Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort

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Life-history theory predicts that differences in reproductive effort and residual reproductive value among species should result in differences in the level of risk that parents are willing to tolerate to themselves versus their offspring. Specifically, highly fecund and shorter-lived species are expected to place greater value in current offspring than themselves, whereas less fecund and longer-lived species are expected to place greater value in their own survival and future breeding opportunities. Here, we test the prediction that parental investment decisions are correlated with life histories by comparing risk-taking behaviour in two species of nuthatch that differ in reproductive effort: the white-breasted nuthatch, *Sitta carolinensis* (more fecund, lower survival) and the red-breasted nuthatch, *S. canadensis* (less fecund, higher survival). We experimentally manipulated stage-specific predation risk by presenting models of an adult predator (hawk) and an egg predator (wren) and measured the willingness of males to feed incubating females on the nest. We found that both species of nuthatch responded to predators by increasing the length of time between visits and aborting more visits to the nest. However, as predicted by their life histories, *S. carolinensis* displayed a significantly stronger response to the egg predator, whereas *S. canadensis* responded more strongly to the adult predator. Thus, species can differ in their willingness to tolerate risk to themselves and their young, and such differences appear to be related to differences in investment in current reproduction and the probability of future survival.

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Life-history theory predicts that variation in parental risk taking should reflect differences in the proportion of resources allocated towards reproduction (i.e. an organism's reproductive effort; Williams 1966; Trivers 1972; Curio 1988; Montgomerie & Weatherhead 1988; Clutton-Brock 1991; Martin 1992; Roff 1992; Stearns 1992). In particular, adults of longer-lived and less fecund species should be less willing to place themselves at risk compared with their offspring because investment in current reproduction is reduced and the probability of future breeding opportunities is high, whereas adults of shorter-lived, less fecund species should be less willing to place their offspring at risk compared with themselves because investment in current reproduction is high and future breeding opportunities are limited. These predictions are based on the underlying trade-off between reproduction and survival, resulting in species with higher reproductive effort also having lower residual reproductive value (e.g. Charlesworth 1980). However, while trade-offs between

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fecundity and survival among species are commonly observed (e.g. Bennett & Harvey 1988; Saether 1988; Martin 1995), correlated changes in parental investment strategies along the fecundity-survival trade-off function have gone largely untested. Variation in risk-taking behaviour among species may be a particularly effective indicator of parental investment strategies. Indeed, empirical studies of risk taking within species suggest that parents are capable of (1) recognizing predators as threats, (2) assessing the fitness value of the current brood relative to the value of future broods and (3) making 'appropriate' parental investment decisions (e.g. Coleman et al. 1985; Redondo & Carranza 1989; Dale et al. 1996; Candolin 1998). However, few studies have attempted to separate between risk to the parents attempting to provide care versus risk to vulnerable offspring (but see Dale et al. 1996), and no study to date has examined whether risk taking in response to such stage-specific predators (predators of adults versus offspring) differs among species with different life-history strategies.

Here we test the influence of fecundity and survival on parental investment strategies by comparing male risk-taking behaviour in two coexisting nuthatches: the white-breasted, *Sitta carolinensis*, and red-breasted,

S. canadensis, nuthatch. Fecundity is higher in the single-brooded *S. carolinensis,* which has a mean clutch size of 7.3 eggs (Pravosudov & Grubb 1993), than the similarly single-brooded *S. canadensis* which has a mean clutch size of 5.7 eggs (Ghalambor & Martin 1999). Estimated mean $\pm$ SE annual adult survival for *S. carolinensis* from Maryland is 0.35 ± 0.01 (Jolly-Seber model with constant capture and survival probability; Karr et al. 1990). An identical model for our study sites in Arizona yielded an even lower value of 0.12 ± 0.06, but sample size was low ($N=33$; T. E. Martin, unpublished data). Estimated mean annual adult survival for *S. canadensis* on our Arizona study site ranged from 0.46 ± 0.19 (Jolly-Seber model that excludes an irruptive migration year) to 0.87 ± 0.33 (Jolly-Seber estimate that controls for first year capture effects; $N=196$, T. E. Martin, unpublished data). Although survival estimates vary, in all cases the estimated mean annual survival of *S. canadensis* is greater than that of *S. carolinensis,* as predicted by their fecundity. Thus, these two species are ideal for comparative studies that use standardized experiments because they differ in fecundity and survival, are closely related phylogenetically (Sibley & Ahlquist 1990), and are ecologically similar (i.e. cavity nesting; insectivorous; socially monogamous; biparental care).

