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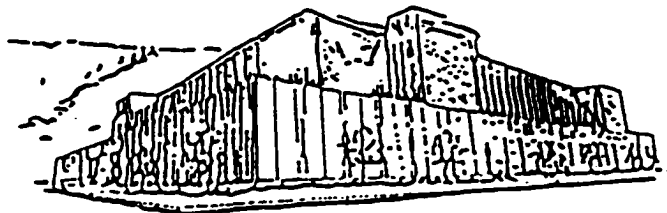
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ECOLOGICAL AND EVOLUTIONARY DETERMINANTS OF INCUBATION
STRATEGIES IN THREE SYMPATRIC NUTHATCHES (*Sittidae*)

by

Cameron K. Ghalambor

B.A., University of California, Los Angeles, 1991

Presented in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

UNIVERSITY OF MONTANA

1998

Approved by:



Chair, Board of Examiners



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ABSTRACT

Ghalambor, Cameron K., Ph.D., Spring 1998

Organismal Biology and Ecology

Ecological and evolutionary determinants of incubation strategies in three sympatric nuthatches (*Sittidae*) (128 pp.)

Advisor: Thomas E. Martin *TEM*

Incubation is a fundamental form of parental care where parents must resolve a trade-off between spending time on the nest to maximize egg survival versus time off the nest meeting their own nutritional needs. Variation in nest microclimate, predation risk, and breeding opportunities can influence this trade-off and lead to variation in incubation tactics within and among species. In a comparison of three sympatric nuthatches, I find that parental activity at the nest decreases and percentage of time females spend on the nest increases with increasing risk of nest predation and decreasing opportunities for re-nesting, while there is no relationship between nest microclimate and incubation behavior among species. Nest microclimate explains some within-species variation. Three sets of experiments support this conclusion. First, when nest-predation risk was experimentally increased using a taxidermic mount of a common nest predator, the three species of nuthatch decreased activity at the nest through reduced incubation feeding. Second, when nest temperature was experimentally increased and decreased by pumping compressed air into nest cavities, the species most limited in its breeding opportunities, *Sitta carolinensis*, did not modify either nest attentiveness or incubation feeding rates. In contrast, the species least limited in breeding opportunities, *Sitta canadensis*, responded as predicted by increasing nest attentiveness and incubation feeding rates when the nest was cooled, and decreased these behaviors when the nest was warmed, thus exhibiting greater behavior plasticity in response to changes in temperature. Therefore, the proximate response to temperature appears to differ among species, and I suggest that limited breeding opportunities result in the maintenance of a fixed and high level of attentiveness in *Sitta carolinensis* as a tactic to defend cavities from competitors and predators. Finally, in a third experiment in which *Sitta carolinensis* and *Sitta canadensis* were exposed to taxidermic mounts of a predator of eggs and a predator of adults, *Sitta carolinensis* responded more strongly to the egg predator where *Sitta canadensis* responded more strongly to the adult predator. These results support the hypothesis that evolutionary differences in life-history strategies associated with limited breeding opportunities directly influence proximate responses within species.

ACKNOWLEDGMENTS

I am truly grateful to have had the opportunity to pursue a graduate education in Biology. I began graduate school with a naive enthusiasm for science and my ability to understand the natural world. Six years later, I finish graduate school with my naive enthusiasm still intact. The more I learn, the more easily impressed I am by the diversity of adaptations organisms possess, yet today I am skeptical of ever being able to fully understand the complexities of the natural world. As I have grown as a scientist, naturalist, and person over the last six years I am indebted to many people who have helped me along this arduous path towards enlightenment.

My advisor Tom Martin gave me the opportunity to pursue a graduate education by accepting me into his lab at the University of Arkansas in 1993. He provided me not only with the financial and logistic support I needed to carry out my research, but also with the intellectual tools to think critically about questions. Tom's "teas" were integral in helping me to think on my feet and in teaching me about humility. I finish my dissertation fully aware of the strong influence Tom has had on my life, and I am grateful for all his guidance and support.

Over the years I have also benefitted from being surrounded by some of the most amazing and talented people I have ever known. The "Martinheads" have inspired and propelled me in so many ways, I don't know where I would be without them. Shannon and Lindy Garner, Courtney Conway, Dave and Patti Barber, Alison Banks, Josh Tewksbury, Alex Badyaev, and Paul Martin have all been so important to my development through the examples they have set for me, and through their many helpful discussions.

They are all great people I am privileged to have been able to spend my graduate years surrounded by them.

I benefitted from having the guidance of a great dissertation committee, Joe Ball, Ken Dial, Bill Derrick, Eric Greene, Del Kilgore, and Jeff Marks all provided me with the support and help I needed to carry out my research. In the field, many field assistants gave generously of their time, but in particular Pam Watts and Chris Ormond were most helpful in helping me conduct experiments on nuthatches. At home, my housemates over the years, Paul Martin, John MacKay, Chavez del Agua, Stacy Drasen, Elizabeth Leaf, and Ben Conard were all influential in providing feedback on my research, as well as putting up with many hours of Tom Waits. In particular, I would like to thank Paul Martin for being there to remind me of why I decided to be a graduate student, and the importance of getting “dirty.”

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PREFACE

The chapters presented here represent a chronological process in time, and in my own thought development on the ideas I describe and discuss, thus each chapter builds upon ideas presented in previous chapters. Upon reflecting on all these chapters, I tried to ask a simple question: Why do species exhibit different incubation behaviors? I have learned that there is no simple answer. However, in summary, the common big picture theme that brings all my research together is the distinction that patterns in nature are hierarchical; ecological variation leads to proximate changes within species, but these proximate changes are subject to evolutionary constraints among species which interact in a manner far more complex than Hutchinson's simplistic theater and play. Thus, although these chapters my at times seem unrelated, they are tied together in my attempt to understand the processes that cause variation in incubation behaviors within and across species.

Chapter I review different hypotheses and describes natural patterns in the incubation behaviors of the three species of nuthatch that are the primary focus of my research. Natural variation among species suggests that the commonly held view that nest temperature effects are responsible for differences in incubation behaviors was not supported. Rather, it appears that in the three species studied variation in risk of nest predation and excavation ability are responsible for differences among species. Chapters II, III, and IV are experimental tests of the patterns presented in Chapter I. I am particularly excited by the results of these chapters because they suggest that proximate

responses to experiments observed within species, reflect evolutionary differences among species. While this may sound simplistic, I can find very few examples in the literature of studies which make this point explicitly. For example, in Chapter II the proximate response to risk of nest predation risk in the three nuthatches reflects differences among species in historic rates and consequences of nest predation. However, I should note that the measure of nest predation among the three species varies between Chapters I, II and III. In Chapter I, I use nest predation rates for the entire nesting period, this data is from Tom Martin's long term study of these three species. In Chapter II and III, I use nest predation rates only during the incubation period resulting in very different values. The confidence of nest predation rates during incubation is lower because of logistic difficulties in monitoring cavity nests. I am currently in the process of reviewing and improving the confidence of these data.

Chapter III documents that the proximate response to temperature within species is also constrained by differences in evolutionary history among species in excavation ability. And finally in Chapter IV, I find that the response to adult and egg predators also varies among species as a function of excavation ability and life-history strategies. In short, no single ecological factor (temperature, egg predator, adult predator) has a similar affect among species and it is only through comparative studies and experiments that this can be revealed.

One final point is that this dissertation was written so that each chapter could be submitted as a separate publication. Accordingly, each chapter was written in the format of a particular journal for which it was targeted. This approach results in repetition across

chapters of some information, such as methods and study site. Because each chapter has a terminal list of citations, some references are listed more than once. Also, throughout this work I refrain from using the word “I” and instead use “we” to describe any action taken. This is done because all the work presented represents a collaborative effort that “I” alone cannot take credit for.

