that the relative importance of the benefits differs under **a** good conditions for breeding and **b** bad conditions for breeding. The optimal level of risk taking occurs where the net benefit ($B_{rv} + B_m - C$) is highest. Under both kinds of breeding conditions $B_{rv}(O) > B_{rv}(Y)$ and $B_m(Y) > B_m(O)$ where O designates old offspring and Y young offspring. However, the absolute differences $[B_{rv}(O) - B_{rv}(Y)$ and $B_m(Y) - B_m(O)]$ differ under the two conditions (see text for reasons). Thus, when conditions are good $B_{rv}(O) + B_m(O) > B_{rv}(Y) + B_m(Y)$ and it follows that $R(O) > R(Y)$. Hence, parents should take greater risks for older nestlings and lesser risks for younger nestlings. On the other hand, when conditions are bad $B_{rv}(Y) + B_m(Y) > B_{rv}(O) + B_m(O)$ and it follows that $R(Y) > R(O)$. Hence, parents should take greater risks for younger nestlings and lesser risks for older nestlings

Kind of predator

What effect does the kind of predator have on the relative importance of the reproductive value of offspring hypothesis and the harm to offspring hypothesis? One obvious effect of predator type is to change the cost to parents of risk taking. Exposure to a predator of adult birds would lower the optimal level of risk taking relative to a nest predator. However, a change in cost does not affect the relative importance of reproductive value and harm to offspring since this is determined by the sum of the two kinds of benefits {i.e. which of the two solid lines [$B_{rv}(Y) + B_m(Y)$ or $B_{rv}(O) + B_m(O)$] in Fig. 2 is above the other}. A change in predator type does, however, have another effect which we so far have not considered. If a parent is injured or killed by the predator during nest defence or feeding under a predator threat, this may endanger the survival of the offspring. Thus, the benefit of risk taking in terms of reproductive value of the offspring will be reduced in proportion to the parent's risk of being killed, and the reduction in benefit will be larger when the value of the offspring is larger (Lazarus and Inglis 1986). This means that situations involving a high parental predation risk may select for reduced risk taking with increasing reproductive value of the offspring, especially if the parents' chances of reproducing again are low (Lazarus and Inglis 1986). On the other hand, the marginal benefit of caring for offspring will probably not, or only to a small extent, be affected by parental risk of being killed. If parents attempt to reduce their own predation risk (and thus the risk of endangering the survival of the offspring) by delaying the resumption of feeding, this would cause a decrease in the condition of the nestlings. Hence, a reduced cost would be accompanied by a reduced benefit, and no clear change in parental behavior is therefore expected. The overall effect of changing the kind of predator would be that parents should typically take greater risks for offspring of higher reproductive value when faced with a nest predator [$B_{rv}(O) + B_m(O) > B_{rv}(Y) + B_m(Y)$], whereas the opposite pattern [$B_{rv}(Y) + B_m(Y) > B_{rv}(O) + B_m(O)$, or no relationship] should be found when parents are under the threat of a predator of adult birds (Fig. 3). This means that the harm to offspring hypothesis can be expected to increase in importance relative to the reproductive value of offspring hypothesis with increasing predator threat to parents.