Males of both species provide indirect care of the young by commonly feeding females during incubation (rates can be as high 20 feeds/h), providing an important food source that allows females to spend more time on the nest, and in turn shortens the incubation period and increases hatching success of eggs (e.g. Lyon & Montgomerie 1985, 1987; Martin & Ghalambor 1999). However, visits to the nest by the male to feed the incubating female also pose a cost. Frequent visits to the nest increase the risk to offspring because visual nest predators can use parental activity to find nests (e.g. Martin & Ghalambor 1999). In addition, frequent visits to the nest also increase risk to the male from visual adult predators such as hawks (e.g. Lima 1987; T. E. Martin, unpublished data). Here, we test the prediction that male *S. carolinensis* should tolerate more risk to itself and be less willing to put its offspring at risk, because of its higher investment in current reproduction relative to *S. canadensis* (sensu Curio 1988; Magnhagen 1990; Dale et al. 1996). In contrast, male *S. canadensis* should be less willing to put itself at risk and more willing to put its young at risk, because of its reduced investment in current reproduction and greater probability of future breeding. To isolate and test predation risk to the male versus the offspring independently, we measured the willingness of males to feed incubating females in the presence of both an adult predator and an egg predator.

METHODS

Study sites were high-elevation (2600 m) snow melt drainages on the Mogollon Rim, Arizona, U.S.A. A detailed description of the vegetation on these study sites is provided in Martin (1998). Study sites were searched for nests from May through to late June of 1996 and 1997. All nests were in natural cavities and were intensively monitored to assess breeding stage (i.e. egg laying, incubation, nestling). In order to separate between risk to parents and young we presented models of a predator of eggs and a predator of adults at nests of incubating *S. carolinensis* and *S. canadensis.* A total of 19 nests were found for both species ($N=9$, *S. carolinensis*; $N=10$, *S. canadensis*), and all experiments were carried out between days 6 and 10 of the incubation period. The majority of males and females used in this study were uniquely colour banded and there was never any indication of more than a single male visiting the nest to feed the incubating female.

The goal of model presentations was to increase the perceived risk of predation near the nest without eliciting nest defence behaviour, such that males would continue to feed incubating females. We chose two common predators that naturally occur on these study sites: the house wren, *Troglodytes aedon,* a common predator of eggs (Belles-Isles & Picman 1986; personal observation) but of no threat to adults, and the sharp-shinned hawk, *Accipiter striatus,* a common predator of adults but not of eggs. We compared the response to predator models to a control model of a small sparrow, the dark-eyed junco, *Junco hyemalis,* which represents no known threat to adults or eggs. We assume that males flying to the nest in the presence of the hawk risk attracting attention to themselves, thus increasing their own predation risk, whereas flying to the nest in the presence of the wren attracts attention to the nest site and increases the risk of nest predation. A number of theoretical and empirical studies suggest that these are reasonable assumptions (e.g. Skutch 1949; Lima 1987; Lyon & Montgomerie 1987; Martin 1992; Martin & Ghalambor 1999; Martin et al. 2000). We compared behavioural responses to taxidermic mounts of a wren, hawk and sparrow that were presented in a stratified random order on three consecutive days. To control for possible time-of-day effects, observations of each individual were started at the same time each day. Models were attached to a small quaking aspen (*Populus tremuloides*) or canyon maple (*Acer grandidentatum*) sapling within 6–8 m of the nest tree, and the location was held constant for each model. In addition, we played taped vocalizations for each model species from a cassette player placed at the base of the sapling where the model was perched to increase detectability of the models. Use of vocalizations with the model is also particularly effective in preventing habituation to the model alone (unpublished data).

