

Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses

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The evolution of different parental care strategies is thought to result from variation in trade-offs between the costs and benefits associated with providing care. However, changing environmental conditions can alter such fitness trade-offs and favor plasticity in the type or amount of parental care provided. Avian incubation is a form of parental care where parents face changing environmental conditions, including variation in the risk of nest predation. Because parental activity can draw attention to the location of the nest, a reduction in nest visitation rates is a predicted response to an increased, immediate predation risk. Here, we experimentally increased the risk of nest predation using model presentations at nests of five coexisting species that differ in their ambient levels of nest predation. We examined whether individuals detect changes in nest predation risk and respond by reducing visitation to the nest. We also tested whether this behavioral response differs among species relative to differences in their ambient risk of nest predation. We found that males of all species detected the increased predation risk and reduced the rate at which they visited the nest to feed incubating females, and the magnitude of this change was highly correlated with differences in the risk of nest predation across species. Hence, as the vulnerability to nest predation increases, males appear more willing to trade the cost of reduced food delivery to the female against the benefit of reduced predation risk. Our results therefore suggest that nest predators can have differential effects on parental behaviors across species. We discuss how the comparative nature of our results can also provide insight into the evolution of behavioral plasticity. *Key words:* *Certhia*, incubation feeding, nest predation, parental care, phenotypic plasticity, *Poecile*, *Sitta*. [*Behav Ecol* 13:101–108 (2002)]

The evolution of parental care strategies is thought to result from trade-offs between the fitness costs and benefits associated with providing care (Clutton-Brock, 1991; Roff, 1992; Stearns, 1992). Different environmental conditions can alter these fitness trade-offs and lead to variation among species and populations in the amount or type of parental care provided (e.g., Badyaev and Ghalambor, 2001; Clutton-Brock, 1991). However, environments also tend to be highly variable, such that no single behavioral phenotype is consistently optimal. Such dynamic conditions require plasticity in behavior as a means of tracking environmental change. For example, in response to a perceived risk of predation, individuals of many species exhibit adaptive changes in behavior that reduce the probability that they will be predated (e.g., Lawler, 1989; Lima, 1998; Lima and Dill, 1990; Sih et al., 1992). Yet, few studies have considered the plastic behavioral responses of parents providing care for their offspring, making it important to understand the theoretical and empirical basis in which parents make behavioral adjustments to changing environmental conditions (e.g., Brodie, 1989; Carlisle, 1982).

Avian incubation of eggs is a fundamental form of parental care that requires parents to resolve time and energy trade-offs in response to changing environmental conditions. In passerine species with uniparental incubation, females must

leave the nest during incubation to feed and meet their own nutritional requirements, but absences from the nest can negatively affect egg temperatures and subsequent embryo development, as well as the ability to protect eggs against predators (e.g., Conway and Martin, 2000a,b; Haftorn, 1988; Moreno, 1989; Weathers and Sullivan, 1989; White and Kinney, 1974; Williams, 1996). By feeding females on the nest (i.e., incubation feeding), males can help ameliorate the trade-off between time on the nest incubating and time off the nest foraging. Indeed, the additional food provided by the male has been shown to increase female nest attentiveness, resulting in shortened incubation periods and improved hatching success (e.g., Halupka, 1994; Lifjeld and Slagsvold, 1986; Lyon and Montgomerie, 1985; Smith et al., 1989; von Haartman, 1958). Yet, the benefits of incubation feeding can be offset by the cost of higher nest predation, which increases with the frequency that males visit their nests (Lyon and Montgomerie, 1987; Martin and Ghalambor, 1999; Martin et al., 2000a,b; Skutch, 1949). Thus, parents incubating eggs must resolve a number of conflicting demands in response to changing environmental conditions.

Most previous work has examined the extent to which parents modify incubation behaviors in response to changes in temperature and energetic demands (Haftorn, 1988; Weathers and Sullivan, 1989; White and Kinney, 1974; Williams, 1996). Yet incubating parents are also faced with changes in the immediate risk of nest predation (e.g., the approach of a predator near the nest), which should favor modifications in behavior that reduce the risk of predation (reviewed in Lima and Dill, 1990; Martin, 1992; Montgomerie and Weatherhead, 1988). Because nest predation can increase with increasing parental activity near the nest (e.g., Martin et al., 2000a,b),

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Received 23 August 2000; revised 9 April 2001; accepted 15 April 2001.

parents faced with an increased, immediate risk are predicted to decrease visitation rates to the nest to reduce drawing attention to the location of the nest (Ghalambor and Martin, 2000, 2001). We assume that such behavioral plasticity in response to an immediate predation threat is under stronger selection in species more vulnerable to nest predation from visually oriented predators such as corvids and squirrels. For example, when a predator approaches a nest, species that use vulnerable nest sites (e.g., open-cup nests) should be under selection to reduce nest visitation rates more relative to species that use safer nest sites (e.g., cavity nests) because predators can more easily access the nest (Martin and Ghalambor, 1999). Thus, the costs of reduced food delivery are offset by the benefits of reduced predation risk, and differences among species in the risk of nest predation should alter this cost-benefit trade-off. Behavioral comparisons of populations or species that differ in their risk of predation can therefore provide insight into the degree to which parental decision making evolves.

We experimentally tested whether incubating parents can perceive changes in predation risk and modify their behavior accordingly. Predation risk was manipulated using model predator presentations near the nests of five species that differ in their ambient nest predation risk. We tested two predictions within and across species. First, we tested whether species exhibit adaptive plasticity in their incubation behaviors when faced with increased, immediate predation risk; male incubation feeding should decrease when the perceived risk of predation increases as a strategy to minimize drawing the attention of the predator to the nest (see above; see also Martin and Ghalambor, 1999). Second, we tested whether the change in incubation feeding rates in response to predator presentations is greater in species with higher ambient risk of nest predation, which presumably reflects greater selection intensity on phenotypically plastic traits (e.g., Doughty, 1995; Giles and Huntingford, 1984; Gotthard and Nylin, 1995).