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CHAPTER I

ECOLOGICAL AND EVOLUTIONARY DETERMINANTS OF AVIAN INCUBATION STRATEGIES: EFFECTS OF BODY SIZE, MICROCLIMATE, AND NEST PREDATION

INTRODUCTION

Variation in life-history strategies across species is thought to result from evolutionary solutions to fitness trade-offs imposed by different ecological conditions (Williams 1966, Southwood 1988, Reznick et al. 1990, Lessels 1991, Roff 1992, Stearns 1992, Martin 1995, Martin and Clobert 1996). Such trade-offs can exist at many levels of an organism's life history, including parental care decisions for species that care for altricial young (Williams 1966, Trivers 1972, Horn and Rubenstein 1984, Clutton-Brock 1991, Lima and Dill 1990, Clutton-Brock and Godfray 1991, Lessels 1991, Martin 1992). Avian incubation presents a classic example of trade-offs in parental care decisions that influence individual fitness. For example, in passerine species with intermittent incubation, females must regularly leave the nest during incubation to feed and meet their own nutritional requirements. Such absences from the nest may cause egg temperatures to reach levels that impair embryo development or even cause embryo mortality, and absences from the nest may restrict the female's ability to protect eggs against predators (Skutch 1957, 1962, Ricklefs 1969, 1974, Drent 1975, White and Kinney 1974, Carey 1980, Martin 1987, 1992, Haftorn 1988, Montgomerie and Weatherhead 1988, Moreno 1989a,b, Weathers and Sullivan 1989). Thus, incubating females must optimize their time on and off the nest to resolve the trade-off between egg survival and self maintenance (i.e. an "incubation strategy").

Comparisons of distantly and closely related bird species reveal a wide diversity of incubation strategies (Lack 1940, Kendeigh 1952, Skutch 1957, 1962), but the critical factors underlying differences among species have not been identified. We believe that

comparative field studies are essential for testing and advancing our understanding of the causes for differences among species. Here, we review alternative hypotheses and predictions for variation in incubation strategies within and among passerine species where females intermittently incubate and then we test these alternatives.

Egg Temperature and Nest Microclimate

Intraspecific variation in the amount of time females spend on and off the nest is often attributed to the demands of regulating egg temperature under different nest microclimates (reviewed in Ricklefs 1974, Drent 1975, Williams 1991, 1996). For example, a cold nest microclimate can cool unattended eggs rapidly and thereby constrain the amount of time females can spend off the nest (Kluyver 1950, von Haartman 1958, White and Kinney 1974, Haftorn 1978, 1979, 1981, 1983, 1984, 1988, Biebach 1984, Haftorn and Reinertsen 1985, Morton and Pereyra 1986, Moreno 1989a, Weathers and Sullivan 1989, Cowie and Novack 1990). Yet, for small passerines that rely primarily on exogenous food resources, limited energy reserves limit the amount of time that females can remain on the nest without feeding (e.g. Royama 1966, Walsberg 1983, Lyon and Montgomerie 1985, 1987, Martin 1987, Moreno 1989a, Smith et al. 1989). Male incubation feeding (i.e. males feeding the female on the nest while she incubates) thus serves as a significant food source that ameliorates energetic limits to female nest attentiveness (von Haartman 1958, Royama 1966, Krebs 1970, East 1981, Lyon and Montgomerie 1985, 1987, Lifjeld and Slagsvold 1986, Lifjeld et al. 1987, Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994). Thus, within a species, microclimate may drive variation in both female incubation rhythms and male incubation feeding rates. Yet,

alternative mechanisms and even the general importance of microclimate and egg temperature regulation on incubation strategies across species remains largely untested.

Body Size

Body size has long been thought to directly influence reproductive energetics (see reviews in Calder 1974, Ricklefs 1974, Williams 1991, 1996, Moreno 1989b, Tatner and Bryant 1993) and may interact with egg temperature and nest microclimate to influence incubation strategies across species in two opposing ways. First, because egg size increases with body size (Blueweiss et al. 1978), larger females may be expected to spend more time off the nest, because with all other things being equal, unattended larger eggs will retain heat longer and cool more slowly than smaller eggs (Turner 1985). However, larger-bodied species can also store more energy reserves and are expected to have lower mass-specific self-maintenance costs (e.g. Blem 1990, Swain 1991); therefore, larger birds might be expected to spend more time on the nest than smaller birds. Thus, the potential opposing effects of egg size and body size make the consequences of size differences across species unclear. Indeed, most comparative studies have not explicitly tested or identified body size as being an important determinant of interspecific differences in female incubation rhythms or rates of male incubation feeding (Lack 1940, Kendeigh 1952, Skutch 1957, 1962, Johnston 1962, Verner and Willson 1969, Silver et al. 1985, Lyon and Montgomerie 1987, Thompson and Raveling 1987, Ricklefs 1993, Baltosser 1996, but see Williams 1991).

Nest Predation

Nest predation is a potential alternative explanation for variation in avian

incubation strategies. Attendance of eggs is widely believed to reduce predation rates on offspring in invertebrates, fishes, amphibians, and reptiles (see Willson 1984, Gross and Sargent 1985, Zeh and Smith 1985, Shine 1988, Clutton-Brock 1991). Yet, the influence of nest predation on avian incubation strategies has been neglected. This neglect is surprising because theoretical arguments suggest that parent birds may reduce the probability of egg predation during incubation by: (1) decreasing the number of trips to the nest to reduce the probability of visual predators finding the nest (Skutch 1949, 1962, Snow 1970, Lyon and Montgomerie 1987, Martin 1987, 1992, 1996, Weathers and Sullivan 1989), or (2) increasing nest attentiveness to provide greater protection against predators that find the nest (Skutch 1949, 1962, Marzluff 1985, Westmoreland and Best 1986, Thompson and Raveling 1987, Moreno 1989b, Martin 1992). Nest predation and parental activity during incubation may therefore interact at different levels. Within a species, the ecological consequence of individuals with increased parental activity at the nest should be increased nest predation from visual predators (see Lawler 1989 for an example with anurans). However, within an evolutionary context, selection should favor decreased parental activity at nests of species with higher predation rates (e.g. Martin 1992, 1996). For example, open-nesting bird species might be constrained to spend less time off the nest and make fewer trips to the nest than cavity-nesting species, because open-nesting species have inherently higher nest predation rates (Lack 1968, Martin and Li 1992, Martin 1992, 1995, 1996).

Ideally what is needed to separate between these competing hypotheses are closely related species that differ in opposing directions with respect to nest microclimate, body

size, and nest predation risk (Harvey and Pagel 1988, Brooks and McLennan 1991, McLennan 1991).

Predictions from a Model System

In this study, we test predictions from the *nest microclimate*, *body size*, and *nest predation hypotheses*. We focus on small (less than 25g), insectivorous cavity-nesting passerines to minimize ecological effects due to body size, diet, and nest sites. We examine variation in incubation strategies (i.e. female on-bout duration, female off-bout duration, nest attentiveness, and male incubation feeding rates) using two approaches. First, we reviewed published studies of incubation behavior from the literature to investigate the role of body size as a determinant of interspecific variation in incubation strategies (Appendix I). Second, we identified a model system within the family Sittidae to field test alternative hypotheses. The Sittidae are represented in North America by four different species, all of which exhibit female incubation and male incubation feeding. Three of these species, Pygmy Nuthatch (*Sitta pygmaea*), Red-breasted Nuthatch (*S. canadensis*) and White-breasted Nuthatch (*S. carolinensis*) breed sympatrically in mixed conifer forests in central Arizona, U.S.A., where they all nest in natural tree cavities (Martin 1988, Li and Martin 1991). Despite their close phylogenetic relationships, these species differ in body size, clutch size, and egg size (Table 1, Appendix II). In addition, data collected over the last 10 years show a gradient in nest predation rates at these sites (Table 1), where White-breasted experience the highest nest predation and Pygmy Nuthatches experience the lowest. Differences in nest predation risk across species appear to be driven by excavation ability, nest height, cavity age, cavity dimensions, ability of

predators to access nests, and vigilance of adults (Li and Martin 1991, Ghalambor and Martin unpublished data).

We test predictions based on nest microclimate, body size and nest predation by contrasting within and among species variation in incubation behaviors, and recognize that these hypotheses are not necessarily mutually exclusive. The *nest microclimate hypothesis* predicts that within and among species, incubation feeding rate and nest attentiveness should increase with decreasing temperature, whereas off-bout duration should decrease (Fig. 1a). The *body size hypothesis* makes two sets of interspecific predictions. First, because ability to store energy increases with body mass, we predict that the similar-sized Red-breasted and Pygmy nuthatches should have lower nest attentiveness and higher incubation feeding rates and off-bout durations than the larger White-breasted Nuthatch (Fig. 1b). Second, because small eggs cool more rapidly than large eggs, White-breasted Nuthatches should exhibit lower nest attentiveness, longer off-bouts, and lower incubation feeding rates than Red-breasted and Pygmy nuthatches (Fig. 1c). Body size effects are also tested within a phylogenetically corrected comparison of a larger number of species based on data from the literature. The *nest predation hypothesis* predicts that because White-breasted Nuthatches use nests that have higher predation rates, they should exhibit the lowest total activity at the nest, through reduced incubation feeding, higher nest attentiveness, longer off-bouts, and shorter off-bouts (Fig. 1d). Alternatively, Pygmy Nuthatch should exhibit the highest incubation feeding rate, lowest nest attentiveness, and longest off-bouts resulting in the highest total activity at the nest, whereas Red-breasted Nuthatches should be intermediate in their behaviors (Fig. 1d). We do not test the

prediction that higher activity leads to higher nest predation within a species.