We measured two response variables as an index of risk taking. First, we focused on the male's willingness to visit the nest and feed the female. We recorded the amount of time elapsed from the time the nest was exposed to the model until the time when the nest was visited by the male (see also Dale et al. 1996). Nests were observed from a blind ca. 20 m from the nest tree. To control for any observer effects, observations began after the male had fed the female at least five times. Following the fifth feeding visit, the model was presented and vocalizations of the model species were broadcast. The second variable measured was the number of aborted visits to the nest by the male during the time from when the model

presentations started until the nest was visited by the male. A visit was characterized as 'aborted' if the male approached the nest with food but then abandoned his attempt to feed the female and did not visit the nest within the following 60 s. Because males frequently vocalize while foraging, in almost every case we were able to follow the location of the male after aborting the visit. In those cases where the feeding visit was aborted, the male retained the food item in his bill and continued to forage at a distance greater than 20 m from the nest tree. Observations ended after the male fed the incubating female.

To test for differences in behavioural response to the different models, we first compared the response of both species to the different models (i.e. control, egg predator and adult predator) using analysis of variance (ANOVA). We then compared the difference in response between the control and egg predator, and the control and adult predator for both nuthatches using a paired t test. This method allowed us to compare the response of the nuthatches to the different predator models while controlling for individual variation within each species.

RESULTS

The mean elapsed time between nest visits in the presence of the control model (ca. 5 min) was similar for both nuthatch species (Fig. 1a) and similar to that observed under natural conditions (Ghalambor 1998), suggesting that the sparrow represents a good control. However, both nuthatch species increased the amount of time between nest visits and the number of aborted visits in response to the egg and adult predator (Fig. 1a, b). Elapsed time between visits increased to as much as 63 min in response to the hawk model and as much as 38 min in response to the wren model. *Sitta canadensis* males aborted feeding visits as many as three times in the presence of the hawk model, whereas *S. carolinensis* males aborted visits as many as two times in the presence of the wren model. Indeed, both *S. carolinensis* and *S. canadensis* aborted feeding visits only in the presence of predators, and were never observed aborting a nest visit in the presence of the control model (Fig. 1b). The order in which models were presented did not have a significant effect on either the elapsed time between visits (ANOVA: $F_{5,49}=1.14$, $P=0.035$) or the number of aborted visits (ANOVA: $F_{5,49}=1.05$, $P=0.40$), and there was no significant interaction effect between order of presentation and species. However, mean elapsed time between male nest visits and the number of aborted visits both showed a significant model type by bird species interaction indicating differing responses to the two predator types by the nuthatch species (Fig. 1a, b). Comparisons of responses within each species of nuthatch show *S. carolinensis* took significantly more time to visit the nest and aborted more visits in the presence of the egg predator than the adult predator (Fig. 2a, b). In contrast, *S. canadensis* took significantly more time to visit the nest and aborted more visits in the presence of the adult predator than the egg predator (Fig. 2a, b).
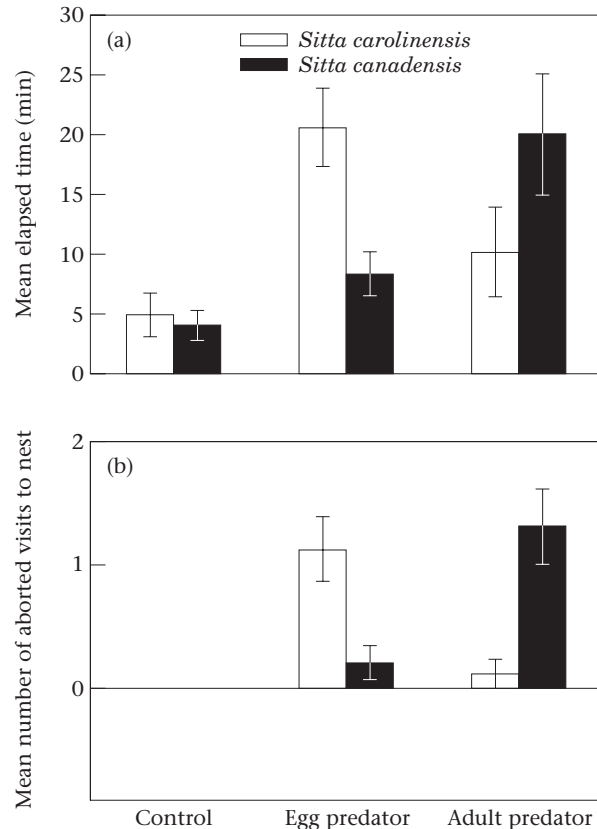