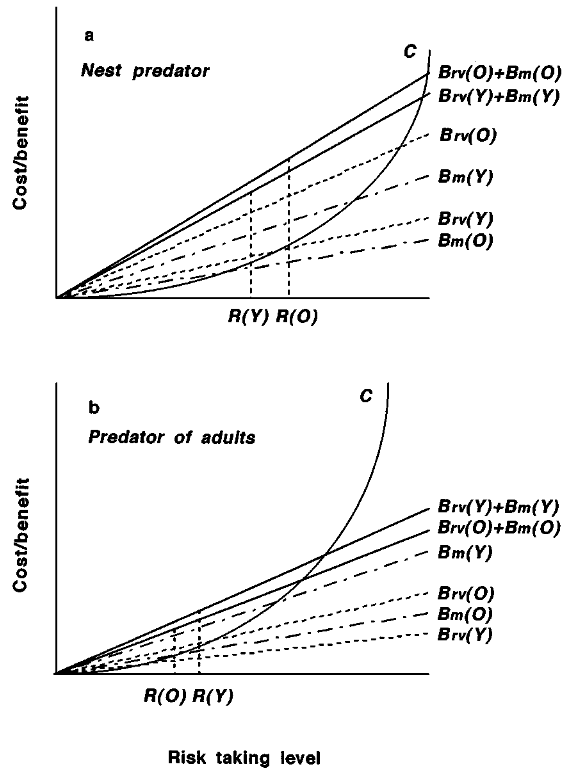

Fig. 3 Effect of **a** a nest predator and **b** a predator of adult birds on the relative importance of two kinds of benefits [reproductive value of offspring (B_{rv}) and marginal benefit to offspring of being fed (B_m)] on risk taking. The optimal level of risk taking occurs where the net benefit ($B_{rv} + B_m - C$) is highest. The marginal benefit of feeding young offspring [$B_m(Y)$] is larger than of feeding old offspring [$B_m(O)$], and is the same for both kinds of predators. However, the reproductive value of young offspring [$B_{rv}(Y)$] is smaller than that of old offspring [$B_{rv}(O)$]. In addition, the benefit in terms of reproductive value of offspring is decreased when the predator can kill the parents because the survival of the offspring is endangered if parents are killed. Thus, in case of a nest predator $B_{rv}(O) + B_m(O) > B_{rv}(Y) + B_m(Y)$ and it follows that $R(O) > R(Y)$. Hence, parents should take greater risks for older nestlings and lesser risks for younger nestlings. On the other hand, in case of a predator of adult birds $B_{rv}(Y) + B_m(Y) > B_{rv}(O) + B_m(O)$ and it follows that $R(Y) > R(O)$. Hence, parents should take greater risks for younger nestlings and lesser risks for older nestlings

Simultaneous variation in both breeding conditions and predator type may give a more complex set of predictions. The predictions are obvious in case of a nest predator during good breeding conditions, or in case of a predator of adult birds during bad breeding conditions. In these cases parental behavior will be determined by the reproductive value of the offspring, and by the harm that offspring would suffer if they were not cared for, respectively. However, cases of a nest predator during bad breeding conditions, or a predator of adult birds during good breeding conditions do not give clear predictions in our model. The parental investment pattern shown may then depend on the specific cost and benefit functions for each species combination of parents and predators.

Sex of parent

In many species of birds with biparental care, there is a sex difference in parental behaviour because it is often only the female that incubates the clutch or broods the offspring. Under the threat of a predator of adult birds this means that females have to take risks that males do not need to take. Thus, from the harm to offspring hypothesis we predict that females should often take greater risks than males during the incubation and brooding periods when faced with a predator of adult birds.

However, in case of a nest predator this may be quite different. Nest defence such as alarm calling and attacks on the nest predator can be done by both parents with some risk of being killed or injured.

Table 1 Predictions from three hypotheses of risk taking of adult pied flycatchers when exposed to a sparrowhawk model near their nest (*sec* secondary females, *mono/prim* monogamous and primary females combined; "$x < y$" means that x is predicted to resume feeding earlier than y)

Variable	Hypotheses		
	Risk to parents	Reproductive value	Harm to offspring
Sex of parent	–	–	Females < Males
Female mating status	Mono/prim < Sec	–	Sec < Mono/prim
Brood size	–	Large < Small	–
Nestling body mass	–	Heavy < Light	Light < Heavy
Nestling age	–	Older < Younger	Younger < Older
Time of season	–	Early < Late	–

However, the cost to the parents of a certain predation risk may not be independent of the sex of the bird that is killed, because of the difference in parental behaviour mentioned above (Regelmann and Curio 1986). If the male is killed the female may still be able to raise some offspring, but if the female is killed the clutch or brood will usually die, except very late in the nestling period (Clutton-Brock 1991). Thus, it can be predicted that in nest defence against a nest predator there will often be a sex difference with males taking greater risks than females.

Test of hypotheses

We tested the three hypotheses outlined above on the pied flycatcher (*Ficedula hypoleuca*). This was done by presenting stuffed models of a predator of adult flycatchers (a sparrowhawk, *Accipiter nisus*) close to the nest when the parents were feeding their young. We recorded the time elapsing until the parents resumed feeding after the sparrowhawk was removed. We compared the responses towards the sparrowhawk with those towards a great spotted woodpecker (*Dendrocopos major*), which is a predator of nestlings, but poses little threat to the parents, and a fieldfare (*Turdus pilaris*) which is completely harmless to both adults and nestlings. We also used a nest predator because we looked at how quickly parents would resume feeding *after* models had been presented, not on intensity of nest defence *during* presentations of models. This gives a much more direct measurement of the harm to the nestlings caused by predator presentations. This was regarded important for the study since no evidence so far is available to evaluate the harm to offspring hypothesis.

We expected that the sparrowhawk would cause a long delay in feeding since it is a serious risk to the parents, and that variation in the time elapsing until feeding was resumed would be related to one of the three hypotheses (see Table 1 for specific predictions). On the other hand, we expected feeding to continue sooner when woodpecker and fieldfare models were used since they represent no threat to the parents, at least when they are not present any longer (woodpecker). Variation in the time elapsing until feeding in woodpecker and fieldfare trials should therefore be unrelated to any of the three hypotheses.

