

Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*)

Sönke Eggers,^{a,b} Michael Griesser,^{a,b} and Jan Ekman^a

^aEvolutionary Biology Centre, Department of Population Biology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden, and ^bDepartment of Biology, Section of Ecology, University of Turku, FIN-20014 Turku, Finland

Bird nestlings may be at risk not only from starvation but also from predators attracted to the nest by parental feeding visits. Hence, parents could trade reduced visitation rates for a lower predation risk. Here, through field data and an experiment, we show plasticity in daily patterns of nest visitation in the Siberian jay, *Perisoreus infaustus*, in response to predator activity. In high-risk territories, jay parents avoided going to the nest at certain times of the day and compensated by allocating more feeding effort to periods when predators were less active. Such modifications in provisioning routines allowed parents in high-risk habitat to significantly lower the risk of providing visitation cues to visually oriented corvid nest predators. These results indicate that some birds modify their daily nest visitation patterns as a fourth mechanism to reduce predator-attracting nest visits in addition to the clutch size reduction, maximization of food load-sizes, and prevention of allofeeding suggested by Skutch. *Key words*: allofeeding, antipredator behavior, nest activity, nest defense, nest predation, parental care, phenotypic plasticity, predation risk allocation hypothesis, Skutch's hypothesis. [*Behav Ecol*]

In altricial bird species, parents need to provide their growing nestlings with food to prevent starvation, ensure proper development, and minimize any negative effects of a poor start in life (Daan et al., 1990; Metcalfe and Monaghan, 2001; Nilsson, 1990; Richner, 1989, 1992). However, malnutrition is not the only threat to the offspring. Provisioning visits may impose a cost in risk of predation if parental activity alerts predators to the location of the nest. This cost in risk of predation must be balanced against the risk of starvation, and it can therefore be expected to constrain the rate at which parents visit the nest. Skutch (1949, 1961) was the first to identify this risk and to suggest three possible ways that visitation (and hence predation risk) might be reduced, namely (1) lowering clutch sizes, (2) maximizing food-load sizes, and (3) eliminating allofeeding (feeding by nonbreeding "helpers"). Although some have failed to document a link between nest activity and predation rates (Farnsworth and Simons, 1999; Roper and Goldstein, 1997), more recent work provides support for Skutch's ideas, especially when the variable effects of nest site are controlled (Martin et al., 2000b).

Predation risk may have an important influence, not only on reproductive success per se but also on the evolved roles of parents and nonbreeders in providing care to offspring. Siberian jays are unusual in having delayed dispersal of offspring but preventing them from allofeeding (Ekman et al., 1994). This behavior is also found in the Nearctic gray jay, *Perisoreus canadensis* (Strickland, 1991), except that, in this species, allofeeding may be allowed during the fledgling period (Waite and Strickland, 1997). To explain the suppression of allofeeding seen in *Perisoreus* and other small corvids, Strickland and Waite (2001) proposed that parental aggressiveness serves to dissuade nonbreeders from allofeeding and increase the exposure of nests to predators. In a meta-analysis of corvids, they confirmed predictions derived from their predator-avoidance hypothesis that species that prevent

allofeeding should be characterized by lower clutch sizes and parental nest visitation rates than those seen in allofeeding species. Thus, species that are least able to dissuade nest predators because of small size and/or small nonbreeder complements are the species most likely to use some or all of the three tactics suggested by Skutch to reduce nest visitation and the risk of betraying the nest location to predators.

A fourth potential parental tactic to reduce the risk of attracting nest predators could be to allocate nest visits and antipredator efforts across different risk situations. In theory, parents should allocate more antipredator efforts to high-risk situations and more feeding visits to low-risk situations when the relative degree of risk in high-risk situations increases (predation risk allocation hypothesis; Lima and Bednekoff, 1999). We provide evidence here that Siberian jays actually do use this countermeasure to reduce the risk of nest predation.

METHODS

Reproductive success

We studied reproductive success in a population of individually color-banded Siberian jays northwest of Arvidsjaur, northern Sweden (65°40' N, 19°0' E), starting in 1989. In March each year, jay females were caught and fitted with radio transmitters (1.85 g; Holohil), and nest sites could be located by radio tracking the incubating females in April. To minimize visits to the nest, the continued progress of a breeding attempt was monitored by observing the incubating female at a distance. We climbed to nests to band chicks or when there were obvious signs of nest predation and the parents had deserted. Predation was signified by visible disruption of the nest or its contents. In the period 1998–2001, nests were monitored daily when video cameras were being serviced (see below). Successful reproduction was confirmed by observation of fledglings in company with their parents.

Nest predators

Information on the identity of nest predators is given in Eggers (2002). Less than one nest out of two (proportion

Address correspondence to S. Eggers. E-mail: sonke.eggers@ebc.uu.se, sonegg@utu.fi.