METHODS

Study species and study site

We focused on five coexisting species that are ecologically similar (i.e., hole-nesting, insectivorous, socially monogamous, with similar body mass and behavioral repertoires) and closely related phylogenetically (Harrap and Quinn, 1995; Sibley and Ahlquist, 1990): pygmy nuthatch (*Sitta pygmaea*; Sittidae), red-breasted nuthatch (*Sitta canadensis*; Sittidae), white-breasted nuthatch (*Sitta carolinensis*; Sittidae), mountain chickadee (*Poecile gambeli*; Paridae), and brown creeper (*Certhia americana*; Certhidae). Long-term research on these five species reveals that they experience different levels of ambient nest predation, and these differences appear to be related to variation in nest-site characteristics (Martin and Ghalambor, 1999, unpublished data; Martin and Li, 1992). These species also exhibit a wide range of variation in incubation feeding rate, which is also tightly correlated with their nest predation rates (Figure 1; Martin and Ghalambor, 1999). Thus, these species provide an ideal system to experimentally test whether the correlation between nest predation and incubation feeding reflects causality.

Study sites were high-elevation (2600 m) snow-melt drainages on the Mogollon Rim, Arizona, USA. A detailed description of the vegetation is provided in Martin (1998). We searched study sites for nests of the five focal species from May through late June 1994–1998. All nests were in natural cavities and were intensively monitored to assess breeding stage (i.e., egg laying, incubation, nestling). A total of 52 natural nests were found for use in experiments ($n = 11$, *Sitta*

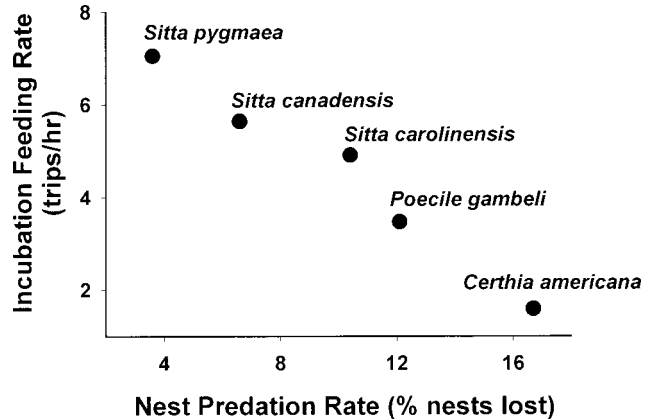


Figure 1 Relationship between male incubation feeding rate (mean over 6 h) versus ambient nest predation rate during incubation period for five coexisting species in this study (data extracted from Martin and Ghalambor, 1999).

pygmaea; $n = 13$, *S. canadensis*; $n = 11$, *S. carolinensis*; $n = 8$ *Poecile gambeli*; $n = 9$ *Certhia americana*), and all experiments were carried out between days 6 and 11 of the incubation period. The majority of males and females were uniquely color banded, and we had no indication that the same birds were resampled in subsequent years. In addition, each experiment was carried out on a different territory to minimize any potential territory quality effects.

Experimental manipulation of predation risk

To test effects of predation risk on incubation behavior, we presented a taxidermic model of a common nest predator. The goal of model presentations was to increase the perceived risk of nest predation near the nest site without eliciting nest defense behavior, such that males would continue to feed incubating females. We chose to present a taxidermic model of a mammalian predator, the red squirrel (*Tamiasciurus hudsonicus*), because it is the most common nest predator of the five focal species in this study and has been observed using parental activity as a cue to finding nests (Martin, 1993, unpublished data; Martin and Li, 1992). Response to the predator model was compared to a control model of the largely granivorous bird, the dark-eyed junco (*Junco hyemalis*), which represents no predation threat. Depending on the composition of the understory, mounts were attached to nearby tree saplings (either a quaking aspen, *Populus tremuloides*, or canyon maple, *Acer grandidentatum*) and placed 6–8 m from the nest tree, with the location held constant for each model. In addition, we played taped vocalizations of either squirrels or juncos from a cassette player placed at the base of the sapling where the model was perched to increase detectability of the models. To simulate the movements of a real squirrel and junco, a thin twine was attached to the base of the sapling and used to sway the sapling during presentations in an effort to give the impression that the model was moving. Use of vocalizations with the moving model is particularly effective in preventing habituation to the model alone (Ghalambor and Martin, 2000, 2001).

Experimental design and behavioral observations

We compared behavioral responses of the five bird species to squirrel and junco models that were presented in a stratified random order on consecutive days for each nest. Time of day

and ambient temperature are highly correlated with each other, and both are in turn correlated with incubation behaviors in these species (Ghalambor, 1998, unpublished data). Therefore, we started all observations at the same time each day (0600 h) to control for any possible effects of time or temperature on parental behavior. The design consisted of an initial control period of 90 min followed by a 90-min model presentation period of either the predator or the control. We measured two behaviors in response to model presentations. First, we measured the change in male incubation feeding rate between the pre-presentation control period and the model presentation period. Second, because the food delivered to the female can increase her time on the nest (e.g., Martin and Ghalambor, 1999) and females may increase attentiveness in response to increased predation risk (e.g., Beissinger et al., 1998; Thompson and Raveling, 1987), we also measured changes in female nest attentiveness (% time on nest). The change in incubation feeding and nest attentiveness between the pre-presentation and model presentation periods represents the magnitude of change in each species and allows for a standardized comparison across species.