Figure 1. (a) Mean±SE elapsed time (min) until the nest was visited by males in response to three different models: control: *Junco hyemalis*; egg predator: *Troglodytes aedon*; adult predator: *Accipiter striatus*. The interaction term between model type and species was highly significant (ANOVA: $F_{4,17}=3.61$, $P<0.05$). (b) Mean±SE number of aborted visits to the nest by males in response to the three different models (as above). The interaction term between model type and species was also highly significant (ANOVA: $F_{4,17}=12.62$, $P<0.001$).

DISCUSSION

Differences among species in reproduction and survival schedules can influence the fitness value of current and future offspring leading to differences in how parents value their own survival versus the survival of their offspring. Comparative studies of life-history strategies have largely focused on the covariation of fecundity and survival (e.g. Ekman & Askenmo 1986; Bennett & Harvey 1988; Saether 1988; Martin 1995), while correlated changes in parental investment patterns have received less attention. In this study we found that both species of nuthatch were risk averse in response to predator models compared with a control model as measured by the amount of time elapsed between nest visits after models were presented and in the number of aborted visits to the nest (Figs 1, 2). These results suggest that both species of nuthatch recognized predator models as possible threats and were capable of adjusting their behaviour accordingly. However, *S. carolinensis* aborted more visits and took more time before visiting the nest in the presence of an egg predator compared with an adult predator,
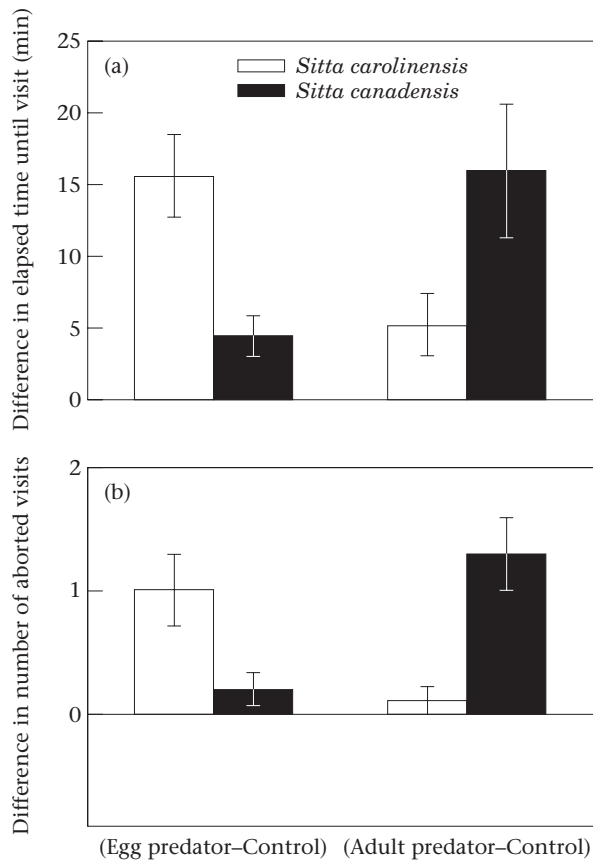
Figure 2. (a) Difference in the amount of time elapsed between nest visits (control–egg predator) and (control–adult predator) for both species of nuthatch. In comparisons of the difference between the control model and the two predator types, *S. carolinensis* took significantly longer to visit in the presence of the egg predator (paired *t* test: $t_8 = -2.75$, $P = 0.02$), whereas *S. canadensis* took significantly longer to visit the nest in the presence of the adult predator (paired *t* test: $t_9 = 3.29$, $P < 0.01$). (b) Difference in the number of aborted visits to the nest (as above) for both species of nuthatch. *Sitta carolinensis* aborted significantly more visits in response to the egg predator (paired *t* test: $t_8 = -2.53$, $P = 0.03$), whereas *S. canadensis* aborted significantly more visits in response to the adult predator (paired *t* test: $t_9 = 3.97$, $P < 0.01$).