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0.46, $n = 185$) succeeded in producing fledged offspring, and about two-thirds of failed nests showed signs of nest predation, being somewhat displaced with the rim of small damaged twigs. There are several sources to the identity of the nest predators. There are direct observations of corvids attacking nests, video recordings, and the results of an experiment using 24 collected Siberian jay nests provided with one chicken and one plasticine egg to identify predators (Eggers, 2002). Other corvids (Eurasian jay, *Garrulus glandarius*; hooded crow, *Corvus corone*; and raven, *Corvus corax*) stand out as the main nest predators. The only indications we have of nest predation by any other animals are video recordings of a sparrow hawk, *Accipiter nisus*, and a squirrel, *Sciurus vulgaris*, eating broods. Unlike the corvids, raptors or squirrels are rare in the study area, and there is no further evidence of their roles as nest predators. To assess corvid activity, we counted the number of corvids for a 5-min interval on our daily visits to nest sites for video maintenance. These visits were balanced to yield a variety of visit times throughout the day. We counted predators for 30 min by observing the surrounding of the nest site before we actually started to raise a ladder to climb the tree with the camera. Habitat structure surrounding the nest had little impact on our counts, because corvids were heard or seen almost exclusively flying over in the vicinity of nest sites.

Territory quality

Our design is based on a priori characterization of territory quality, specifically nest-predation risk. Territorial boundaries were stable over the years, which enabled us to calculate a probability of nest success by combining data across years. To express the relative reproductive success in territories we used a nest success index (NSI) that consists of the sum over all years of the difference between the actual reproductive successes within a given territory (0 indicates failure; 1, success) and the probability of nest success in the population in general (proportion of nests that were successful) for each year (Ekman et al., 2001).

Of the 35 territories in our study area, we identified in this way 17 territories with lower than average risk of nest failure (henceforth low-risk territories). These territories were characterized by more dense forest structure associated with a higher abundance of low spruce (less than 15 m) among the mature trees (Ekman et al., 2001). The remaining 18 territories had higher than average risk of nest failure (high-risk territories), and they were located closer to human settlements, with a more open forest structure. High-risk and low-risk territories were not grouped near one another; hence, they can be regarded as statistically independent. The correlation between forest structure and reproductive success appears to arise because an open forest structure facilitates nest detection for predators guided by visual cues. A preference by Siberian jays for territories of high breeding productivity further suggests that this link is indeed causal and reflects habitat quality (Ekman et al., 2001).

Parental activity

We studied natural variation in parental visitation rates in relation to predator exposure at 18 successful nests monitored by video cameras in the period 1998–2001. We obtained video recordings of activities at the nest continuously from the time we detected the nest, which we normally did as soon as the female started to incubate, up to the time of fledging or nest predation. Passive infrared-motion detectors were used to trigger cameras placed about 2 m from nests to ensure that all visits by parents could be detected. The sensors detected

movements of warm bodies and started the camera, which ran as long as there was activity at the nest and then for another 30 seconds after the last impulse. These video recordings allowed us to determine the date of the first chick's hatch and the times and durations of parental visits to the nest. The cameras were inspected daily, and new tapes were inserted if we estimated that there was not enough tape left to record all visits in the ensuing 24 hours. Video recordings from the nestling stage were scored for the number of trips to and from the nest by both parents.

We compared the visitation rates of parents at nests where the parents successfully raised a brood in high-risk ($n = 9$) and low-risk ($n = 9$) territories. To study daily nest visitation patterns in relation to the activity of potential nest predators, we sampled nest visit times and durations. The pooled time of recordings per nest was on average 26 ± 2 h (mean \pm SE). For the analysis we used a repeated-measures design in which parental visitation rates were recorded at five different time blocks in each territory. The parents were observed on successive occasions in both high-risk ($n = 9$) and low-risk ($n = 9$) territories to see whether corvid activity (covariate) might affect visitation rates.

Playback experiment

To test whether Siberian jay parents specifically respond to cues signaling the presence of corvids, we simulated their presence by playback of a mixture of calls (Eurasian jay, hooded crow, and raven) in 2000. We presented parents in seven low-risk territories with playback from 1400–1600 h (1 corvid call/6 min, TDK endless cassette, EC-12M) so that the exposure mimicked how corvid activity varied over the day in high-risk habitat. Tape recorders were placed on the ground, hidden under spruce branches, at a distance of 10 m from nesting trees. For each nest there was an exposure period of 3 days and a control period of 3 days. For four of the nests, which were chosen randomly, the control period (C) preceded the exposure period (E), and for the remaining three nests, the control period followed after the exposure to corvid calls to exclude any order effect. We incorporated the order effects of control and experimental sessions as a between-subjects factor in the statistical analysis (C-E versus E-C). To control for the effect of nestling age on daily visitation patterns, we timed manipulations by starting the experimental period (either control or exposure first) when females stopped sitting on the chicks and both parents began contributing to feeding the nestlings.