Data analysis

We plotted the behavioral response of each species using standard plots of the behavioral means against the pre-presentation and model presentation time periods. Before analysis, incubation feeding rate was log-transformed and percent nest attentiveness was arcsine transformed to normalize the data. We first tested whether male incubation feeding rates were correlated with female nest attentiveness within the five species to assess independence of the two variables. We tested this using an ANCOVA with nest attentiveness as the dependent variable, incubation feeding rate as a covariate, and species as a grouping variable. We repeated this test for both the pre-presentation and model presentation periods. We then tested for a significant order of presentation effect (i.e., whether the squirrel or the junco was presented first) using a repeated-measures ANOVA that tested the effect of order and the interaction of order and species on incubation feeding rate and nest attentiveness. All species and the difference in their responses between the pre-presentation and model presentation time periods for days when a squirrel or junco were presented were then included in a repeated-measures ANOVA. We tested whether the difference in incubation feeding rate and nest attentiveness differed between model types and whether there was an interaction between these behavioral responses and species. To directly compare how much each species modified its behavior in response to the predator model, we compared incubation feeding rates and nest attentiveness during the pre-presentation and model presentation time periods on days when only the squirrel was presented. As above, we used a repeated-measures ANOVA and tested for a significant time effect (pre-presentation versus presentation) and a time-by-species interaction effect.

The five species exhibit large differences in their baseline rates of incubation feeding (Figure 1). Large differences in baseline rates make comparisons of behavioral plasticity among species complicated because the same absolute change in one species may not be equivalent to the same changes in another. For example, *Sitta pygmaea* males may feed incubating females more than 10 times per hour, whereas *Certhia americana* males rarely feed females more than 4 times per hour. Thus, a reduction by 2 feeds per hour in these two species would represent either a 20% or 50% change in food delivery to the female, respectively. We therefore standardized responses across species by converting absolute changes in each behavior to percent changes between the pre-presentation

period and the predator presentation time periods. We then tested the relationship across species between response to the predator and variation in the risk of nest predation using a nonparametric Spearman rank correlation test because the small number of species resulted in a non-normal distribution.

RESULTS

We expected to find a close relationship between incubation feeding and nest attentiveness; however, we found no correlation between these traits in any of the five species during the pre-presentation control period (ANCOVA, $F = 0.53$, $df = 1, 47$, $p = .82$) or the model presentation period (ANCOVA, $F = 0.009$, $df = 1, 47$, $p = .93$), and thus we treated these two behaviors as independent variables (see Discussion). We then tested for order effects in presentation experiments and found that the order in which models were presented had no effect on incubation feeding rates (repeated-measures ANOVA; $F = 6.05$, $df = 1, 39$, $p = .41$), and there was no order-by-species interaction effect (repeated-measures ANOVA; $F = 11.55$, $df = 4, 39$, $p = .28$). We found the same result for nest attentiveness; there was no order effect ($F = 0.824$, $df = 1, 40$, $p = .37$) or order-by-species effect ($F = 1.09$, $df = 4, 40$, $p = .37$), so we dropped this term from further analyses.

There was a significant effect of model type on male incubation feeding rates when all species were grouped together (repeated-measures ANOVA; $F = 39.96$, $df = 1, 48$, $p < .0001$), reflecting that incubation feeding rates dropped more in the presence of the predator model than in the presence of the control (Figure 2). Indeed, in the presence of the squirrel model, we observed males of all five species arriving in the vicinity of the nest (< 10 m) with food in their bills, then leaving the vicinity of the nest without feeding the female. We never observed this behavior in the presence of the control model, suggesting that males recognized squirrels as a potential threat and were hesitant to visit the nest when a squirrel was present. In no case did we observe males attacking or exhibiting any type of nest defense behavior toward either the predator or control models. In contrast to male incubation feeding rates, female nest attentiveness did not significantly change in response to model presentations (Figure 3; ANOVA, $F = 1.99$, $df = 1, 43$, $p = .17$). During sessions off the nest, females of all species were occasionally observed perching and foraging directly above the squirrel model, but no clear difference in female behavior was observed in response to the predator and control models. In no case were females observed attacking the predator or the control models.

When only the response to the predator model was considered (Figure 4a), feeding rates significantly differed between the pre-presentation and predator presentation periods for all species (repeated-measures ANOVA, $F = 139.05$, $df = 1, 46$, $p < .0001$). The change in incubation feeding rate significantly differed among species (repeated-measures ANOVA, $F = 76.14$, $df = 4, 46$, $p < .0001$), and there was a significant species by treatment interaction ($F = 12.14$, $df = 4, 46$, $p < .0001$). The significant interaction between species and treatment was primarily driven by differences in incubation feeding rates in the presence of the nest predator, rather than by large differences in initial feeding rate among species (Figure 4a). Thus, slopes measure the extent of change in incubation feeding rates in the presence of a nest predator (Figure 4a). The same analysis for nest attentiveness (Figure 4b) showed no differences in attentiveness between the pre-presentation and predator presentation periods (repeated-measures ANOVA, $F = 0.872$, $df = 4, 45$, $p = .36$). There was, however, a significant species effect ($F = 21.53$, $df = 4, 45$, $p < .0001$), but no species-by-treatment interaction ($F = 1.104$, $df = 4,$