METHODS

Study Site and Field Observations

Study sites are high elevation (2600 m) snow melt drainages on the Mogollon Rim, Arizona, U.S.A., containing an overstory dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*), and an understory composed primarily of canyon maple (*Acer grandidentatum*) and New Mexican locust (*Robinia neomexicana*) (see Martin 1988, 1997 for a more detailed description of the study area). Study sites were searched for nuthatch nests from May to late July, 1994 to 1996. Time budgets of females and males during the incubation period were recorded using both video cameras focused on the nest cavity and focal observations (focal observations were from a blind approximately 20m from the base of the nest tree). Male and female behavior was recorded from these video tapes. Observations were limited to the morning hours between 05:30 and 12:00 when activity levels at nests generally were highest and daylight ambient temperatures were coolest. Nest microclimate was measured from 1994 to 1996 by climbing nest trees and drilling small holes into the nest cavity through which small thermistors were inserted approximately 2 cm above the incubating female. Nest temperatures were then recorded every minute and stored in an Onset minidatalogger. However, because these species nest high inside of unstable tree snags, most nests were inaccessible to us. Therefore, we were unable to simultaneously measure temperature at nests of all three species, but rather opportunistically sampled nests that were accessible. In addition to nest microclimate

data, we also collected ambient temperature data to assess the general effects of temperature, because ambient temperature is highly correlated with nest temperature and egg cooling rates (e.g. Haftorn 1988). In 1994, average hourly temperature was recorded on the study sites using the average temperature measured across a topographical gradient. In 1995 and 1996, average hourly temperature was obtained from a single meteorological station set up on the study sites. On days when temperature observations were unavailable from the study sites, average hourly temperature was obtained from a government operated weather station approximately 85 km away at the Flagstaff airport. Temperature measurements did not differ significantly between the study sites and the airport.

We quantified the following incubation behaviors as a function of time of day and ambient temperature: (1) percent of time an incubating female was on the nest (i.e. nest attentiveness), (2) duration of each on-bout session, (3) duration of each off-bout session, and (4) the frequency of male incubation feeding. We conducted behavioral observations on a total of 44 nests during incubation (12 White-breasted; 20 Red-breasted, 12 Pygmy). Combined video and focal observations resulted in more than 14,400 minutes of behavioral observations for the three species combined.

Statistical Analysis

To test for interspecific differences among nuthatches in their incubation behaviors, we first used a nested analysis of variance with the transformed incubation behavior as the dependent variable, species as a fixed main effect, and individuals within species as a random nested effect to control for individual variation. Differences in nest

microclimate among the three species were tested in a similar manner, with nest temperature as the dependent variable. Temperature effects were further explored by looking at relationships within each species. Because nest microclimate was correlated with ambient temperature ($r = 0.614$, $p < 0.000$) and time of day ($r = 0.493$, $p < 0.000$), we compared incubation behaviors within each species with the larger sample of ambient temperature and time of day. To control for individual variation when testing for effects of time of day and ambient temperature on within species incubation behaviors, we used an analysis of covariance model and blocked on different individuals within each species. We then tested whether time of day or temperature were significant covariates. In order to separate between the effects of time of day and ambient temperature we divided individuals within each species into two temperature groups based on the mean ambient temperature experienced from 05:00 to 07:00. Observations were then categorized as being on either cold or warm days if they were above or below the median ambient temperature. We then tested whether temperature or time of day had a greater effect on incubation behaviors by using a nested analysis of covariance (NANCOVA), with the transformed incubation behavior as the dependent variable, temperature group (cold vs. warm) as a fixed main effect, different individuals within species as a random nested effect, and time of day as a covariate (Bennington and Thayne 1994, GLM option, SPSS 7.0, 1995). If temperature determines incubation behavior, then observations on colder days should differ from observations on warmer days. Finally, because time-of-day effects were more important determinants of within-species variation in incubation behavior, we controlled for time of day to test for differences among nuthatches using a NANCOVA as

above, with the transformed behavior as the dependent variable, species as a fixed main effect, individuals within species as a random nested effect, and time of day as a covariate.

Because there are only three species of nuthatch for examining body size effects, we increased our scope of inference by looking at a larger sample of 18 additional cavity-nesting passerines where only females incubate and males are known to exhibit incubation feeding (Appendix I). Incubation data from the literature are based on reported species means and are not standardized for time of day or temperature. When more than one study was available, reported values were averaged. To control for non-independence due to species relatedness, we used the independent contrast method of Felsenstein (1985) and the CAIC software package of Purvis (1991). The phylogenetic hypothesis constructed was based on summarizing published systematic data (Gill et al. 1989, 1993, Sibley and Ahlquist 1990, Gill and Slikas 1992, Slikas et al. 1996, Appendix II). Because data come from different sources using different approaches, branch lengths were set as equal, and a punctuated model was assumed. No significant correlations were found between standardized contrasts and variances of the untransformed contrasts, justifying the use of equal branch lengths (Purvis 1991). All relationships examined using independent contrasts were linear regressions, where the regression line was forced through the origin due to the use of standardized contrasts (see Garland et al. 1992). In addition, observed on-bout durations were compared to predicted values based on a regression model developed by Williams (1991) for species where males do not feed the incubating female. Williams did not control for phylogeny in developing this model, so we use phylogenetically non-transformed data for comparative purposes. This comparison

tests the prediction that observed on-bout durations should be longer in species with male incubation feeding because the additional food represents an added nutritional benefit.

RESULTS

Determinants of Interspecific Variation

Nuthatches differed significantly in only two of four incubation behaviors when no covariates were used in the model (Table 2). Pygmy Nuthatches had the highest male incubation feeding rates, the lowest nest attentiveness, and the shortest on-bout durations (Table 2). White-breasted Nuthatches had the lowest incubation feeding rates, the highest nest attentiveness, the shortest off-bout durations, and the longest on-bout durations, whereas Red-breasted Nuthatches consistently were intermediate between the other two species (Table 2). These results are consistent with predictions of the *nest predation hypothesis*, because increasing nest-predation risk is predicted to favor lower incubation feeding rates, higher nest attentiveness, and shorter off-bout durations in these species (Tables 1, 2). Additionally, the nest predation hypothesis predicts that total activity at the nest should be inversely related to predation risk, and we find strong support for this prediction (Fig. 2).

Body size cannot explain these patterns because the two similar sized species, Red-breasted Nuthatch and Pygmy Nuthatch, differed from each other in all incubation behaviors, except for off-bout duration (Table 2). Furthermore, body mass did not explain any significant variation in male incubation feeding rate, female nest attentiveness, off-bout duration, or on-bout duration among the larger sample of cavity-nesting passerines we examined (Fig. 3). Observed on-bouts of these 21 species where males commonly feed

the incubating female were significantly longer than predicted values generated from body size of species where incubation feeding is absent ($p < 0.0005$, see Fig. 4). This comparison shows that incubation feeding clearly is associated with longer incubation on-bout lengths independent of body size.

Finally, differences in incubation behavior were not related to any significant differences in nest microclimate across these three nuthatch species (Table 3). We found a mean nest temperature difference of less than one degree, and after controlling for individual effects, there was no significant difference in nest temperatures among nuthatches (Table 3).

Determinants of Intraspecific Variation

Although our results do not support nest microclimate as being a determinant of incubation behaviors across species, temperature and time of day had clear effects on incubation feeding rates, nest attentiveness and off-bout duration within certain species (Tables 4, 5). For example, as predicted by the *nest microclimate hypothesis*, incubation feeding rates and nest attentiveness by Red-breasted Nuthatches were negatively correlated with ambient temperature and time of day, whereas off-bout duration was positively correlated (Tables 4, 5). Nest attentiveness and off-bout durations by Pygmy Nuthatches, and incubation feeding rates by White-breasted Nuthatches also responded to changes in temperature and time of day effects as predicted; however, these patterns were not always significant (Tables 4, 5). Furthermore, White-breasted Nuthatch nest attentiveness and off-bout duration, and Pygmy Nuthatch incubation feeding rates clearly were not correlated with temperature and time of day as predicted.