Pied flycatchers are sometimes polygynous, and the brood of the second female attracted by a male (secondary female) is assisted less than that of the first mate (primary female) and those of monogamous females (Lundberg and Alatalo 1992; Slagsvold and Lifjeld 1994). This also means that polygynous males are less often present at their secondary than primary nest and so secondary females would have less help in being warned by the mate in case of danger. Hence, from the risk to parents hypothesis we expected secondary females (uniparental care) to resume feeding later than primary and monogamous females (biparental care) in trials with the sparrowhawk (Table 1).

From the reproductive value of offspring hypothesis we expected parents with larger broods and larger, older offspring to take greater risks than those with smaller broods and smaller, younger offspring. We also expected early breeders to resume feeding sooner than late breeders (Table 1).

In cases of polygyny in the pied flycatcher, the brood of the secondary female is assisted less than that of the primary female and those of monogamous females. Nestlings of secondary females are therefore usually of poorer condition (Stenmark et al. 1988; Slagsvold and Lifjeld 1994). Hence, from the harm to offspring hypothesis we expected that secondary females would resume feeding sooner than primary and monogamous females. This prediction is opposite to that from the risk to parents hypothesis regarding uni- or biparental care. Furthermore, we expected the predictions from the harm to offspring hypothesis to be opposite those of the reproductive value of offspring hypothesis as regards nestling body mass, and offspring age. Finally, since only females brood the nestlings in the pied fly-catcher (Lundberg and Alatalo 1992), we expected a sex difference in risk taking from the harm to offspring hypothesis. Females should return to the nestbox sooner than their mates when the offspring were small and in need of brooding, but this should not be the case when the offspring were older and brooding had ceased.

Methods

Study area and study species

The study was carried out near Oslo in south-eastern Norway, during the breeding season of 1993. The vegetation in the study area consists of a mixture of conifers and deciduous trees. The study area contained nestboxes with an entrance hole diameter of 32 mm, and the nestboxes were fixed to trees about 1.5 m above the ground.

The pied flycatcher is a small, short-lived, insectivorous passerine bird which usually arrives to the breeding grounds in southern Scandinavia in the beginning of May. Nest building and incubation is done exclusively by the female, while the male contributes parental care by feeding the female during incubation, and by feeding the nestlings. During egg-laying or incubation the males often establish secondary territories, usually some distance from their first, where they try to attract a second mate (Lundberg and Alatalo 1992). In this study we combined data for primary and monogamous nests in comparisons with secondary nests, because male parental investment differs little between primary and monogamous nests, whereas secondary females receive significantly less male help than both former groups.

Models

A sparrowhawk represents a serious threat to adult pied flycatchers in our study area (Slagsvold et al. 1995b). Great spotted woodpeckers are able to peck into the nest cavity of hole nesting birds and eat the young (Curio 1975; personal observations). However, great spotted woodpeckers represent a minimal threat to the parent pied flycatchers themselves. Fieldfares represent no threat to either parents or nestling pied flycatchers. One pair of sparrowhawks has nested yearly in the study area, and great spotted woodpeckers and fieldfares are common.

The stuffed specimens of a sparrowhawk (a female) and a fieldfare were both presented in a resting position, while the great spotted woodpecker was in a foraging position on the trunk of a tree. In this study we were primarily interested in risk taking behavior of parents in relation to factors such as sex of parent, mating status, and reproductive value of the brood, and less so in relation to the kind of model presented. Hence, to make trials as comparable as possible, we used only one model of each of the three species tested. The models were exposed for a short time only, reducing the probability of the birds becoming habituated. However, there is little habituation of free-living birds to predators (Curio 1975; Shalter 1975). The distance between neighbouring nestboxes in the study area was at least 25 m. However, when more than one nes was exposed to the sparrowhawk model on the same day, the distances between these nests were usually several hundred meters.