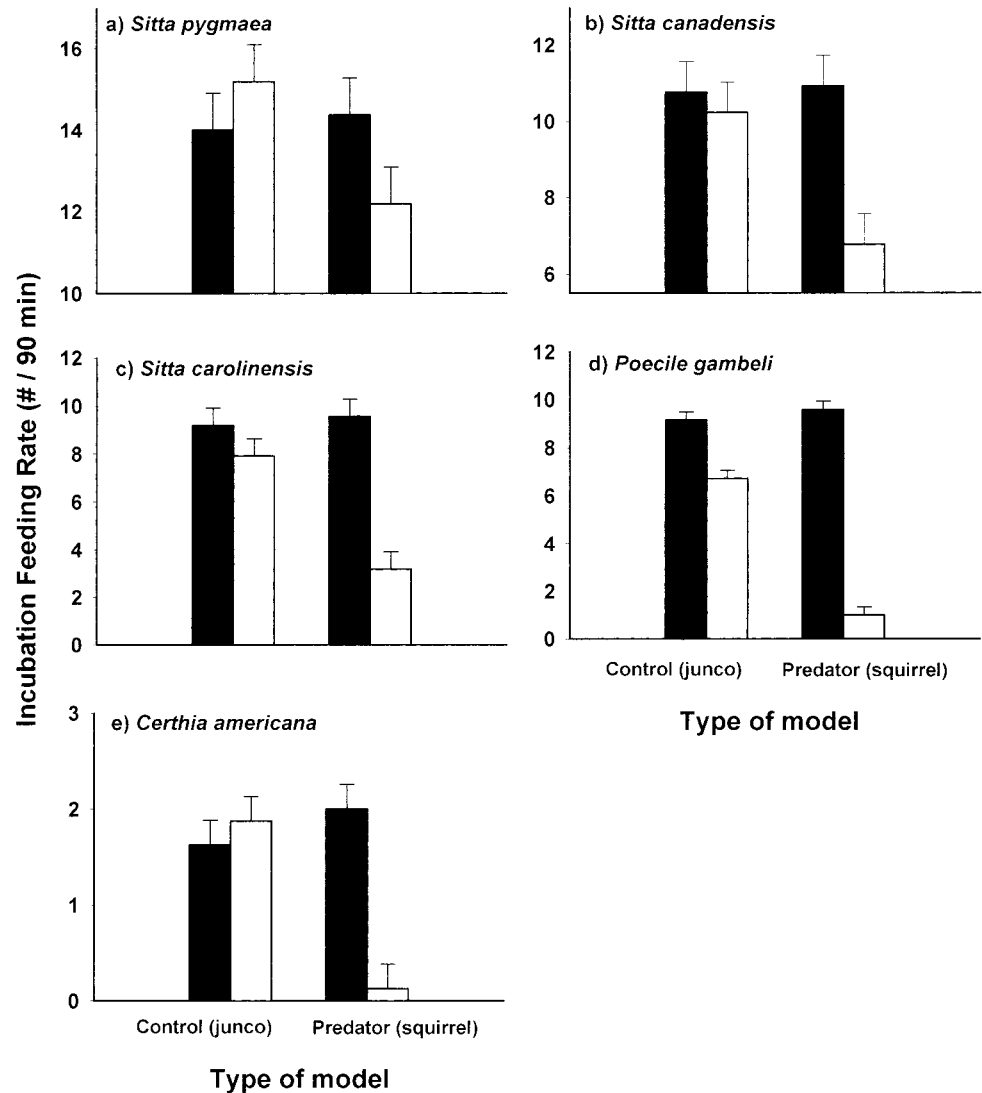


Figure 2
Change in incubation feeding for five closely related species. Shown is the mean (\pm SE) incubation feeding rate during pre-presentation (no model; filled bars) and presentation (model; open bars) time periods for days when a control (junco) and a predator (squirrel) model were presented.

45, $p = .37$), reflecting that species significantly differed in the amount of time spent on the nest but not in their responses to the presentations (Figure 4b). The only species that showed any measurable change in nest attentiveness was *Certhia americana*, which increased its time on the nest in response to the predator presentation (Figure 4b).

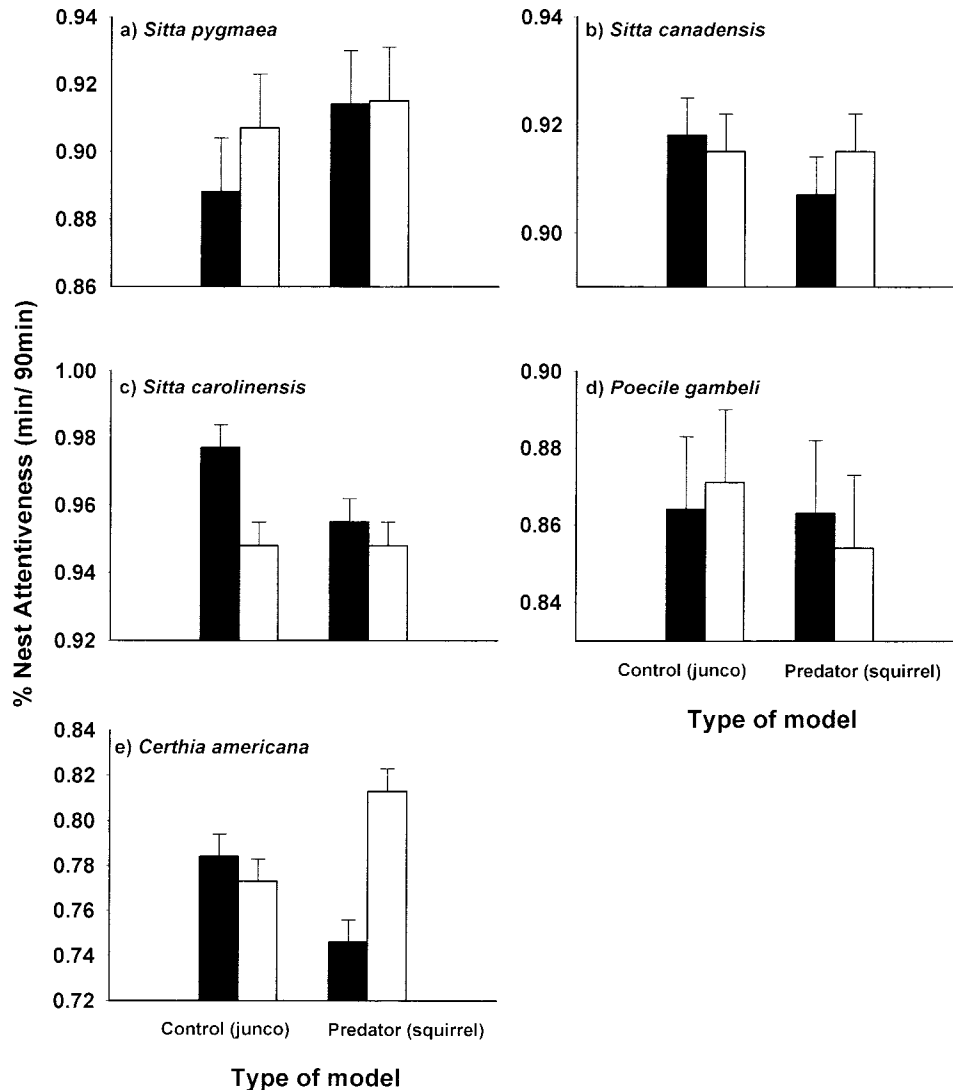
We predicted that the magnitude of decreases in incubation feeding rates in response to the predator model should be greater in species with greater risk of nest predation. We found the magnitude of standardized changes (i.e., decreases) in incubation feeding in response to the predator model were, indeed, larger for species at greater risk of nest predation (Figure 5a; Spearman $\rho = 0.90$, $df = 5$, $p = .019$). Percent change in female nest attentiveness was not related to risk of nest predation (Spearman $\rho = 0.30$, $df = 5$, $p = 0.30$; Figure 5b), and only *Certhia americana* exhibited a percent change that was significantly different from zero (Figure 5b).