Because temperature and time of day are correlated ($r = 0.50$, $p < 0.0005$), we separated temperature and time of day effects by testing for differences in incubation behaviors among individuals on warm and cold days. The prediction was that if temperature effects were greater than time-of-day effects, warm and cold days should differ. Yet, when testing for differences among warm and cold days only 2 of 12 tests yielded significant results. Pygmy Nuthatch on-bout duration was significantly longer on warmer days (NANCOVA, $F = 5.80$, $p = 0.03$, $df = 2$), and Red-breasted Nuthatch nest attentiveness was higher on colder days (NANCOVA, $F = 10.66$, $p < 0.001$, $df = 2$). The lack of significance for 10 of the 12 tests suggests that where correlations exist between incubation behaviors and temperature and time of day, time of day is likely the more important effect.

Time of Day and Nuthatch Incubation Behaviors Re-Examined

Correlations between incubation behaviors and time of day complicate the interspecific comparisons of mean incubation behaviors made above. Therefore, species were compared again using time of day as a covariate in the nested ANOVA model (Table 6). In all cases except on-bout duration, time of day was a significant covariate, and the interaction of time of day by species was significant (Table 6, Figs. 5, 6). Despite the difficulties in interpreting heterogeneous slopes, two striking patterns emerged, (1) White-breasted Nuthatch nest attentiveness does not vary as a function of either time of day or ambient temperature, whereas Red-breasted and Pygmy nuthatches show decreasing attentiveness with time of day and temperature, and (2) unlike the White-breasted and Red-breasted nuthatches, Pygmy Nuthatch incubation feeding rates stay high with

increasing time of day and temperature (Figs. 5, 6). Both of these patterns are inconsistent with predictions from the *nest microclimate hypothesis*, because nest attentiveness and incubation feeding rates are expected to decrease when egg cooling rates are slow. Additionally, body-size effects are not equally manifested across species because the similar sized Red-breasted and Pygmy nuthatches differed significantly in their incubation feeding response (Figs. 5, 6). These results, however, again support predictions from the *nest predation hypothesis* because the species with the highest predation risk, the White-breasted Nuthatch, exhibited continuously high nest attentiveness and low incubation feeding rates, whereas the species with the lowest predation risk, the Pygmy Nuthatch, had continuously high incubation feeding rates independent of time of day or temperature (Figs. 5, 6).

DISCUSSION

Proximate and ultimate fitness trade-offs created by a bird's environment should result in that combination of female and male incubation behaviors that maximizes fitness through increased egg survival, while minimizing associated costs to parents. The challenge of regulating egg temperature under varying microclimates has been treated as the primary determinant of incubation strategies. Yet, our comparison of three sympatric nuthatches yields substantial variation in the importance of temperature and time of day on incubation behaviors within species, with no behavior showing a consistent response across species (Figs. 5, 6). Nonetheless, the pattern of behaviors across species is

consistent with predictions from the *nest predation hypothesis*, despite very different species-specific slopes between incubation behaviors and time of day or temperature. Specifically, higher rates of nest predation are associated with lower male incubation feeding rates, higher female nest attentiveness, and shorter off-bout durations resulting in lower total activity at the nest (Table 2, Figs. 1, 5, 6). Comparisons of these species-specific slopes (Figs. 5, 6) highlight the plasticity of incubation behavior, and provide important insight into the behavioral response of each species to the same range of temperatures and time of day. Interspecific differences may reflect differences in nest predation over evolutionary time. However, the response of each species may also reflect a phenotypic adjustment to the local environment based on the perceived predation risk (Julliard 1997, Martin and Ghalambor in review). For example, White-breasted Nuthatches suffer higher rates of nest predation in part because they use old nest cavities that are relatively easy for nest predators to access (Li and Martin 1991, Ghalambor and Martin in prep). Birds may exhibit phenotypic modifications in their behavior to reduce activity at the nest or choose other strategies that decrease risk, when perceived risk is high. Regardless of whether observed differences across species are fixed or plastic, these results provide evidence that nest predation risk is an important mechanism to determine different incubation strategies.

We found no evidence that nest microclimate alone is a significant determinant of different incubation behaviors across species, because nest temperatures did not differ among the three species (Table 3). However, nest temperature measurements were not controlled for by date, and therefore represent only random observations during the

incubation period. A better experimental design would have simultaneously measured temperature in nests of all three species. Despite this shortcoming, it is unlikely that any of the three species in this study are experiencing significantly different nest microclimates as all three nuthatches build insulated nests within tree cavities.

Although nest temperature did not explain differences across nuthatch species, temperature or time of day effects were important within in each species to some degree. For example, incubation feeding rates tend to be highest early in the morning and when temperatures were coldest in White-breasted and Red-breasted nuthatches (Tables 4, 5). Additionally, nest attentiveness declined and off-bout duration increased with temperature and time of day for Pygmy and Red-breasted nuthatches (Tables 4, 5). These patterns are in part consistent with other single-species studies of cavity nesting birds in the temperate zone (e.g. Haftorn 1978, 1979, 1981, 1988, Cowie and Novak 1990). Yet, it is unclear whether temperature or time of day are driving these patterns because they are correlated with each other, and each could be important in different ways. Cold ambient temperatures may increase constraints on getting off the nest to forage because of rapid egg cooling and simultaneously increase the energetic cost of re-warming eggs which in turn would require greater male incubation feeding (e.g. Vleck 1981, Biebach 1986, Haftorn 1988, Williams 1996). Alternatively, time of day may influence energy limitation, where energy is most limited during the morning because females have fasted over night and depleted their energy stores (Walsberg 1983, Martin 1987, Swain 1991, Williams 1996). Such energy limitation may require females to reduce nest attentiveness and males to increase incubation feeding. Predictions for both temperature and time-of-day effects

are supported by the data (Figs. 5, 6). Therefore, to test whether cold morning temperatures were having an effect independent of time of day, we tested whether behaviors differed between warm and cold days. We found only 2 significant cases out of 12 tested, suggesting that time-of-day constraints on the females energy balance may be more important than ambient temperature on incubation behaviors. This conclusion is supported by experiments conducted by Smith et al. (1989), who were able to increase female nest attentiveness and decrease off-bout duration with supplemental food, but did not simultaneously observe males increasing their incubation feeding rates when ambient temperatures were low. Additionally, experimental manipulations of egg temperatures in other studies have shown that incubating females will only alter nest attentiveness within certain limits, again suggesting that temperature effects alone are not sufficient to explain incubation patterns within a species (e.g. Johnson and Cowan 1974, Haftorn 1979, 1984, Davis et al. 1984). Yet, off-bout duration was shortest early in the morning, which is opposite of predictions from energy limitation alone, but is expected from cold temperatures. Thus, diurnal patterns seem to reflect a large influence of energy limitation related to time of day effects on male incubation feeding rates and female nest attentiveness, but possible effects of cold temperature on off-bout durations (see also Haftorn 1988).

Body size is expected to potentially influence incubation behaviors through differences in the thermal properties of small versus large eggs (Turner 1985), and the ability of larger birds to store more energy (Blem 1990, Swain 1991, Williams 1991, 1996). However, we found no obvious body size effects in this study. For example, the

incubation feeding rates, nest attentiveness and on-bout durations of the similar sized Red-breasted and Pygmy Nuthatch were very different (Table 2, Figs. 4, 5). Yet, the reduced activity of White-breasted Nuthatches achieved through lower rates of male incubation feeding, high female nest attentiveness, and short off-bout durations could be influenced by its slightly larger size and ability to store more lipids (Blem 1990, Swain 1991, Williams 1991, 1996). However, body size alone did not explain any significant variation among 18 additional cavity nesting passerines that exhibit female incubation and male incubation feeding (Fig. 2). Furthermore, body size effects were also absent in a comparative study of incubation feeding and nest attentiveness that contrasted 20 co-existing open- and cavity-nesting passerine species (Martin and Ghalambor in review). Thus body size effects maybe small, for small incubating passerines that rely on exogenous rather than endogenous energy resources, (Martin and Ghalambor in review). Indeed even among incubating waterfowl that rely on stored lipid reserves, nest predation may also be of greater importance than body size to the evolution of incubation strategies. Thompson and Raveling (1987) in a comparison of arctic nesting geese, concluded that interspecific differences in mean nest attentiveness were best explained by the interaction of nest predation risk and body size among species, rather than body size alone.