Experimental design

Males were captured on arrival and ringed with a metal ring and an individual combination of two or three colour rings, which enabled us to recognize them in the field. In addition, we made biometrical measurements of the males and scored their plumage color according to the Drost scale (Drost 1936). By daily observations in the field we collected data on the mating status of all birds (males: monogamous or polygynous; females: monogamous, primary or secondary), date of laying of the first egg, clutch size, hatching date and brood size. The day of hatching was taken as day 0 when ageing the young. Nests were grouped into experimental blocks in order to control for potential effects of male and female quality on risk taking behavior. We used male plumage color as a measure of male quality (Sætre et al. 1994, 1995), and clutch size as a measure of female quality. Males were grouped into bright (colour scores 1.5–2.5), intermediate (colour scores 2.8–4.0) and dull (colour scores 4.5–6.0) individuals. The clutch sizes of monogamous and primary nests (see below regarding secondary nests) were categorized as small (4–6 eggs) or large (7–8 eggs). This resulted in six experimental blocks. Pairs were assigned to blocks in chronological order according to hatching date. Within each block, the first six pairs to be tested were shown the sparrowhawk (four pairs), woodpecker (one pair) and fieldfare (one pair). The bias towards trials with sparrowhawks was because this was most important for testing the predictions of the hypotheses. The models' order within the group of six pairs was chosen randomly. The next six pairs in the same block got the same order of presentations. In each of the other five blocks a different, randomly chosen order of presentation was used. A total of 57 monogamous and primary nests were tested (37 trials with sparrowhawk, 10 with woodpecker, and 10 with fieldfare).

Secondary females were categorized only with regard to clutch size, which was divided into small clutches (3–5 eggs) and large clutches (6–8 eggs). This size limit differed from that of monogamous and primary females (see above) because secondary females initiated nesting later, and, hence, had smaller clutches on average. Within each experimental block of secondary females the first four females to be tested were shown the sparrowhawk (two females), woodpecker (one female) and fieldfare (one female). Order of presentation was chosen randomly in each of the two blocks in the same way as was described above. In total, 25 secondary females were tested. However, in four cases the male was present during the presentation of the model, and these cases were excluded from the analyses. The sample size used for statistical analyses was thus reduced to 21 secondary females (11 trials with sparrowhawk, 6 with woodpecker and 4 with fieldfare).

Models were presented when nestlings were 6 days old, except for the tests of the effect of offspring age in which trials were also done at an age of 12 days (see below). However, in the trials to be done at 6 days age, 9 of the 78 presentations were moved 1 day back or forward to avoid accumulation of trials on certain days. The results were not affected by moving of trials (U-tests of the time elapsing until the first nestbox visit in moved trials versus trials at day 6, $P > 0.88$ for both sexes). All trials were therefore pooled in the analyses. In order to measure the effect of offspring age, trials were also done late in the nestling period. Each pair, or secondary female, was submitted to the same kind of test as they had been submitted to on day 6, which enabled us to do pairwise tests. The second trial was done when the nestlings were 12 days old. In the meantime some birds had been used for the purpose of another study which affected the condition of the nestlings. Because of this they were not tested to ensure a homogeneous sample of birds. Thus, 12 trials were done at monogamous and primary nests (6, 2 and 4 pairs were presented with sparrowhawk, woodpecker and fieldfare, respectively), whereas 14 trials were done at secondary nests (6, 5 and 3 with sparrowhawk, woodpecker and fieldfare, respectively). No trials were moved in time at this stage.

During the trials the model was placed on the roof of the nestbox, and the observer retreated to an observation post, at least 10 m from the nestbox. The model was removed when both parent birds were assumed to have seen it as indicated by their presence less than 10 m from the nestbox, or alarm calling. Observations started when the observer had returned to the observation post after removing the model. We recorded the time elapsing until the first nestbox entry (usually to feed the nestlings) of each parent, and this time was used as a measure of risk taking of the parents. Observations were ended when both parents had entered the nestbox at least once. Thereafter the number of nestlings was recorded, and the whole brood was weighed. One or both parents were often present when models were put up on the nestbox roof. This extra disturbance could affect the results since humans may also be regarded as nest predators. However, all birds were subjected to the same experimental procedure, and thus one would not expect systematic differences between groups.

All statistical tests are two-tailed.

Table 2 Time (min) elapsing until pied flycatchers returned to visit the nest after presentations of three kinds of models near the nest during two stages of the nestling period (*sec* secondary females, *mono/prim* monogamous and primary females combined)

Model and stage	Males			Mono/prim females			Sec females		
	Median	Range	*n*	Median	Range	*n*	Median	Range	*n*
Sparrowhawk									
Day 6	19	6–58	37	13	3–63	37	11	0–47	11
Day 12	26	11–87	6	24	7–83	6	4	2–8	6
Woodpecker									
Day 6	9	1–26	10	8	2–29	10	5	1–31	6
Day 12	10	8–11	2	14	7–20	2	7	1–24	5
Fieldfare									
Day 6	1	0–9	10	2	0–19	10	4	1–9	4
Day 12	2	1–35	3	4	2–12	4	4	1–7	3

Results

Response to models

During the presentations of the sparrowhawk model, the birds usually stayed in the tree where the nest was or in the adjacent vegetation and made alarm calls. They never attacked the model, but always stayed at some distance from it. Even after the model was removed the birds still showed signs of excitement such as occasional alarm calling. On the other hand, the flycatchers harrassed or even attacked the woodpecker model. On two occasions the birds attacked the model so fiercely that it fell off the nestbox. In one trial with a secondary female, a live woodpecker appeared. The woodpecker was attacked and chased away. The fieldfare model was never attacked, and the birds showed no sign of stress due to its presence. On a few occasions the flycatchers even fed while the fieldfare was still present. This never happened when the sparrowhawk and woodpecker models were presented.