DISCUSSION

Studies of phenotypic plasticity have historically been limited to environmentally induced changes in morphology and life histories, while plasticity in behavioral traits has been relatively understudied (Carroll and Corneli, 1999). Yet understanding the factors that influence behavioral plasticity may play an es-

sential role in understanding the selective pressures creating variation in parental care strategies within and across species. Here we experimentally tested whether parents of five coexisting, cavity-nesting species were able to perceive an increase in the risk of nest predation and adjust their behavior accordingly. We found strong evidence that males of all species recognize a potential nest predator and respond by reducing their incubation feeding rates (Figures 2 and 4a). A reduction in incubation feeding is assumed to be an adaptive strategy that reduces the risk of drawing the attention of visually oriented predators to the nest (see also Ghalambor and Martin, 2000, 2001; Martin et al., 2000a,b). By conducting experiments in a comparative framework, we were also able to test and demonstrate that the slope of the behavioral responses (Figure 4a) and the magnitude of change (Figure 5a) in incubation feeding rates increased as the risk of nest predation increased across species. Thus, differences in the risk of nest predation across species predict variation in both the mean incubation feeding rates (Figure 1) and plasticity in incubation feeding rate in the presence of a nest predator (Figures 4a and 5a). These results are consistent with the previously proposed hypothesis that variation in incubation feeding rates among species has evolved in response to differences in the ambient risk of nest predation (Martin and Ghalambor, 1999).

In contrast to male incubation feeding rates, females did

**Figure 3**

Change in nest attentiveness for five closely related species. Shown is the mean (\pm SE) nest attentiveness during pre-presentation (no model; filled bars) and presentation (model; open bars) time periods for days when a control (junco) and a predator (squirrel) model were presented.

not generally modify their time on the nest incubating eggs in response to nest predator presentations, despite a reduction in the amount of food received from the male (Figures 3 and 4b). Below we discuss the implications of these results for our understanding of parental care tactics during incubation and for behavioral plasticity in general.

Response to predation risk within species

Strategic or adaptive changes in behavior that affect fitness often depend on the ability of an individual to monitor changes in the environment (e.g., Moran, 1992). We found reductions in feeding visits by males in the presence of the squirrel model, but a lack of response to the control model, indicating that birds are able to track changes in immediate predation risk (Figure 2). Males were never observed attacking the predator model or engaging in other types of behavior near the nest, suggesting that males trade the benefits of food delivery to the female against the costs of attracting attention to the nest by reducing visits to the nest in the presence of a nest predator. Yet, a reduction in food delivered to females is also predicted to have costs in the form of reduced female nest attentiveness because females are forced off the nest to forage for themselves. Numerous studies have found that nest attentiveness by females is highly responsive to changes in food

delivered by males (e.g., Lifjeld and Slagsvold, 1986; Lyon and Montgomerie, 1985; von Haartman, 1958). Yet only *Certhia americana* showed a change in nest attentiveness between days when a predator and a control model were presented (Figure 3), and, contrary to our prediction, attentiveness increased rather than decreased (see also Figure 4b). We see two possible explanations for this discrepancy. First, a lack of reduction in female nest attentiveness may simply reflect the short-term (90 min) duration of the presentations, where females were able to maintain nest attentiveness without compromising their energy balance. Second, females, like males, may perceive the increased risk of nest predation and maintain nest attentiveness as a strategy to reduce risk to eggs (Beissinger et al., 1998; Kleindorfer and Hoi, 1997; Marzluff, 1985; Thompson and Raveling, 1987). Incubating females of the three nuthatch species are very effective at deterring squirrels using antipredator displays at the nest (see Ghalambor and Martin, 1999; Kingery and Ghalambor, 2001), but no comparable data are available for the other two species. In response to both an increased risk of nest predation and a reduction in food from the males, females may be faced with the conflicting pressures of needing to get off the nest to forage versus spending time on the nest for defense, independent of the thermal requirements of the eggs (see also Beissinger et al., 1998; Thompson and Raveling, 1987). Similar