The lack of significant body size effects contrast with Williams (1991) who found a positive relationship between female body mass and on-bout duration (Fig. 3, predicted line). This discrepancy in results could be due in part to: (1) our use of phylogenetically controlled data, (2) the larger subset of body sizes used in Williams (1991), or (3) our use of only species where male incubation feeding is present. Indeed, one important result

that we found is that on-bout durations in species where male incubation feeding is present is significantly longer than in species where it is absent (Fig. 4). These results support other studies that have shown incubation feeding or supplemental food to be an important nutritional supplement to incubating females allowing for more time on the nest within species (Royama 1966, Krebs 1970, Lyon and Montgomerie 1985, 1987, Lifjeld and Slagsvold 1986, 1989, Nilsson and Smith 1988, Smith et al. 1989, Moreno 1989b, Halupka 1994) and among species (Martin and Ghalambor in review). Given that male incubation feeding can in part explain patterns of female nest attentiveness, factors that influence male parental care should be considered in future studies of incubation.

We tested three possible mechanisms for differences in nuthatch incubation strategies, but other untested factors remain. For example, male incubation feeding may decrease with reduced confidence in paternity or when males engage in other behaviors such as seeking extra-pair copulations, which in turn can reduce female nest attentiveness (Lifjeld and Slagsvold 1986, Lyon and Montgomerie 1987, Badyaev 1997). One major difference among the species in this study is that Pygmy Nuthatches breed cooperatively at up to 30% of their nests (Sydeman 1989), whereas Red-breasted and White-breasted nuthatches are socially monogamous. Helpers may reduce parentage and confidence of paternity among primary males (e.g. Whittingham et al. 1997), and helpers may also explain the high rates of incubation feeding found in Pygmy Nuthatches (Table 2, Figs. 5, 6). Because we have no genetic data on paternity in these nuthatch species, this remains an untested hypothesis. Yet, among a banded population of Pygmy Nuthatches, Storer (1973) reported that helpers never incubated and rarely fed the incubating female,

suggesting that the role of helpers during incubation may be limited in this species. Either way, helpers do not explain the differences in incubation behaviors between Red-breasted and White-breasted nuthatches. Moreover, if helpers are important, it is interesting to note that they may act indirectly through nest predation, because helpers can reduce nest predation (e.g. Vehrencamp 1978), which may explain higher nest success in Pygmy Nuthatches and in turn explain the higher incubation feeding rate.

Finally, nest predation is commonly believed to be the primary source of nesting mortality in birds (Ricklefs 1969, Martin 1992b, Martin 1993a). Differences in nest predation risk are largely driven by differences in nest-site choice (e.g. open vs. cavity, colonial vs. solitary), which in turn are strongly correlated with life-history traits (Martin 1995, Martin and Clobert 1996). Therefore, it is not surprising that nest predation is correlated with different aspects of parental effort, such as nestling development rates, nestling provisioning rates, and incubation (e.g. Skutch 1949, Lack 1968, Martin 1987, 1992, 1996, Ricklefs 1984, Li and Martin 1992, Bosque and Bosque 1995, Martin and Ghalambor in review, this study). Differences in nest-site choice among species might parental care strategies such as incubation. The three nuthatches in this study differ in their nest site choices in one significant way. White-breasted Nuthatches rely completely on pre-existing holes, whereas Red-breasted and Pygmy nuthatches excavate at least some of their own cavities (Martin 1993b). Non-excavating species that rely on existing cavities for breeding generally are considered to be limited in their breeding opportunities, resulting in strong competition for nest sites (Nilsson 1984, Brawn et al. 1987, Balda and Brawn 1988, Bock et al. 1992, Martin 1993b). Thus, the fitness cost of nest predation

may be substantially higher for White-breasted Nuthatches than for Red-breasted and Pygmy nuthatches because not only are nest-predation rates higher, but re-nesting opportunities may be more limited (Beissinger and Waltman 1991, Martin and Li 1992, Martin 1992, 1993b). Nest-site limitation, therefore, might also interact with nest predation, resulting in selection for the constantly high nest attentiveness patterns exhibited by female White-breasted Nuthatches, despite lower incubation feeding rates (Figs. 5, 6). Indeed, the greater nest attentiveness exhibited by White-breasted Nuthatches are opposite to results from a companion study which show a positive relationship between incubation feeding rate and nest attentiveness across 20 coexisting species on the same study sites as the nuthatches in this study (Martin and Ghalambor in review). Therefore, non-excavating species could be under strong selection to maintain high nest attentiveness not only to reduce the probability of egg predation, but also deter nest competitors.

In summary, attention has long focused on the proximate effects of temperature in explaining variation in avian incubation strategies, whereas alternative explanations for interspecific differences has received only limited attention. Our results suggest that temperature and time-of-day effects may explain some within species variation, but differences in nest predation and possibly nest-site competition may play a more important role in determining differences among species and deserve more attention in future research.

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APPENDIX I

Summary of incubation behaviors gathered from the literature for cavity-nesting passerines under 25 grams; body mass (mass) from Dunning (1993), mean incubation feeding rate per hour (feed rate), mean on-bout duration (on-bout), mean off-bout duration (off-bout), and percent female nest attentiveness (attentiveness)

Species	Mass (g)	Feed rate (per h)	On-bout (min)	Off-bout (min)	Attentiveness (%)	References
<i>Picedula hypoleuca</i>	11.60	3.90	15.80	4.80	77	Lundberg and Alatalo (1992)
<i>Parus ater</i>	9.1	N/A	35.40	4.23	89	Haftorn (1984)
<i>Parus atricapillus</i>	10.8	2.80	20.25	7.25	74	Smith (1986)
<i>Parus bicolor</i>	21.6	1.50	29.75	11.10	73	Grubb and Pravosudov (1994)
<i>Parus caeruleus</i>	13.3	2.90	29.13	6.32	82	Cowie and Novack (1990)
<i>Parus carolinensis</i>	10.2	2.20	16.50	5.20	76	Brewer (1963)
<i>Parus cinctus</i>	12.4	3.55	41.35	8.40	83	Haftorn and Hailman (1995)
<i>Parus ludsonianus</i>	9.8	0.65	32.90	8.00	80	McLaren (1975)
<i>Parus inornatus</i>	17.5	N/A	28.50	8.50	77	Dixon (1949)
<i>Parus major</i>	19.0	0.94	29.65	9.01	77	Hinde (1952); Haftorn (1981)
<i>Parus montanus</i>	10.2	N/A	20.90	6.45	76	Haftorn (1979)
<i>Parus palustris</i>	10.6	2.36	37.90	7.10	84	Nilsson and Smith (1988)

Appendix I. continued

<i>Protonotaria citrea</i>	15.6	N/A	50.50	12.17	81	Walkinshaw (1953)
<i>Sitta canadensis</i>	9.7	5.76	34.69	4.81	88	This study
<i>Sitta carolinensis</i>	21.1	4.56	37.69	3.88	91	This study
<i>Sitta europea</i>	22.0	1.00	25.00	10.00	71	E. Matheyson, communication
<i>Sitta pygmaea</i>	10.6	7.94	30.01	4.85	86	This study
<i>Sitta pusilla</i>	10.2	1.00	41.90	11.40	79	Norris (1958)
<i>Thryomanes bewickii</i>	9.90	N/A	17.50	29.60	37	Kendeigh (1952)
<i>Thryothorus ludovicianus</i>	18.70	1.10	68.38	32.64	68	Kendeigh (1952)
<i>Troglodytes aedon</i>	10.9	0.20	12.10	8.50	59	Kendeigh (1952)

APPENDIX II.

Phylogenetic hypothesis for cavity-nesting passerines used in comparative analysis (See Methods for citations).