The time that elapsed until the birds visited the nestbox was significantly longer when the birds were presented with the sparrowhawk model than for the fieldfare model on day 6 in the nestling period (Mann-Whitney *U*-tests; males: $z = -4.68$, $n_1 = 37$, $n_2 = 10$, $P < 0.0001$; monogamous and primary females: $z = -4.06$, $n_1 = 37$, $n_2 = 10$, $P < 0.0001$; Table 2). However, the difference was not significant regarding secondary females (*U*-test: $z = -1.44$, $n_1 = 11$, $n_2 = 4$, $P = 0.15$), even though the time was nearly 3 times longer in the trials with the sparrowhawk model than in the trials with the fieldfare model (Table 2). Similarly, the nestbox was visited significantly later in sparrowhawk trials compared to woodpecker trials (*U*-tests; males: $z = -3.04$, $n_1 = 37$, $n_2 = 10$, $P = 0.0024$; monogamous and primary females: $z = -2.24$, $n_1 = 37$, $n_2 = 10$, $P = 0.025$; Table 2), except regarding secondary females (*U*-test: $z = -0.91$, $n_1 = 11$, $n_2 = 6$, $P = 0.37$).

There was also a significant difference in the time that elapsed until the nestbox was visited in woodpecker trials compared to fieldfare trials (*U*-tests; males: $z = -2.42$, $n_1 = 10$, $n_2 = 10$, $P = 0.016$; monogamous and primary females: $z = -2.68$, $n_1 = 10$, $n_2 = 10$, $P = 0.007$; Table 2). However, the difference regarding secondary females was again not significant (*U*-test; $z = -0.64$, $n_1 = 6$, $n_2 = 4$, $P = 0.52$; Table 2).

In several cases, only one parent was present when the models were placed on the nestbox, and the parents were therefore unequally exposed to the models, which could be a cause of variance in the results. In the trials with the sparrowhawk model, the time the birds were exposed to the model varied from 1 to 24 min (median 3 min, $n = 66$, including both sexes in each pair). The pair member which had been exposed for the longest time entered the nestbox first in 12 of the 33 pairs (binomial test, $P = 0.16$), indicating that there was no strong effect of exposure time on risk taking.

We expected that the time elapsing until feeding when the woodpecker and the fieldfare were presented would not be related to any of the factors investigated (sex, mating status, brood size, nestling body mass and age, time of season). No significant relationships were found ($P > 0.07$ in each of 17 tests with woodpecker, $P > 0.08$ in each of 21 tests with fieldfare).

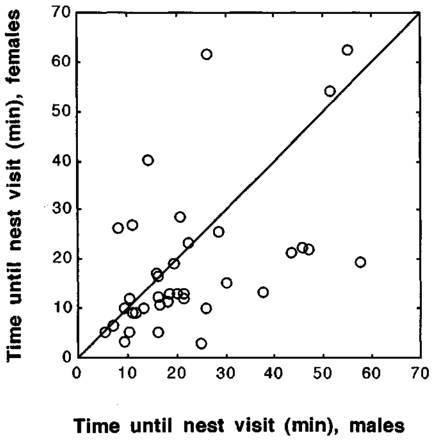

Fig. 4 Risk taking of pied flycatchers in relation to sex of parent. Risk taking was measured as the time elapsing until parents returned to visit the nest after presentation of a sparrowhawk model near the nest on day 6 of the nestling period. *Circles above the diagonal line* indicate that the female returned later than her mate, whereas *circles below the line* indicate that the female returned before her mate

This assures that if differences were found when the sparrowhawk was presented, this would be an effect of the trial model and not of any prior differences in relation to any of the factors mentioned above.

Comparison of males and females

Paired comparisons of pair members showed that females returned to visit the nest before males in trials with a sparrowhawk model when nestlings were 6 days old (Fig. 4). In 25 cases the female returned first, whereas in 12 cases the male returned first (Wilcoxon signed-ranks test; $z = -2.18$, $n = 37$ pairs, $P = 0.029$). Among pairs tested when nestlings were 12 days old, the female returned first in four cases, whereas the male returned first in two cases ($z = -0.94$, $n = 6$ pairs, $P = 0.35$, same test). These results are in line with the prediction from the harm to offspring hypothesis since there was a significant sex difference early in the nestling period.