Because we played corvid calls only in the afternoon, even in the exposure group there was no cue of increased corvid presence until late in the first day of playback. It was thus only on the second day of playback that the parents had an opportunity to respond and modify their entire daily visitation pattern. Measures of responses to playback in daily visitation patterns therefore have to be displaced in time and delayed for 1 day after the exposure to corvid calls. Thus, our recording of responses in daily visitation patterns runs from the second day of playback to include the first day with no playback after the days of exposure. Likewise, the first day after a 3-day period of exposure to corvid calls cannot be used for control, as the parents might be expected to be responding still to the cue from the previous day. Therefore, we postponed the control period and waited 1 day without playback before we observed the behavior of our controls. Monitoring by video cameras of the nest to be manipulated began when the female started to incubate and continued to the end of the nestling period. We visited these nests daily to check cameras, inspect nests, and assess the presence of corvid nest predators.

Table 1

Estimated change of exposure to corvid nest predators for parents in high-risk territories ($n = 9$) if their daily nest visitation patterns were not adjusted to the activity of corvids but maintained the mean rate of provisioning, and if parents in low-risk territories ($n = 9$) did adjust their daily visitation patterns as in high-risk territories while they maintained their mean rate of provisioning

Nest	No. of cues ^a provided per day					
	High risk of nest predation			Low risk of nest predation		
	Observed	Without daily routine	Change	Observed	With daily routine	Change
1	2.46	2.94	0.48	0.84	0.63	-0.21
2	0.47	0.73	0.26	0.99	0.9	-0.09
3	1.23	1.38	0.15	0.36	0.3	-0.06
4	1.35	1.5	0.15	0.33	0.3	-0.03
5	3.6	4.8	1.2	0.33	0.33	0
6	0.69	0.78	0.09	0.39	0.39	0
7	0.7	0.74	0.04	0.42	0.45	0.03
8	1.77	2.64	0.87	0.45	0.48	0.03
9	0.6	0.72	0.12	1.35	1.41	0.06
Mean \pm SE	1.43 \pm 0.35	1.8 \pm 0.47	0.37 \pm 0.13	0.61 \pm 0.12	0.58 \pm 0.12	-0.03 \pm 0.03

For explanation of design, see Methods. In high-risk habitat, there was an increase (0.37 ± 0.13 [mean \pm SE] visitation cues per day; paired t test, $t = -2.77$ and $p < .025$) in the number of cues to other corvids without the daily routine of visitation rates. Parents in low-risk habitat would not gain in reduced rate of cues from a daily routine in the nest visit rate with an estimate decrease of only -0.03 ± 0.03 cues provided per day (paired t test, $t = 1.09$ and $p = .31$).

^a Nest visit when corvid (Eurasian jay, hooded crow, raven) was in sight of the nest within the same 5-min sampling block.

Calculating the risk of providing visitation cues

This calculation is based on the assumption that the risk of predation is a compound effect of parental activity and the activity of corvids. The risk of giving away the location of the nest to a predator is then a conditional probability in that a nest visit can reveal the position of the nest only if there is a predator around. Therefore, the risk of giving away the location of the nest to a predator can be expressed as the number of visits by the parents when there is a corvid in sight. This does not necessarily imply that the nest is detected, but it is an assessment of how often the parents are at risk of providing a cue that allows a visual hunter to locate the nest. We first calculated the nest visitation rate as the probability that either parent would visit in a 5-min interval. The likelihood that a corvid was in sight of the nest was likewise estimated for 5-min intervals. The probability that a parent visiting the nest would provide a cue would then be as follows:

$$\text{probability (providing cue)} = \text{probability (parent provisioning)} \\ \times \text{probability (corvid present)}.$$

Nest visitation rates and corvid observations were sampled for 3-h blocks (0300–0600 h, 0600–0900 h, 0900–1200 h, 1200–1500 h, and 1500–1800 h). These probabilities of providing a cue were translated into the number of visits when another corvid was present by multiplying them by 36 (3×12 separate 5-min intervals). The sum over all five blocks of 3 h gives the total number of nest visits with another corvid in sight per day.

Estimating the effect of modified parental activity on exposure

We estimated to what extent reduction in parental activity could reduce the risk of nest predation by comparing what would happen if parents in high-risk habitat behaved as did

those in low-risk habitat and vice versa (Table 1). To calculate the hypothetical nest visitation rates of parents that do not vary visitation rates at different times of the day, we used the relative proportion of parental nest visits observed amongst the five blocks of 3 h in high-risk territories ($n = 9$; block of 3 h, proportion of nest visits: 0300–0600, 0.27; 0600–0900, 0.27; 0900–1200, 0.18; 1200–1500, 0.18; 1500–1800, 0.10). For parents in high-risk territories that vary visitation rates, we used the same rate at different times of the day while still maintaining their mean rate of provisioning.