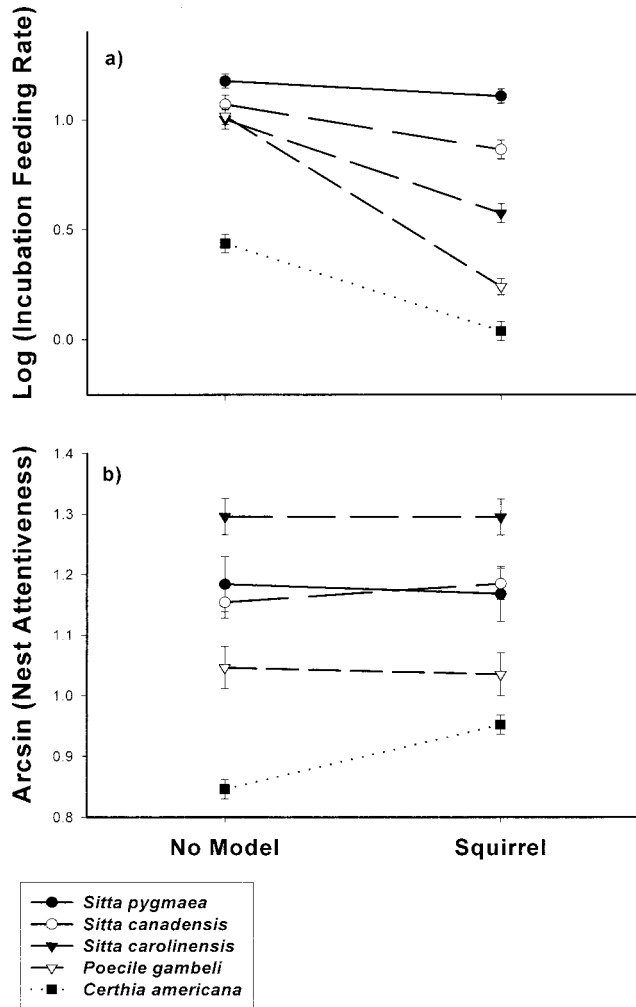


Figure 4
Interspecific comparison of the slope of change in behavioral responses for (a) incubation feeding and (b) nest attentiveness during pre-presentation (no model) and predator presentation time periods.

experiments to those conducted here on species where males do not feed females could test the effects of nest predation risk on female behavior independent of changes in male food delivery.

The observed responses to predator presentations should also be sensitive to the type of nest predator encountered. We chose to use a squirrel model for our predator presentations because squirrels are the most common nest predator of all cavity-nesting birds on our study site (Martin, 1993; Martin and Li, 1992) and because squirrels have been observed using parental activity as a cue to finding the location of nest sites (Ghalambor and Martin, unpublished data). However, nest predators may differ in the level of risk they pose and how that risk is perceived by nesting birds. For example, Steller's jays (*Cyanocitta stelleri*) are also highly visual and common nest predators at this study site, but they have difficulty accessing the deeper cavity nests of *Sitta pygmaea* and *Sitta canadensis* (Ghalambor and Kingery, 2001; Ghalambor and Martin, 1999). Had we used a Steller's jay model, it is possible that *S. pygmaea* and *S. canadensis* would have not modified their incubation feeding rates. Indeed, in other experiments we have shown that cavity-nesting species respond less strongly to a jay model than do coexisting, open-cup-nesting species (Ghal-

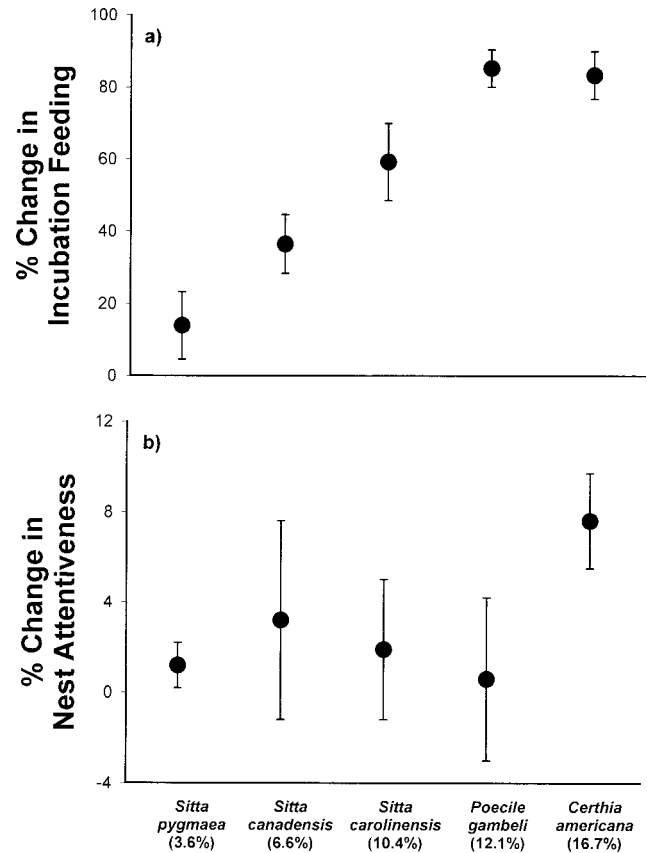


Figure 5
Interspecific comparison of standardized changes in (a) incubation feeding rate and (b) nest attentiveness in response to predator presentations. Species are arranged by order of nest predation risk (percent nest predation in parentheses under species name).

ambor and Martin, 2001). Thus, the type of predator encountered near the nest may elicit different responses, and future studies should explore how birds alter their behavior to the suite of predators with which they coexist.