Effect of female mating status

There was no significant difference in the time elapsing until the nest was visited between secondary females and monogamous and primary females combined when nestlings were 6 days old, though the trend was in the direction predicted by the harm to offspring hypothesis (sparrowhawk model; *U*-test; $z = -1.46$, $n_1 = 11$, $n_2 = 37$, $P = 0.14$; Fig. 5). However, when nestlings were 12 days old there was a significant difference; secondary females returned to the nest sooner (*U*-test; $z = -2.56$, $n_1 = 6$, $n_2 = 6$, $P = 0.01$; Fig. 5). This suggests that secondary females take greater risks, at least when nestlings are older. This provides support for the harm to offspring hypothesis but not for the risk to parents hypothesis.

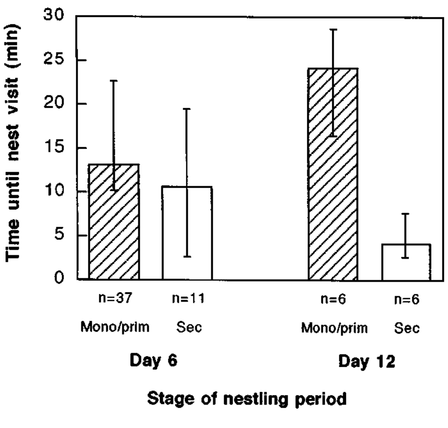

Fig. 5 Risk taking of female pied flycatchers in relation to stage of the nestling period (day 6 and day 12 after hatching) and mating status. Risk taking was measured as the time elapsing until females returned to visit the nest after presentation of a sparrowhawk model near the nest. *Bars* indicate median values, *lines* indicate 25–75 percentile range (*Mono/prim* monogamous and primary females combined, *Sec* secondary females)

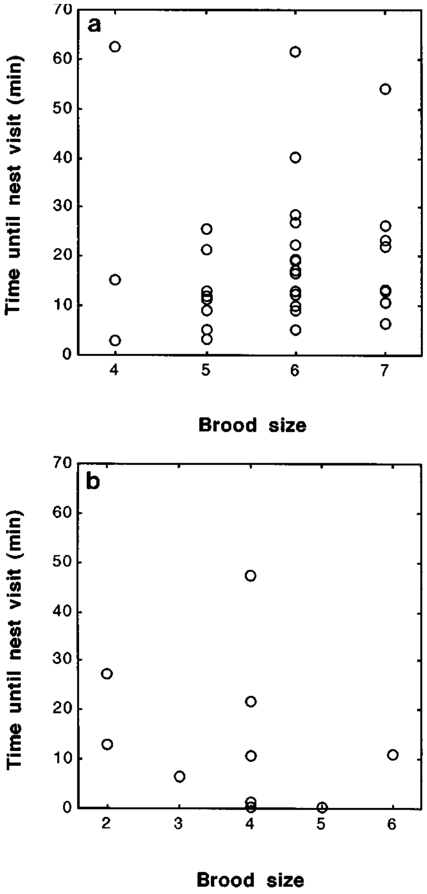

Fig. 6 Risk taking of **a** monogamous and primary females and **b** secondary female pied flycatchers in relation to brood size. Risk taking was measured as the time elapsing until females returned to visit the nest after presentation of a sparrowhawk model near the nest on day 6 of the nestling period

Effect of brood size

For monogamous and primary females there was a positive correlation between brood size and the time that elapsed until the nest was visited after presentation of a sparrowhawk (Fig. 6a). This was in the opposite direction of what was predicted from the reproductive value of offspring hypothesis, but the trend was not significant (nestlings 6 days old; Spearman rank correlation: $r_s = 0.26$, $n = 37$, $P = 0.11$). For secondary females there was a non-significant negative correlation between brood size and the time that elapsed until the nest was visited ($r_s = -0.32$, $n = 11$, $P = 0.31$; Fig. 6b). No relationship was found for males ($r_s = -0.01$, $n = 37$, $P = 0.81$). Furthermore, no significant relationships were found between brood size and the time that elapsed until the nest was visited when nestlings were 12 days old (Spearman rank correla-