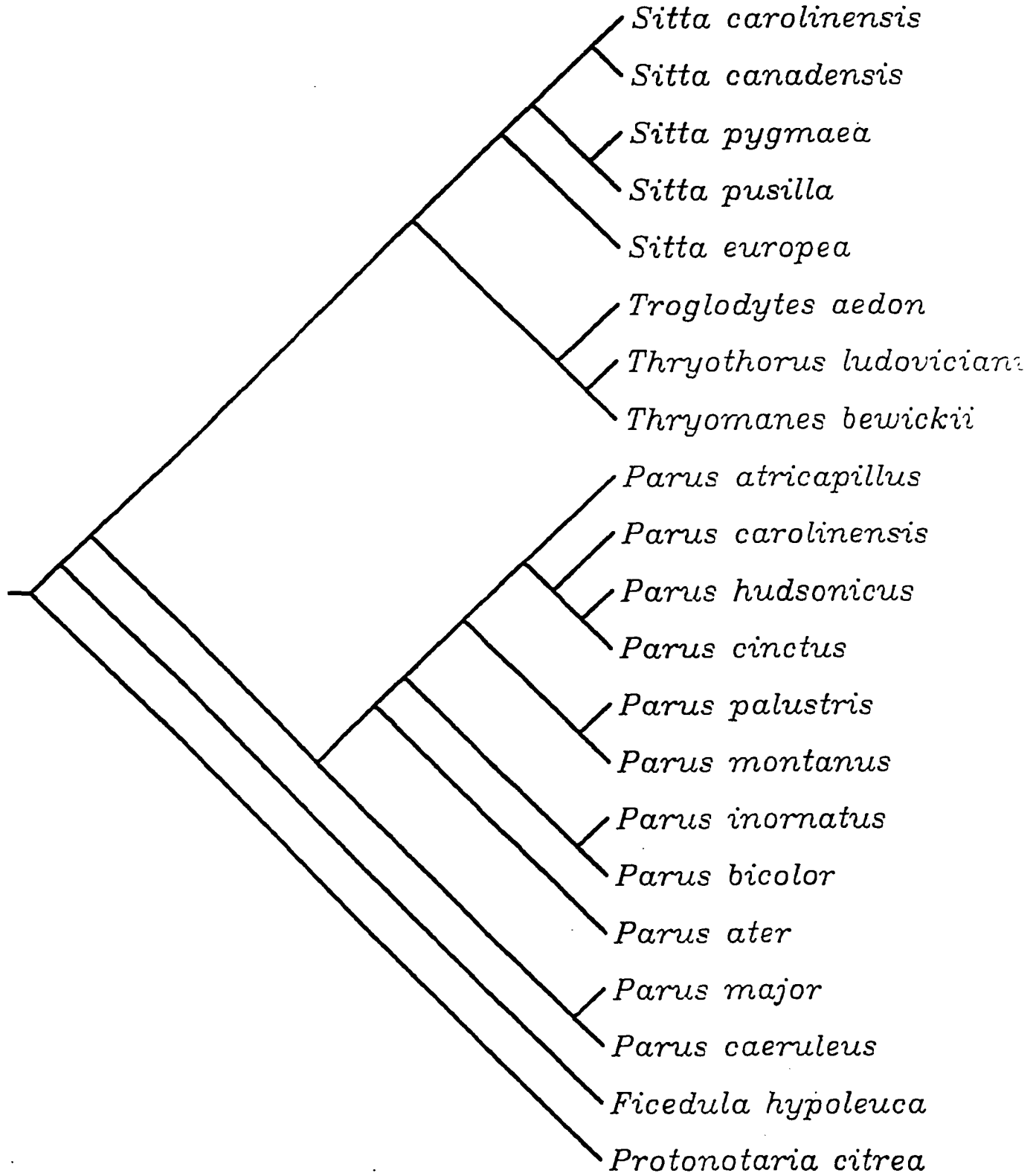


Table 1. Comparison of ecological and life-history traits for nuthatches on the Mogollon Rim, Arizona U.S.A.

	White-breasted Nuthatch (<i>Sitta carolinensis</i>)	Red-breasted Nuthatch (<i>Sitta canadensis</i>)	Pygmy Nuthatch (<i>Sitta pygmaea</i>)
Mean Initiation Date ^a	133.0	140.0	133.0
Nest Predation ¹ (%)	39.8	25.9	13.2
Mean Clutch Size ¹	7.3	5.5	6.5
Length of Incubation ¹ (d)	12.0	12.0	16.0
Mean Body Mass ² (g)	21.1	9.8	10.6
Body Length ² (cm)	15.0	11.0	11.0
Egg Dimensions ² (mm)	19.3 x 14.5	15.2 x 11.9	15.4 x 12.0

^a Martin, unpublished data; ¹ Martin (1995), Pravasudov and Grubb (1993); ² Dunning (1993), ³ Harrap and Quinn (1995).

Table 2. Descriptive statistics for nuthatches on the Mogollon Rim, Arizona 1994-95. Shown are non-transformed estimated marginal means (+/- se). Nested One-way ANOVA results for transformed data using Type IV sums of squares due to an unbalanced design with missing cells.

	WBNU ¹	RBNU ²	PYNU ³	Nested ANOVA ⁴
Incubation Feeding Rate (#/hr)	3.62 (0.37) ^a	4.20 (0.36) ^a	6.38 (0.42) ^b	F = 4.35, p = 0.018, df = 2, 50
Nest Attentiveness (%)	0.93 (0.02) ^a	0.90 (0.01) ^b	0.86 (0.01) ^b	F = 1.52, p = 0.231, df = 2, 44
Off-Bout Duration (min)	3.72 (0.36) ^a	4.86 (0.31) ^b	4.88 (0.39) ^b	F = 3.77, p = 0.029, df = 2, 61
On-bout Duration (min)	39.33 (2.79) ^a	37.04 (2.26) ^a	31.00 (3.11) ^b	F = 1.66, p = 0.199, df = 2, 67

¹ N= 12 individuals for all behaviors except N= 11 for Nest Attentiveness.

² N= 20 individuals for all behaviors except N= 18 for Nest Attentiveness.

³ N= 12 individuals for all behaviors.

⁴ Error term used to calculate F values is based on estimated sample sizes using the Satterthwaite approximation due to an unbalanced design with missing cells (see Sokal and Rolf, 1995, SPSS 7.0 1996, GLM option). Scheffe post-hoc results testing differences among species are denoted with letters following each mean. Shared letters denote no significant difference.

Table 3. Descriptive statistics for nuthatch nest microclimate on the Mogollon Rim, Arizona 1994-1996. Shown are the mean (SE), minimum, and maximum nest temperatures for all daylight hours (05:00 through 21:00) during the incubation period.

	WBNU ¹	RBNU ²	PYNU ³	Nested ANOVA
Mean ⁴	25.25 (0.16)	25.05 (0.14)	25.19 (0.16)	F = 0.001, p = 0.999, df = 2
Maximum	37.18 (4.10)	34.54 (2.90)	34.94 (4.10)	F = 0.036, p = 0.965, df = 2
Minimum	6.03 (3.24)	10.35 (2.30)	13.12 (3.24)	F = 1.407, p = 0.272, df = 2

¹ N = 5 different nests, and 325 observations.

² N = 6 different nests, and 390 observations.

³ N = 5 different nests, and 325 observations.

⁴ One-way nested ANOVA, with individual as a random nested effect to control for individual variation.

Table 4. Results from within species ANCOVAs testing the significance of time of day on incubation behaviors. Individual effects were controlled by blocking on different individuals within each species, then testing time of day as a covariate in the model. Analyses were performed on transformed data and Type IV sums of squares are used due to an unbalanced design with empty cells.

	White-breasted Nuthatch	Red-breasted Nuthatch	Pygmy Nuthatch
	Incubation feeding rate		
Slope	-0.06	-0.13	0.04
P-value (Error, df)	0.08 (1, 104)	<0.00* (1, 111)	0.65 (1, 68)
	Nest attentiveness		
Slope	-0.00	-0.05	-0.07
P-value (Error, df)	0.53 (1, 32)	0.07 (1, 39)	0.03 (1, 33)
	Off-bout duration		
Slope	0.02	0.07	0.14
P-value (Error, df)	0.74 (1, 57)	<0.00* (1, 75)	<0.00* (1, 47)
	On-bout duration		
Slope	-0.03	0.05	0.09
P-value (Error, df)	0.58 (1, 43)	0.65 (1, 59)	0.27 (1, 35)

* denotes significance after Bonferroni correction (Rice 1989).