Response to predation risk across species

Differences among species in behavioral responses to the predator model are most obvious for incubation feeding (Figure 4a). For example, incubation feeding rates drop to almost zero in the presence of the predator model in *Poecile gambeli*, a species with a relatively high risk of predation, whereas feeding rates decrease only slightly in *Sitta pygmaea*, the species with lowest risk of nest predation (Figure 4a). These differences in behavioral plasticity exist despite presentation of the same standardized predator stimulus. Such results may reflect that behavioral plasticity has evolved in response to different predation rates (see below). Other comparative studies of behavioral plasticity among populations and species have found similar support for variation in plastic responses as an adaptation to different environmental conditions (Blouin, 1992; Giles and Huntingford, 1984; Rodd et al., 1997). Ultimately, however, data on the heritabilities of these behavioral responses are needed before we can conclude whether the differences in plasticity among species reflect evolved or learned differences. In contrast to the male response, the absolute change and the percent change in female nest attentiveness did not vary among any of the species except *Certhia americana*, which increased its nest attentiveness in response to the

predator model (Figures 4b and 5b). Further investigation into the behavioral changes of incubating females in response to nest predators is clearly warranted, particularly in the majority of species where females must resolve the trade-off between time on the nest incubating and time off the nest foraging without male assistance.

One interesting aspect of our results that warrants discussion is the relationship between mean incubation feeding rates and associated plasticity. Increased levels of nest predation are associated with lower mean incubation feeding rates among species (Figure 1; Martin and Ghalambor, 1999). A consequence of low baseline incubation feeding rates is that the potential for plasticity is reduced in species at very high risk of nest predation because males feed females infrequently. This is the case for *Certhia americana*, where males feed incubating females at a much lower rate than the other four species (Figure 4a). Thus, although in response to the predator model *C. americana* males reduced feeding visits to near zero, the absolute change in feeding was relatively small compared to the other species (Figure 4a). The slope of change measuring the plastic response in incubation feeding is therefore more shallow in *C. americana* than expected given its risk of nest predation. We attempted to correct for this effect by converting absolute changes in incubation feeding to percentage changes in order to standardize the response across species (Figure 5a). These standardized responses also show a strong relationship between the magnitude of change and risk of nest predation that asymptotes as incubation feeding approaches zero in the presence of the predator (Figure 5a). However, it is important to recognize that the same absolute change will have a larger standardized effect in species that feed less frequently, such as *C. americana*, making even standardized comparisons across species problematic if large differences exist in baseline feeding rates. In terms of the costs and benefits associated with incubation feeding under the risk of predation, what we ultimately need to know is how much absolute versus relative reductions in food to the female influence both the probability of nest predation and the female's energetic demands in different species.

Implications for the evolution of behavioral plasticity

Behavioral traits, like other phenotypic traits, vary as a function of the interaction between genes and the environment (see Carroll and Corneli, 1999). The norm of reaction or set of phenotypes expressed across a range of environments by a single genotype is the conceptual framework most often used in studies of plasticity (e.g., Stearns, 1989). However, reaction norms can also be considered properties of any genetically related group of individuals, such as clones, populations, or species. To the extent that reaction norms are heritable, comparisons of the slopes of reaction norms provide insight into the evolution of plastic traits (e.g., Doughty, 1995; Gotthard and Nylin, 1995; Scheiner, 1993). Nonparallel norms of reaction can be used as evidence for the evolution of phenotypic plasticity to different selective environments (Blouin, 1992; Carroll and Corneli, 1999; Doughty, 1995; Gotthard and Nylin, 1995; Thompson, 1999). In the present study we found strong evidence for nonparallel norms of reaction among species with respect to male incubation feeding rate but weak evidence for female nest attentiveness (Figure 4). Had the slopes for changes in incubation feeding been parallel, our results would have suggested that, while mean differences exist in incubation feeding, the behavioral response to a potential predator was similar among species. The nonparallel slopes we observed suggest that plasticity associated with incubation feeding has diverged among species, and this divergence is strongly associated with differences in the risk of nest

predation across species. Because manipulative experiments in behavioral ecology are typically carried out on single species and within single populations, the comparative results observed here are rare, yet they may be highly informative regarding the environmental forces responsible for variation in behaviors. Had we carried out this study on only *S. pygmaea*, we may have concluded that nest predators have a weak to marginal effect on parental behavior; whereas if we had studied only *S. carolinensis*, we would have concluded that predation risk has a very strong effect. Only by placing these experiments within a comparative context is the relationship between parental behavior and nest predation revealed. Indeed, we have recently conducted similar experiments during the nestling period on 10 species that fall along a nest predation gradient and found similar results to those presented here (Ghalambor and Martin, 2001, unpublished data). Thus, there appears to be a general pattern between how strongly birds respond to nest predators and their ambient risk of nest predation.

We thank Pam Watts, Paul Martin, and Chavez del Agua for help with the predator presentation experiments and many field assistants for help collecting the other field data that made this study possible. We thank the Arizona Game and Fish Agency, Blue Ridge Ranger Station of the Coconino National Forest, and the Apache-Sitgreaves National Forest for their support of this work. This study was supported by grants to T.E.M. from the National Science Foundation (DEB-9407587, DEB-9527318, DEB-9707598), and the BBIRD (Breeding Biology Research and Monitoring Database) program under the Global Change Research Program of the U.S. Biological Resources Division. C.K.G. was supported in part by a doctoral dissertation improvement grant from the National Science Foundation (IBN-9701116). This manuscript was improved by discussions and comments from Farrah Bashey, Alex Badyaev, Scott Carroll, Michael Bryant, Dionna Elder, David Reznick, Paul Martin, Trevor Price, David Westneat, Marlene Zuk, and one anonymous reviewer.