RESULTS

Predator activity

Siberian jay parents encountered corvid nest predators (Eurasian jay, raven, and hooded crow) more frequently in the high-risk territories where reproductive success was low and the open forest structure favors nest detection by predators that hunt by using visual cues. The overall activity of corvid species was about three times as high in high-risk habitat with an average of 1.70 observation per hour compared with 0.56 observations per hour in low-risk habitat on our visits ($p < .0025$, repeated-measurement ANOVA) (Figure 1). However, there was not only a difference in overall level of corvid activity between habitats, but there was a daily pattern in the timing of corvid activity in high-risk habitat that we could not find in low-risk habitat. The level of predator activity was of the same magnitude in both types of habitat during the morning (0300–0900 h). After that time, predator activity increased substantially in high-risk habitat and remained on that higher level for the rest of the day. Corvid activity in low-risk habitat did not show any corresponding pattern over the day, as revealed by a significant habitat \times time of day interaction (Figure 1). Predator activity in low-risk habitat throughout the day remained on the same low level as in the morning, and this lack of a daily pattern in corvid

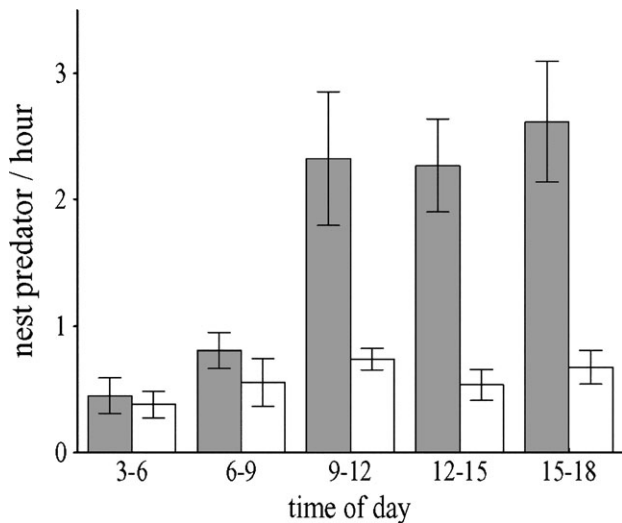


Figure 1
Diurnal pattern of corvid (Eurasian jay, hooded crow, raven) activity in low-risk (open bars, $n = 9$) and in high-risk (shaded bars $n = 9$) territories. Number of corvid nest predators observed per 5-min intervals and hour sampled for five 3-h blocks between 0300–1800 h in Siberian jay territories. The activity of corvids in territories with higher than average risk of nest predation (high-risk habitat) increased significantly with time but did not do so in territories with lower than average risk of nest predation (low-risk habitat). Overall, corvid activity was higher in high-risk habitat compared with low-risk habitat (habitat: $df = 1$, $F = 14.3$, $p < .0025$; habitat \times time of day: $df = 4$, $F = 4.6$, $p < .025$; time of day: $df = 4$, $F = 8.4$, $p < .0025$, repeated-measurement ANOVA, balanced design, nine low-quality and nine high-quality territories, five time-blocks each).

activity accounted for the difference in overall level between habitats.

Visitation patterns

Corvid activity in low- and high-risk habitat affected nest visitation rates of Siberian jay parents unequally (habitat \times corvid activity: $df = 1$, $F = 41.4$, $p < .001$; habitat: $df = 1$, $F = 0.01$, $p = .91$ [ns], repeated-measurement ANOVA adjusted for covariate corvid activity: $df = 1$, $F = 2.8$, $p < .05$, balanced design) (Figure 2a,b). The nest visit rate of Siberian jay parents declined during times of high corvid activity in high-risk habitat ($df = 1$, $F = 51.3$, $p < .0001$) (Figure 2a). With its overall lower level of corvid activity in low-risk habitat (Figure 1), there was less of a variation in risk for parents to respond to, and we could not find any correlation between visitation rate and corvid activity in low-risk habitat ($df = 1$, $F = 0.03$, $p = .87$) (Figure 2b). The inverse relationship between visitation rates and corvid activity in high-risk habitat indicates that parents visited the nest more intensively in the morning when corvid activity was low. Parents reduced the risk of nest predation in high-risk habitat by directing their visits to times of the day with lower corvid activity, whereas the total number of visits per day was not adjusted to the difference in corvid activity between high- and low-risk habitats ($p = .76$, repeated-measurement ANOVA) (Figure 3). Hence, although we found no difference between habitats in the overall rate of nest visits, there was a strong habitat \times time of day interaction (Figure 3). We can exclude differences in reproductive investments as the reason for between habitat differences in the response, as there was no appreciable difference in clutch size (mean \pm SE = 3.0 ± 0.59) in high-risk and low-risk habitat (3.1 ± 0.37 ,