whereas the reverse was true for *S. canadensis* (Figs 1, 2). These differences reflect the different life-history strategies of these two species and suggest *S. carolinensis* places relatively greater value in its current offspring, while *S. canadensis* places greater value in its own survival and future breeding opportunities. Thus, our results support predictions from two theoretical life-history models that specifically address parental care behaviour: (1) parental risk taking increases with reproductive effort and reduced residual reproductive value (Curio 1988), and (2) when the risk of predation is directed to parents rather than young, species with reduced residual reproductive value should be more willing to place themselves at greater risk, and less likely to withhold care (Dale et al. 1996).

The risk of predation to parents or offspring has long been thought to constrain parental investment strategies (e.g. Skutch 1949; Lima 1987; Martin 1992). Indeed, we have previously shown that among both open- and hole-

nesting bird species the frequency of males feeding females is negatively correlated with their risk of nest predation (Martin & Ghalambor 1999). Our results here provide experimental evidence that predation risk can indeed reduce incubation feeding rates. Reduced food delivery by the male has been shown to increase the amount of time that females must spend off the nest foraging for themselves both within (e.g. Lyon & Montgomerie 1985) and between species (Martin & Ghalambor 1999). Our results showing a causal relationship between predation risk and incubation feeding suggest that such effects may have extended costs to female nest attentiveness.

Experimental tests of parental investment strategies are typically conducted on single species, whereas comparisons between species are rare. A comparative approach that uses standardized methods and controls for phylogeny, by comparing closely related species that are similar in behaviour and ecology, may provide a particularly useful method for experimentally testing differences in parental investment strategies. For example, in comparisons of risk taking in both tropical-nesting passerines and temperate-nesting ducks, life-history differences among species were correlated with 'risky' behaviour (Ricklefs 1977; Forbes et al. 1994). As predicted, more fecund, shorter-lived species were more willing to put themselves at risk when defending their nests against human intruders (Ricklefs 1977; Forbes et al. 1994). Similarly, in a comparison between short-lived and long-lived gobies reproducing under the risk of predation, Magnhagen (1990) found the shorter-lived species took more risks than the longer-lived species. We have also used an approach similar to the one used in this study across a larger number of species and found as life-history differences become larger, so does the magnitude of response to the predator models (C. K. Ghalambor, M. Bazzalo, S. Peluc, & T. E. Martin, unpublished data). However, interspecific comparisons of risk taking have been cautioned against because species may differ in risk taking for reasons other than their life histories (e.g. Ricklefs 1977; Montgomerie & Weatherhead 1988). Such caution is warranted, particularly because risk taking may differ among species as a correlated response to selection pressures other than those related to an organism's life-history strategy (see Price & Langen 1992). For example, the two species in this study differ in their risk of egg predation (*S. carolinensis* > *S. canadensis*) such that observed differences in response to the egg predator may simply reflect differences in the risk of egg predation (Martin & Ghalambor 1999). However, by partitioning predation risk between parents and young, we were able to isolate and test the effects of egg versus adult predators independently (following Dale et al. 1996). Thus, while caution is necessary in interspecific comparisons, especially when only two species are involved, appropriate experiments among closely related and ecologically similar species can minimize such concerns and allow for greater inference into evolutionary relationships that are difficult to test in single-species studies.

Finally, because variation in stage-specific mortality can drive life-history evolution (Reznick et al. 1990, 1997;

Magnhagen 1991; Martin 1995), understanding the relationship between parental investment decisions and stage-specific predation risk is a critical component of life-history strategies. If parental investment decisions are correlated with reproductive effort as the results here suggest, then future work should consider the degree to which such parental behaviours are genetically correlated with and evolve alongside traditionally measured life-history traits such as clutch size and adult survival (e.g. Brodie 1989).

Acknowledgments

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