REFERENCES

- Badyaev AV, Ghalambor CK, 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* 82:2948–2960.
- Beissinger SR, Tygielski S, Elder B, 1998. Social constraints on the onset of incubation in a neotropical parrot: a nestbox addition experiment. *Anim Behav* 55:21–32.
- Blouin MS, 1992. Comparing bivariate reaction norms among species: time and size at metamorphosis in three species of *Hyla* (Anura: Hylidae). *Oecologia* 90:288–293.
- Brodie ED III, 1989. Behavioral modification as a means of reducing the cost of reproduction. *Am Nat* 134:225–238.
- Carlisle TR, 1982. Brood success in variable environments: implications for parental care allocation. *Anim Behav* 30:824–836.
- Carroll SP, Corneli PS, 1999. The evolution of behavioral norms of reaction as a problem in ecological genetics. In: *Geographic variation in behavior* (Foster S, Endler J, eds). Oxford: Oxford University Press; 53–68.
- Clutton-Brock TH, 1991. *The evolution of parental care*. Princeton, New Jersey: Princeton University Press.
- Conway C, Martin TE, 2000a. Effects of ambient temperature on avian incubation behavior. *Behav Ecol* 11:178–188.
- Conway C, Martin TE, 2000b. Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution* 52:670–685.
- Doughty P, 1995. Testing the ecological correlates of phenotypically plastic traits within a phylogenetic framework. *Acta Oecol* 16:519–524.
- Ghalambor CK, 1998. Ecological and evolutionary determinants of incubation strategies in three sympatric nuthatches (Sittidae) (PhD dissertation). Missoula: University of Montana.
- Ghalambor CK, Martin TE, 1999. Red-breasted nuthatch (*Sitta canadensis*). In: *The birds of North America*, no. 459 (Poole A, Gill F, eds). Philadelphia: The Birds of North America; 1–28.

- 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.
- Giles N, Huntingford, FA, 1984. Predation risk and inter-population variation in anti-predator behavior in the three-spined stickleback. *Anim Behav* 32:264–275.
- Gotthard K, Nylin S, 1995. Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos* 74:3–17.
- Haftorn S, 1988. Incubating female passerines do not let egg temperature fall below the physiological zero temperature during their absences from the nest. *Ornis Scand* 19:97–110.
- Halupka K, 1994. Incubation feeding in the meadow pipit *Anthus pratensis* affects female time budget. *J Avian Biol* 25:251–253.
- Harrap S, Quinn D, 1995. Chickadees, tits, nuthatches, and treecreepers. Princeton, New Jersey: Princeton University Press.
- Kingery H, Ghalambor CK, 2001. Pygmy nuthatch (*Sitta pygmaea*). In: *The birds of North America* (Poole A, Gill F, eds). Philadelphia: The Birds of North America.
- Kleindorfer S, Hoi H, 1997. Nest predation avoidance: an alternative explanation for male incubation in *Acrocephalus melanopogon*. *Ethology* 103:619–631.
- Lawler SP, 1989. Behavioral responses to predators and predation risk in four species of larval anurans. *Anim Behav* 38:1039–1047.
- Lifjeld JT, Slagsvold T, 1986. The function of courtship feeding during incubation in the pied flycatcher *Ficedula hypoleuca*. *Anim Behav* 34:1441–1453.
- Lima SL, 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27:215–290.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Lyon B, Montgomerie R, 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? *Behav Ecol Sociobiol* 17:279–284.
- Lyon B, Montgomerie R, 1987. Ecological correlates of incubation feeding: a comparative study of high arctic finches. *Ecology* 68:713–722.
- Martin TE, 1992. Interaction of nest predation and food limitation in reproductive strategies. *Curr Ornithol* 9:163–197.
- Martin TE, 1993. Nest predation and nest sites: new perspectives on old patterns. *Bioscience* 43:523–532.
- Martin TE, 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* 79:656–670.
- Martin TE, Ghalambor CK, 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? *Am Nat* 153:131–139.
- Martin TE, Li P, 1992. Life history traits of open versus cavity-nesting birds. *Ecology* 73:579–592.
- 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.
- Marzluff JM, 1985. Behavior at a pinyon jay nest in response to predation. *Condor* 87:559–561.
- Montgomerie RD, Weatherhead PJ, 1988. Risks and rewards of nest defense by parent birds. *Q Rev Biol* 63:167–187.
- Moran NA, 1992. The evolutionary maintenance of alternative phenotypes. *Am Nat* 139:971–989.
- Moreno J, 1989. Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe* (L.). *Ardea* 77:107–115.
- Rodd FH, Reznick DN, Sokolowski M, 1997. Phenotypic plasticity in the life history traits of Trinidadian guppies. *Ecology* 78:419–433.
- Roff D, 1992. The evolution of life histories: theory and analysis. New York: Chapman and Hall.
- Scheiner SM, 1993. Genetics and the evolution of phenotypic plasticity. *Annu Rev Ecol Syst* 24:35–68.
- Sibley CG, Ahlquist J, 1990. Phylogeny and classification of birds: a study in molecular evolution. New Haven, Connecticut: Yale University Press.
- Sih A, Kats LB, Moore RD, 1992. Effects of predatory sunfish on the density, drift and refuge use of stream salamander larvae. *Ecology* 73:1418–1430.
- Skutch AF, 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430–455.
- Smith HG, Kallander H, Hultman J, Sanzen B, 1989. Female nutritional state affects the rate of male incubation feeding in the pied flycatcher *Ficedula hypoleuca*. *Behav Ecol Sociobiol* 24:417–420.
- Stearns S, 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 39:436–445.
- Stearns S, 1992. The evolution of life histories. Oxford: Oxford University Press.
- Thompson DB, 1999. Different spatial scales of natural selection and gene flow. In: *Geographic variation in behavior* (Foster S, Endler, J eds). Oxford: Oxford University Press; 33–51.
- Thompson SC, Raveling DG, 1987. Incubation behavior of emperor geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707–716.
- von Haartman L, 1958. The incubation rhythm of the femal pied flycatcher (*Ficedula hypoleuca*) in the presence and absence of the male. *Ornis Fenn* 35:71–76.
- Weathers WW, Sullivan KA, 1989. Nest attentiveness and egg temperature in the yellow-eyed junco. *Condor* 91:628–633.
- White FN, Kinney JL, 1974. Avian incubation. *Science* 186:197–115.
- Williams JB, 1996. Energetics of avian incubation. In: *Avian energetics and nutritional ecology* (Carey C, ed). New York: Chapman Hall, 375–415.