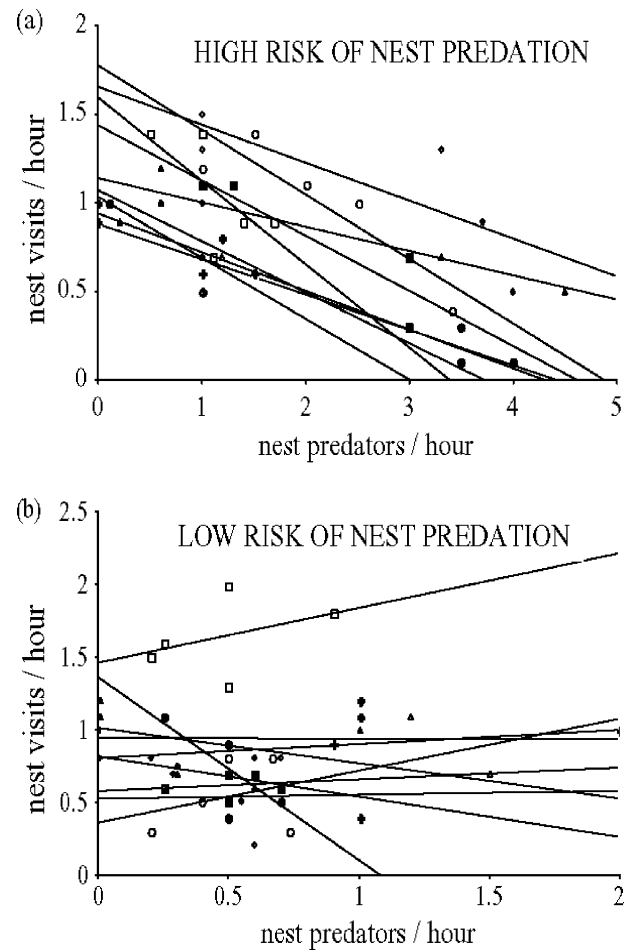


Figure 2
Adjustment to corvid activity in nest visitation rate by Siberian jay parents in high-risk (a) and low-risk (b) habitats. Mean number of nest visits by Siberian jay parents in relation to the mean number of corvids observed per 5-min intervals and hour. Visitation rates sampled between 0300–1800 h for five blocks of 3 h in each of nine territories in low-risk habitat and nine territories in high-risk habitat. Separate regression lines are shown for each territory. Nest visitation rates decreased significantly with increasing corvid activity in habitat with high risk of nest predation ($df = 1$, $F = 51.3$, $p < .0001$), whereas there was no significant response in nest visitation rates in habitat with low risk of nest predation ($df = 1$, $F = 0.03$, $p = .87$, repeated-measurement ANOVA).

$t = -0.2$, $p = .83$), which is consistent with the lack of any difference in the overall visitation rate between habitats.

Experimental test

Diurnal visitation patterns of parents in low-risk habitat converged on those of parents in high-risk habitat after they were given a predation-risk cue in the form of corvid calls (Figure 4). On exposure to playback, the parents in low-risk habitat shifted their activity so that visitation rates were highest during the first half of the day, whereas they reduced their activity at the nest later in the day when playback indicated high corvid activity. Daily visitation patterns of parents in high-risk habitat thus appear to be genuine responses to cues signaling the presence of nest predators. During control periods, parents were exposed to disturbances from our daily camera inspections (when we raised the ladder, climbed trees, worked with the camera, and inspected the nest) without provoking a response in daily visitation patterns.

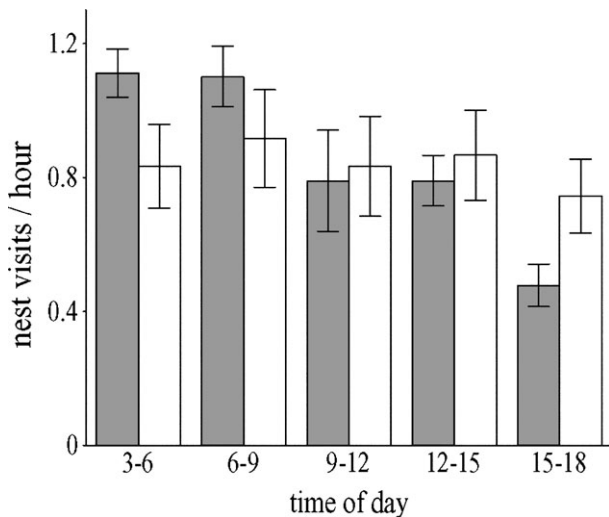


Figure 3
Diurnal nest visitation patterns by Siberian jay parents in low-risk (open bars) and high-risk (shaded bars) habitats. Mean number of nest visits (\pm SE) by Siberian jay parents per hour for five 3-h blocks between 0300–1800 h in territories with high- ($n = 9$) and low- ($n = 9$) risk of nest predation. There was no difference in the overall rate of nest visits between habitats, but time affected visitation rates unequally in high- and low-risk habitats. Visitation rates in high-risk habitat were higher in the morning before the peak in corvid activity, whereas visitation rates in low-risk habitat were more evenly distributed over the day (habitat: $df = 1$, $F = 0.09$, $p = .76$; time: $df = 4$, $F = 13.3$, $p < .001$; habitat \times time: $df = 4$, $F = 6.4$, $p = .004$, repeated-measurement ANOVA, balanced design).

In fact, the birds were very tame and soon came to accept our presence to the extent that some females had to be lifted from the nest on inspections. The change in daily provisioning patterns thus appears to be a response to the playback treatment per se, as there was no corresponding response to the disturbances caused by our presence. We can be less confident, however, that the response is specific to corvid calls. There remains the possibility that the parents would have shifted their daily visitation patterns in response to any playback.