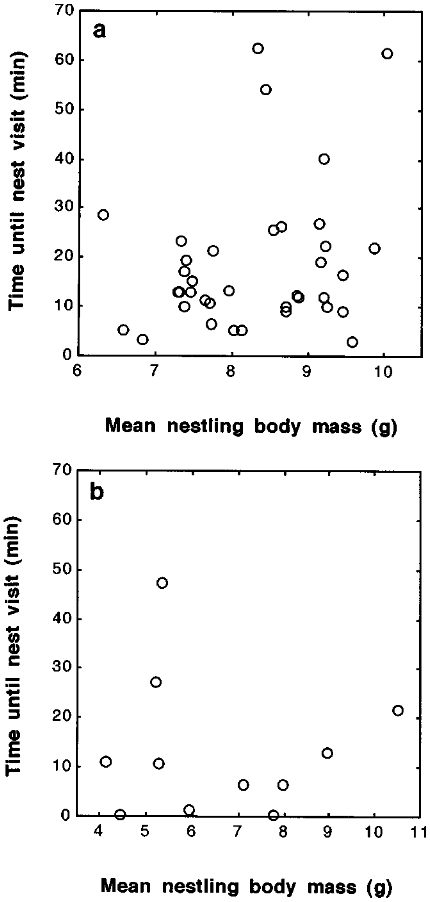

Fig. 7 Risk taking of **a** monogamous and primary and **b** secondary female pied flycatchers in relation to nestling body mass. Risk taking was measured as the time elapsing until females returned to visit the nest after presentation of a sparrowhawk model near the nest on day 6 of the nestling period

tions: $P > 0.70$ for each test of both sexes and all mating categories). Thus, there did not seem to be any support for the prediction from the reproductive value of offspring hypothesis.

Effect of nestling body mass

There were no significant relationships between nestling body mass when nestlings were six days old and the time that elapsed until the birds returned to visit the nest in the trials with the sparrowhawk model (males: $r_s = -0.04$, $n = 37$, $P = 0.81$; monogamous and primary females: $r_s = 0.14$, $n = 37$, $P = 0.41$, Fig. 7a; secondary females: $r_s = 0.05$, $n = 11$, $P = 0.86$, Fig. 7b). Furthermore, no significant relationships were found when nestlings were 12 days old (Spearman rank correlations, $P > 0.40$ for each of three tests). Thus, neither the reproductive value of offspring hypothesis nor the harm to offspring hypothesis were supported.

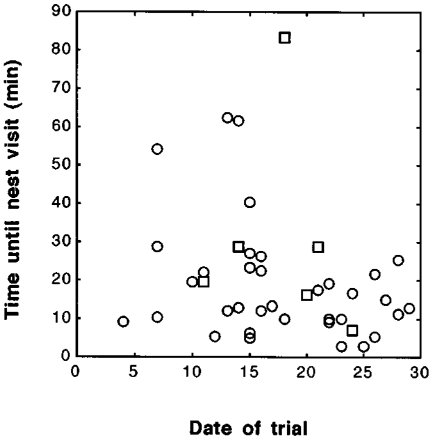

Fig. 8 Risk taking of female pied flycatchers in relation to breeding time (date of trial: 1 = 1 June) in two stages of the nestling period (day 6 after hatching, circles; day 12 after hatching, *squares*). Risk taking was measured as the time elapsing until females returned to visit the nest after presentation of a sparrowhawk model near the nest. Monogamous and primary females only

Effect of nestling age

The effect of nestling age was measured by the difference in the time that elapsed until the nest was visited for the pairs that were tested both when nestlings were 6 and 12 days old. All males which were presented to the sparrowhawk model at day 12 returned to the nest later than they did at day 6 (Wilcoxon signed ranks test; $z = -2.20$, $n = 6$, $P = 0.028$). For monogamous and primary females, five returned later and one sooner on day 12 compared to day 6. However, this difference was not significant ($z = -1.78$, $n = 6$, $P = 0.075$, same test), perhaps due to the small sample size. Among the secondary females, three returned to visit the nest later and three sooner ($z = -0.73$, $n = 6$, $P = 0.46$, same test). The results from the monogamous and primary nests therefore seemed to support the harm to offspring hypothesis and contradict the reproductive value of offspring hypothesis.

Effect of time of season

There was no evidence that pairs which bred early returned to visit the nest before pairs which bred late in the season in trials with the sparrowhawk model (day 6: males: $r_s = -0.06$, $n = 37$, $P = 0.70$, monogamous and primary females: $r_s = -0.24$, $n = 37$, $P = 0.15$ (Fig. 8), secondary females: $r_s = -0.08$, $n = 11$, $P = 0.79$). Sample sizes for similar tests at day 12 were small, and did not show any significant relationships (males: $r_s = -0.09$, $n = 6$, $P = 0.85$, monogamous and primary females: $r_s = -0.49$, $n = 6$, $P = 0.28$ (Fig. 8), secondary females: $r_s = -0.03$, $n = 6$, $P = 0.95$). Hence, the reproductive value of offspring hypothesis was not supported.