Table 5. Results from within species ANCOVAs testing the significance of temperature on incubation behaviors. Individual effects were controlled by blocking on different individuals within each species, then testing temperature as a covariate in the model. Analyses were performed on transformed data and Type IV sums of squares are used due to an unbalanced design with empty cells.

	White-breasted Nuthatch	Red-breasted Nuthatch	Pygmy Nuthatch
	Incubation feeding rate		
Slope	-0.04	-0.08	0.02
P-value (Error, df)	0.02 (1, 104)	<0.00* (1, 103)	0.59 (1, 68)
	Nest attentiveness		
Slope	0.00	-0.02	-0.04
P-value (Error, df)	0.82 (1, 30)	0.07 (1, 39)	0.04 (1, 33)
	Off-bout duration		
Slope	-0.01	0.02	0.06
P-value (Error, df)	0.54 (1, 57)	0.03 (1, 69)	<0.00* (1, 47)
	On-bout duration		
Slope	-0.04	0.05	0.02
P-value (Error, df)	0.18 (1, 43)	0.25 (1, 52)	0.33 (1, 35)

* denotes : significance after Bonferroni correction (Rice 1989).

Table 6. Results from mixed model nested analysis of covariance tests, testing for differences in incubation behaviors among nuthatches, with different individuals within each species as a random nested term, time of day as a covariate, and species x time of day as an interaction term. Type IV sums of squares are used due to an unbalanced design with missing cells. See Figure 4 for comparison of slopes of each species and behavior, and Table 2 for sample sizes of individuals.

Behavior	Species x Time of Day	Species	Individual	Time of Day
Incubation Feeding Rate (#/hr)	F= 3.59, p= 0.03	F= 1.92, p= 0.15	F= 2.20, p< 0.00	F= 6.31, p= 0.01
Nest Attentiveness (min/hr)	F= 2.94, p= 0.06	F= 3.75, p= 0.30	F= 2.36, p< 0.00	F= 3.84, p= 0.05
Off-Bout Duration (min)	F= 4.46, p= 0.01	F= 2.70, p= 0.07	F= 2.08, p< 0.00	F= 11.46, p< 0.00
On-bout Duration (min)	F= 0.83, p= 0.44	F= 1.04, p= 0.36	F= 1.56, p= 0.03	F= 0.28, p= 0.60

FIGURE LEGENDS

Figure 1. Prediction plots for incubation behaviors across species as a function of temperature (a), body size (b), egg size (c), and nest predation risk (d). Differences in body size, egg size, and nest predation risk are used to make a priori predictions for the three nuthatch species in this study. Nest temperature data was unknown prior to this study, therefore no specific predictions are made across nuthatch species. See Introduction for specific descriptions of each hypothesis being tested. WBNU = White-breasted Nuthatch, RBNU= Red-breasted Nuthatch, and PYNU = Pygmy Nuthatch.

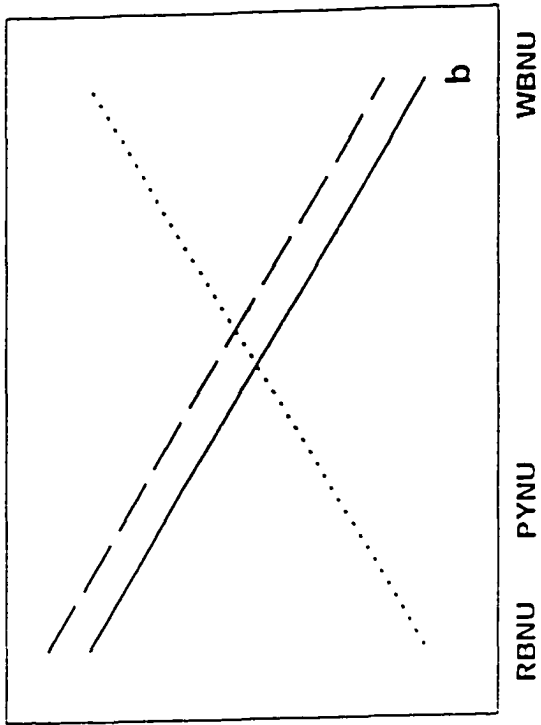
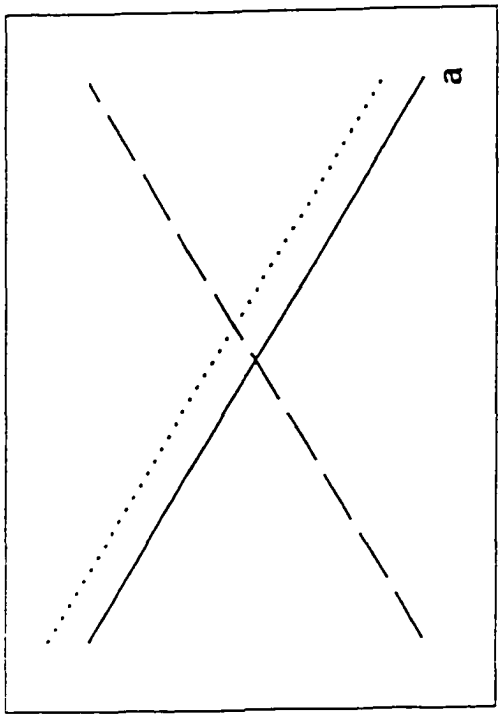
Figure 2. Plot of mean (se) total visits to nests during incubation per hour (combined visits of males and females) in comparison to percent nest loss due to predation (data from Martin 1995). Differences in predation rates appear to be driven by characteristics of the nest sites used by each species (see Introduction). Test between species was done using a nested ANCOVA with time of day as a covariate, individual as a random nested term, and species as a fixed main effect ($F = 6.52$, $p = 0.008$, $df = 2$). Contrasts test the a priori prediction that activity at the nest should decrease with increased predation risk.

Figure 3. Scatterplots of transformed incubation behaviors relative to log transformed body size in cavity nesting passerines when phylogeny is controlled using Felsenstein's (1985) independent contrast method. Beta values represent standardized coefficients. See Appendix I for list of species, values, and references. See Appendix II for phylogenetic hypothesis used in the analysis.

Figure 4. Scatterplot of phylogenetically uncorrected on-bout durations (solid circles) for species where males provide incubation feeding versus solid predicted line for species without incubation feeding. Observed values are significantly larger than predicted (ANOVA, $F= 19.10$, $p < 0.000$, $df = 41$).

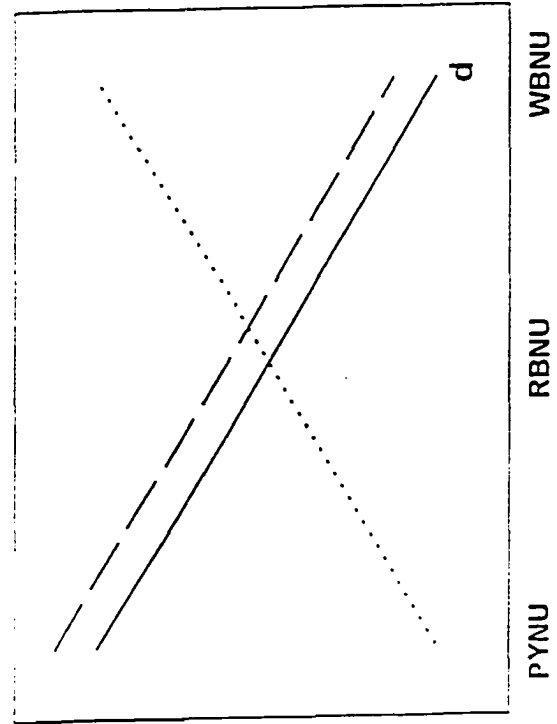
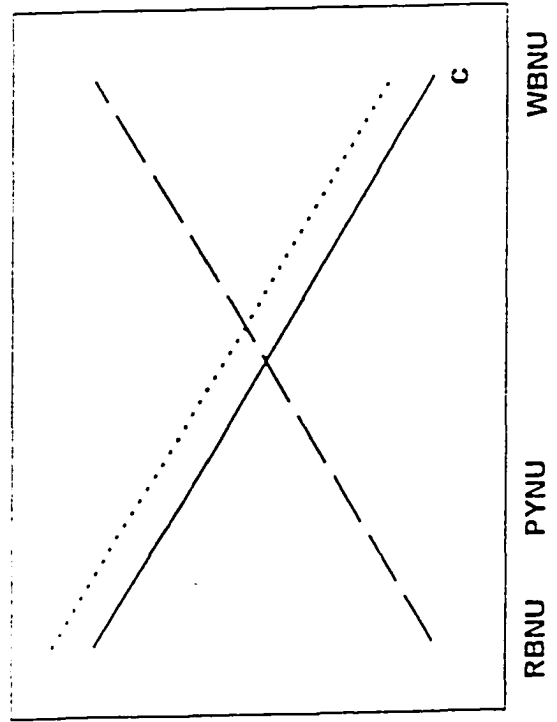
Figure 5. Plots of best fit regression lines for transformed incubation behaviors as a function of time of day. See Table 4 for corresponding significance of each slope.