Modification of daily visitation patterns as an antipredator defense

Both in our observations of natural variation in visitation rates and in the experiment, parents concentrated their visits at times of day when the risk of encountering nest predators was lower. This response is consistent with a parental strategy to reduce the risk of giving away the nest location to predators. However, under natural conditions only parents in high-risk territories showed this response. This difference in response between parents in high- and low-risk habitats raises two questions. First, how effective is the adjustment of the nest visitation rate in high-risk habitat in reducing predation risk? Second, do parents in low-risk habitat forego an opportunity to reduce the exposure of nests to corvid nest predators? Parents in high-risk habitat would, according to our estimate of the probability of giving a visual hunter a cue by visiting the nest (see Methods), run a substantially higher risk of exposing the nest to a predator if they did not modify their daily visitation patterns but instead visited their nest at an even rate over the day. Without daily variations in visitation rates the proportion of visits when they were at risk to give predators a cue would then increase significantly (0.37 ± 0.13 cues to nest predators per day; paired t test, $t = -2.77$ and $p < .025$)

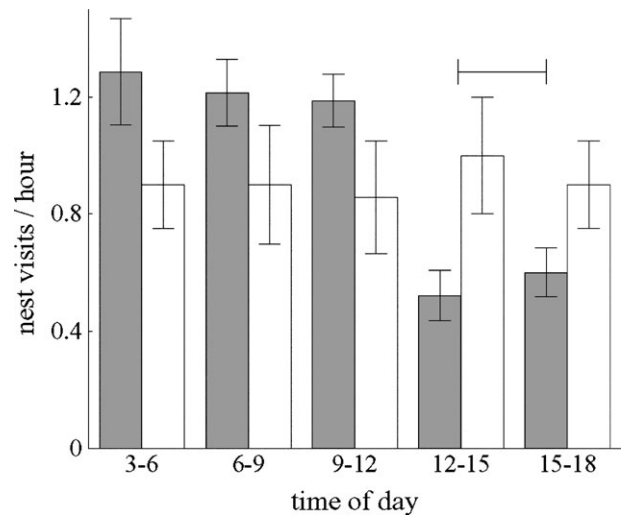


Figure 4
Diurnal nest visitation patterns by Siberian jay parents in low-risk habitat without a cue to corvid activity (no call playback; open bars) and with a cue (playback of corvid calls; shaded bars). Mean number of nest visits (\pm SE) by Siberian jay parents per hour for five 3-h blocks between 0300–1800 h in habitat with low risk of nest predation. Nests were their own control. Parents were exposed to a mixture of corvid playbacks (Eurasian jay, hooded crow, and raven) between 1400–1600 h. (horizontal line) during three consecutive days ($n = 7$ nests). The order of control (C) and experimental (E) sessions was counterbalanced and incorporated in the statistical analysis (C-E, $n = 4$ versus E-C, $n = 3$). The daily provisioning patterns of parents in low-risk habitat responded and converged toward the visitation patterns of parents in high-risk habitat with higher activity in the morning (time of day: $df = 4$, $F = 3.5$, $p = .002$; treatment [control/exposure]: $df = 1$, $F = 0.00$, $p = .98$ [ns]; order [C-E/E-C]: $df = 1$, $F = 3.1$, $p = .08$ [ns]; time of day \times treatment: $df = 4$, $F = 3.6$, $p = .002$; repeated-measurement ANOVA, balanced design).

(Table 1), and the risk of exposure would have increased for all nine pairs breeding in high-risk habitat ($p < .01$, binomial test) (Table 1).

In contrast, there would be no substantial effect of using a modified provisioning pattern in low-risk habitat. Parents in low-risk habitat would, unlike parents in high-risk habitat, not reduce the risk of having their nest detected by varying their activity over the day (paired t test, $t = 1.09$ and $p = .31$) (Table 1). Although the risk of detection would have decreased for four pairs, it would have increased for three. The estimates for the remaining two pairs could not be distinguished at the second decimal and were treated as identical (Table 1).

DISCUSSION

Predation has long been seen as a major selective force in the evolution of adaptations such as cryptic coloration, protective armor, and chemical defense (Edmunds, 1974; Harvey and Greenwood, 1978; Sih, 1987). Furthermore, predation provides a logical selective force for many observed patterns of habitat selection, species coexistence, and life-history traits (Lima and Dill, 1990; Martin, 1986, 1993). However, the rate of nest visits in birds has been attributed mainly to the food requirements of chicks (Briskie et al., 1994; Kilner et al., 1999; Sanz and Tinbergen, 1999; Wright et al., 1998), whereas the risk of nest predation has often not been considered in attempts at explaining differences in parental nest visitation rates (but see Ghalambor and Martin, 2000, 2001; Martin et al., 2000a; Skutch, 1949). This neglect of predation risk as an evolutionary force is surprising because nest predation is

a significant source of mortality in early life (Lack, 1954; Newton, 1998; Ricklefs, 1969).