Discussion

In the present paper we propose that risk taking behavior such as nest defence against predators of offspring, and parental investment (incubation, feeding or brooding) under the threat of a predator of adult birds, may be explained by the following hypotheses: (1) the parents' own vulnerability to predation, (2) the reproductive value of the offspring and (3) the harm that offspring would suffer if they were not cared for. We derived predictions from each hypothesis which should make it possible to determine which factor has most effect on parental behavior. Most likely all three hypotheses apply to any species, but their relative importance will vary according to breeding conditions, kind of predator, relative value of current versus future reproduction etc. We tested the hypotheses on breeding pied flycatchers and most support was found for the harm to offspring hypothesis.

One prediction from the risk to parents hypothesis was tested in the present study, but we found that the results were in the opposite direction of what was predicted. We know of only one other study which has obtained data that can be used to test this prediction. Meek and Robertson (1994) found that unaided (widowed) females defended their offspring non-significantly more than paired females, which is also contrary to the risk to parents hypothesis. Thus, even though risk of predation must obviously be important for parents, it seems that this cost is not the major factor affecting variation in parental behavior. We suggest that this may be the case for short-lived species in particular. On the other hand, parents of long-lived species may more often adjust their behaviour according to their own risk of predation because future breeding attempts constitute a greater proportion of their lifetime reproductive success.

Several predictions from the reproductive value of offspring hypothesis were tested, but no evidence supporting the hypothesis was found. However, sample sizes were small in some tests, thus reducing the statistical power of the tests. Even so, regarding nestling age, the results were opposite to what was expected from this hypothesis. This is contrary to a number of other studies which have shown that measures of parental investment, especially nest defence, increase with the reproductive value of the offspring (see reviews by Montgomerie and Weatherhead 1988; Clutton-Brock 1991). On the other hand, many, though not all of the predictions from the harm to offspring hypothesis were supported. Few other data are available to evaluate the latter hypothesis, but it has been found that parental nest or brood defence increases during bad weather (Larson 1960; Regelmann and Curio 1983). This is difficult to explain from the reproductive value of offspring hypothesis, but such a relationship is expected from the harm to offspring hypothesis. The hypothesis also predicted that there should be a sex difference in risk taking such as nest defence when a nest predator is presented (but not when a predator of adult birds is presented, as in the present study), and that the male should then take greater risks than the female. Several studies have found such a pattern (Buitron 1983; Regelmann and Curio 1986; Breitwisch 1988). The explanation proposed for this pattern has been that males need to display their quality and willingness to invest in order to retain their mate for future breeding attempts, perhaps because of a male-biased sex ratio (Breitwisch 1988). However, our model suggests that males taking greater risks in nest defence than females can be explained just as well by sexual differences in costs and benefits of parental investment.

Why did the results of the present study support the harm to offspring hypothesis while previous studies have usually found support for the reproductive value of offspring hypothesis? Many previous studies have looked at nest and brood defence of parents when presented with models of nest predators, whereas our study looked at risk taking under the threat of a predator of adult birds. Our model predicted that the relative importance of the two main hypotheses (reproductive value of offspring and harm to offspring) should change in relation to the kind of predator. Thus, in our field study we were more likely to find an effect relevant to the harm to offspring hypothesis since a predator of adults was used. Perhaps more important, our study differed from previous studies in the way risk taking was measured. The time elapsing until feeding resumes gives a very direct measure of the stress imposed on the nestlings, whereas, for instance, the intensity of alarm calling or mobbing, the closest distance of approach to the predator, latency of approach are not necessarily related to nestling stress at all. In conclusion, we think the experimental design was crucial for detecting an effect relevant to the harm to offspring hypothesis.

Our model also predicted that the conditions for breeding would influence which hypothesis should be most important for explaining parental behavior. When conditions are good parents should invest in relation to the reproductive value of the offspring, whereas when conditions are bad the marginal benefit of parental care should be more important. Our study did not permit a test of this prediction, and it is difficult to say if breeding conditions were worse in our study than in previous studies. Probably, they were not. Since most studies of nest defence have found support for the reproductive value of offspring hypothesis, breeding conditions may have to be quite poor before the marginal benefit of parental care overrides the effect of offspring reproductive value in case of a nest predator. This possibility should be explored in detail in future studies.

In conclusion, we expect that the costs and benefits pinpointed in each of the three hypotheses all contribute in determining parental behavior, but that their relative importance depends on the specific circumstances of each test situation, such as the kind of predator and breeding conditions. The experimental design of a study can also be expected to influence which kind of benefit is likely to be detected.

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