Loss of a year's entire reproductive output is a substantial fitness cost, and especially so for short-lived organisms. The behavior of Siberian jay parents indicates a response to such costs aimed at reducing the risk of losing the offspring. Our data point to a plasticity in the behavior of parents whereby they take advantage of a daily activity pattern among nest predators and they both concentrate their nest-visits to times when predator activity is low and reduce their visit rate when nest predators are most active. This result confirms the predation risk allocation hypothesis, which predicts that animals allocate more antipredator efforts to high-risk situations and more feeding to low-risk situations when the relative degree of risk in high-risk situations increases (Lima and Bednekoff, 1999).

An alternative option to modify the pattern of nest visitation throughout the day would be to reduce the overall visitation rate (Ghalambor and Martin, 2002). From our material based on recordings of the activity throughout the entire active day of Siberian jay parents, they do not appear to use this option, whereas Strickland and Waite (2001) provide evidence from a comparative cross-species comparison for a lower visitation rate in species with high risk of nest predation. These two mechanisms are not mutually exclusive. Predation risk may necessitate a lower overall visitation rate in species with high risk of nest predation, whereas given such a base-line level in the risk of nest loss, our data suggest that there is still room for further antipredator behaviors. Yet, antipredator behaviors do not come without costs. Regardless of whether there is an overall reduction in the visitation rate or just during especially high-risk periods of the day, there must be some compensation or the offspring will be less well fed with an associated higher risk of starvation. Although Siberian jays reduced rates during times of highest predator activity, they still upheld their daily mean visitation rate by increasing their activity during times of low predator activity.

Although Siberian jay parents in high-risk habitat should have gained substantially in reduced risk from their behavioral response (reduction by 0.37 ± 0.13 cues to nest predators per day), parents in low-risk habitat would not have made any appreciable gain and they did not modify their daily visitation patterns. The plasticity demonstrated in high-risk habitat is consistent with parents in that habitat having low reproductive success, and it confirms that visitation rates cannot be understood solely from food abundance and the state of the chicks (Ghalambor and Martin, 2000, 2001; Skutch, 1949).

Corvids are visual hunters that succeed in finding prey more efficiently in an open habitat where relevant cues are more easily observed. Therefore, nest predation risk seems, not surprisingly, to be an interaction between corvid activity and forest structure (Eggers, 2002). Siberian jays prefer high-productivity territories located farther away from human settlements, where they escape exposure to high numbers of corvid nest predators associated with man (Eggers, 2002; Ekman et al., 2001). Although some individuals in territories with high risk of predation cope with the nest predators and reproduce successfully, the high rates of nest failure in these territories suggest that visitation rates cannot be reduced sufficiently by the parents to compensate for the higher exposure to predators in the open habitat. The need to provision the offspring seems to limit their possibilities of coping with higher vulnerability to nest predators. Presumably, both growth and quality of the offspring would deteriorate if the provisioning were reduced any more.

Because birds have determinate growth, their capacity to catch up for a temporary lack of food is limited (Metcalf and

Monaghan, 2001), and Siberian jay parents in high-risk habitat may have paid another hidden cost for the antipredator behavior. The value of food to the offspring is not only a question of volume, but also of timing. To maximize their digestive efficiency, chicks should be provisioned at a steady rate, as they were in the low-risk habitat. If chicks are fed at irregular intervals, the potential of the digestive tract will not be used in full during the critical period of rapid nestling growth and the offspring could fledge at a reduced size and quality, thus suffering reduced fitness (Daan et al., 1990; Eggers, 2002; Nilsson, 1990; Richner, 1989, 1992). The capacity of the digestive tract will also limit the potential for compensatory feeding. Hence, the antipredator behavior forcing Siberian jay parents in high-risk habitat to provision their offspring more irregularly may have entailed a cost, although further studies are required to establish whether the antipredator behavior has a cost in nestlings being less well fed, or alternatively whether the need to feed the chicks properly constrains parents from improving the antipredator behavior further.

Aggression can serve as a defense against nest predators, parasites, and conspecifics in many species (Collias and Collias, 1984; Larsen, 1991; Wiklund, 1990). However, there is growing evidence that nonaggressive behaviors such as the reduction of nest visitation rates through lowering clutch size or maximizing food-load sizes form an important component of nest defense in small corvid species, and presumably in many other birds, with limited capacity to defend the nest by aggression (Eggers, 2002, Strickland and Waite, 2001). Moreover, cooperative breeding is suggested to be restricted mainly to bird species large enough to deter nest predators or have relatively inaccessible nests (Skutch, 1961). This is because cooperative breeding may involve either a net benefit in terms of antipredator defense (Ricklefs, 1980) or a net cost (Skutch, 1961), depending on whether antipredator defense by helpers compensates for the increased conspicuousness of the nest as a result of increased alloparental activity (Strickland and Waite, 2001). In the Siberian jay, parents actively prevent retained offspring from approaching the nest during the breeding period (Ekman et al., 1994). Similar behavior occurs in the North American gray jay (Strickland, 1991), except that allofeeding may be allowed in the postfledging period (Strickland and Waite, 2001; Waite and Strickland, 1997).

In this article we demonstrate that Siberian jays modify their daily provisioning patterns to lower the risk of providing visitation cues to visually oriented corvid nest predators. Our results are consistent with behavior in which the visitation rate has responded with plasticity in visitation rates to the selective pressure exerted by nest predation. This plasticity enables the parents to escape predation by capitalizing on the fact that nest predators are not equally active over the entire day.

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REFERENCES

- Briskie JV, Naugler CT, Leech SM, 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proc R Soc Lond B* 258:73–78.
- Collias NE, Collias EC, 1984. Nest building and bird behavior. Cambridge, Massachusetts: Harvard University Press.
- Daan S, Dijkstra C, Tinbergen JM, 1990. Family planning in the kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour* 114:83–116.
- Edmunds M, 1974. Defense in animals. New York: Longman.
- Eggers, S, 2002. Behaviour and life-history responses to chick provisioning under risk of nest predation (PhD dissertation). Uppsala, Uppsala University.
- Ekman J, Eggers S, Griesser M, Tegelström H, 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. *J Anim Ecol* 70:317–324.
- Ekman J, Sklepkovych B, Tegelström H, 1994. Offspring retention in the Siberian jay *Perisoreus infaustus*: the prolonged brood care hypothesis. *Behav Ecol* 5:245–253.
- Farnsworth GL, Simons TR, 1999. Factors affecting nesting success of wood thrushes in Great Smoky Mountains National Park. *Auk* 116: 1075–1082.
- Ghalambor CK, Martin TE, 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Anim Behav* 60:263–267.
- Ghalambor CK, Martin TE, 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494–497.
- Ghalambor CK, Martin TE, 2002. Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav Ecol* 13:101–108.
- Harvey PH, Greenwood PJ, 1978. Anti-predator defense strategies: some evolutionary problems. In: Behavioral ecology: an evolutionary approach, 1st ed (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates; 129–151.
- Kilner RM, Noble DG, Davies NB, 1999. Signals of need in parent offspring communication and their exploitation by the common cuckoo. *Nature* 397:667–672.
- Lack D, 1954. The natural regulation of animal numbers. Oxford: Clarendon Press.
- Larsen T, 1991. Anti-predator behavior and mating systems in waders: aggressive nest defense selects for monogamy. *Anim Behav* 41:1057–1062.
- Lima S, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lima SL, Bednekoff PA, 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659.
- Martin TE, 1986. Competition in breeding birds: on the importance of considering processes at the level of the individual. *Curr Ornithol* 4:181–210.
- Martin TE, 1993. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43:523–532.
- Martin TE, Martin PR, Olson CR, Heidinger BJ, Fontaine JJ, 2000a. Parental care and clutch sizes in North and South American birds. *Science* 287:1482–1485.
- Martin TE, Scott J, Menge C, 2000b. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc R Soc Lond B* 267:2287–2293.
- Metcalfe NB, Monaghan P, 2001. Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260.
- Newton I, 1998. Population limitations in birds. London: Academic Press.
- Nilsson JÅ, 1990. Establishment success of experimentally delayed juvenile marsh tits *Parus palustris*. *Ethology* 83:73–79.
- Richner H, 1989. Habitat specific growth and fitness in carrion crows (*Corvus corone corone*). *J Anim Ecol* 58:427–440.
- Richner H, 1992. The effect of extra food on fitness in breeding carrion crows. *Ecology* 73:330–335.
- Ricklefs RE, 1969. An analysis of nesting mortality in birds. *Smithson Contr Zool* 9:1–48.
- Ricklefs RE, 1980. “Watch-dog” behavior observed at the nest of a cooperative breeding bird, the rufous-winged flycatcher *Myizetes cayanensis*. *Ibis* 122:116–118.
- Roper RJ, Goldstein RR, 1997. A test of the Skutch hypothesis: Does activity at nests increase nest predation risk? *J Avian Biol* 28:111–116.
- Sanz TJ, Tinbergen TM, 1999. Energy expenditure, nestling age and brood size: an experimental study of parental behavior in the great tit *Parus major*. *Behav Ecol* 10:598–606.
- Sih A, 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: Predation: direct and indirect impacts on aquatic communities (Kerfoot WC, Sih A, eds). Hanover, New Hampshire: University Press of New England; 203–224.
- Skutch AF, 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455.
- Skutch AF, 1961. Helpers among birds. *Condor* 63:198–226.
- Strickland D, 1991. Juvenile dispersal in gray jays: dominant brood member expels siblings from natal territory. *Can J Zool* 69:2935–2945.
- Strickland D, Waite TA, 2001. Does initial suppression of allo-feeding in small jays help to conceal their nest? *Can J Zool* 79: 2128–2146.
- Waite TA, Strickland D, 1997. Cooperative breeding in gray jays: philopatric offspring provision juvenile siblings. *Condor* 99:523–525.
- Wiklund CG, 1990. The adaptive significance of nest defence by merlin, *Falco columbaris*, males. *Anim Behav* 40:244–253.
- Wright J, Both C, Cotton PA, Bryant D, 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. *J Anim Ecol* 67:620–634.