Figure 6. Plots of best fit regression lines for transformed incubation behaviors as a function of ambient temperature. See Table 5 for corresponding significance of each slope.



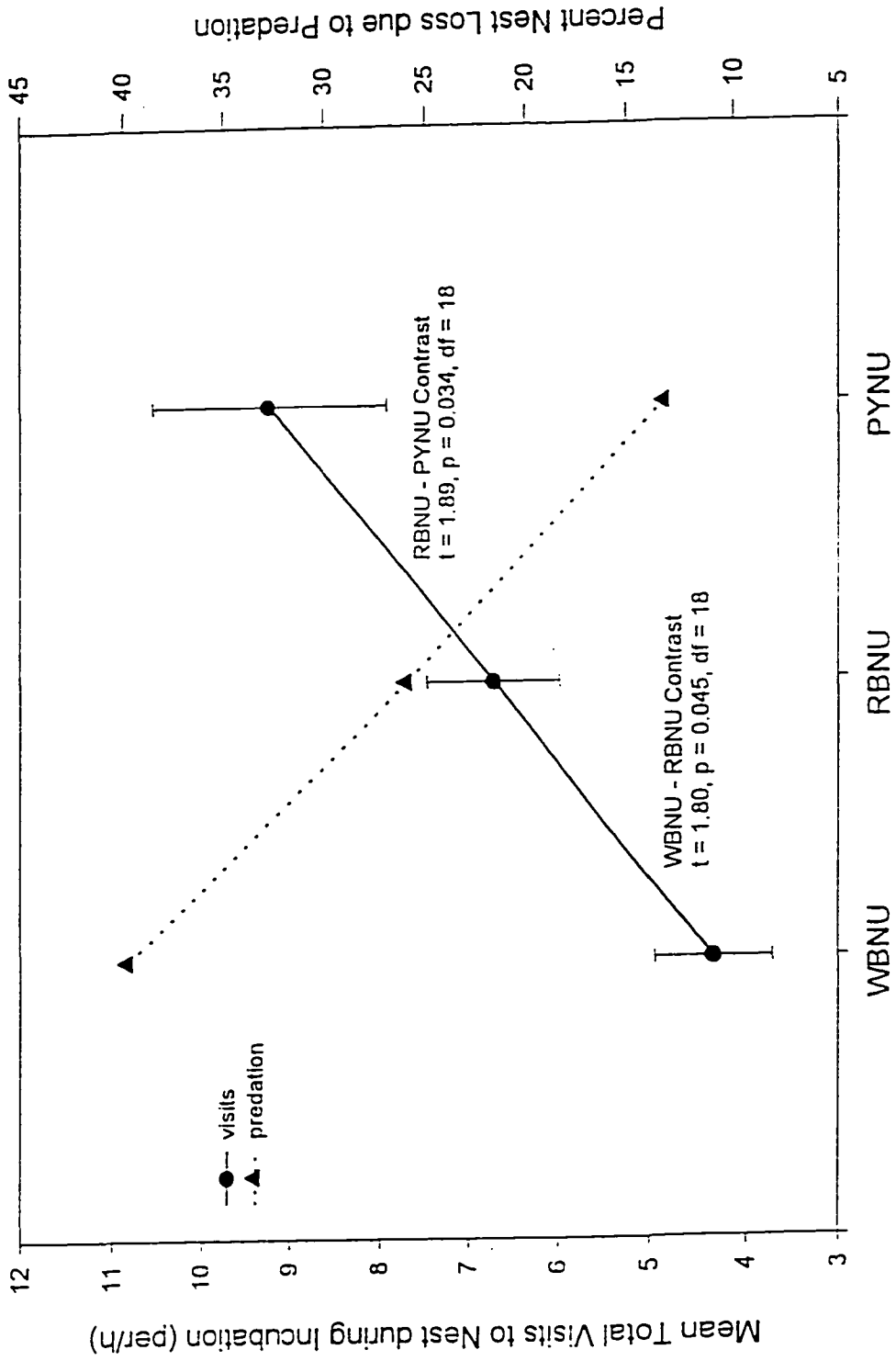
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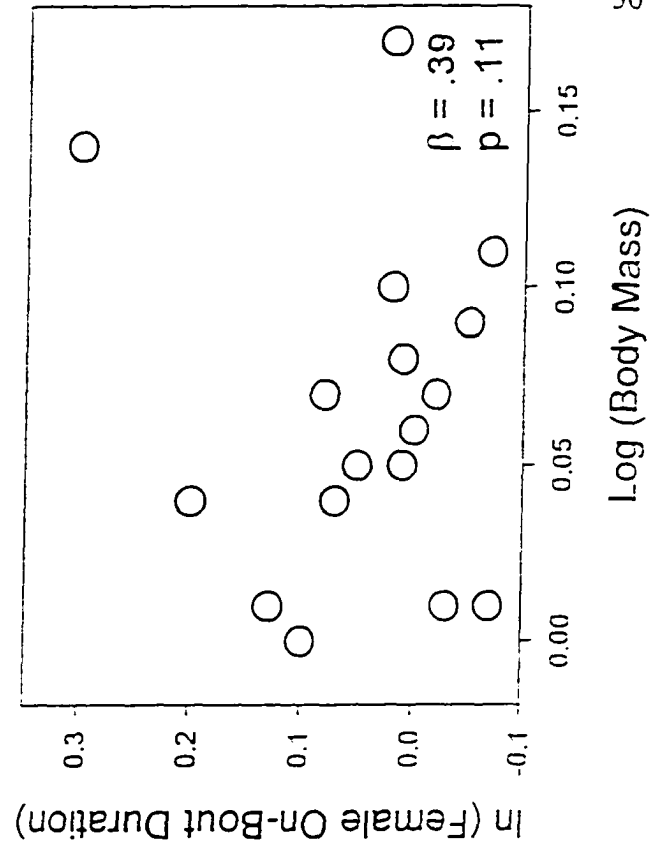
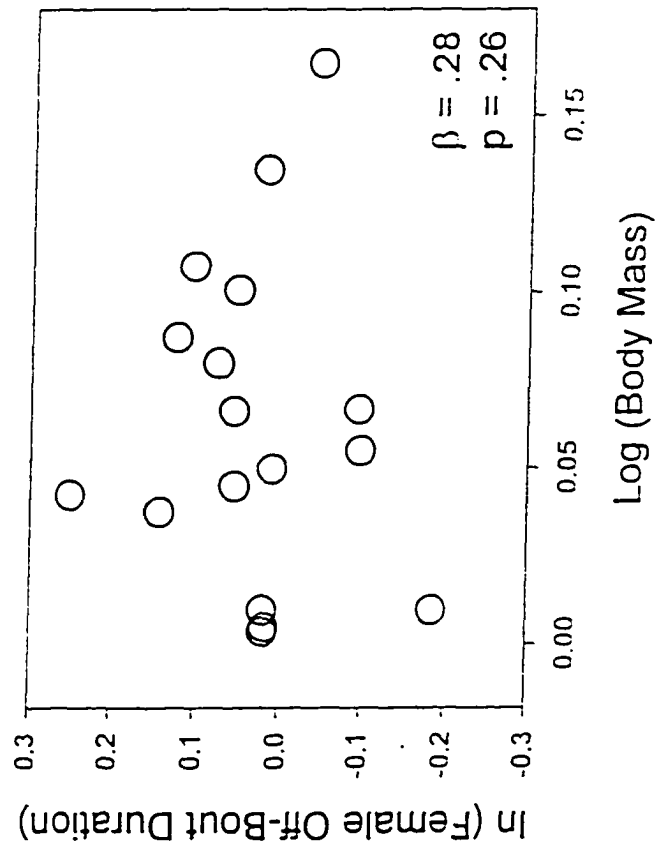
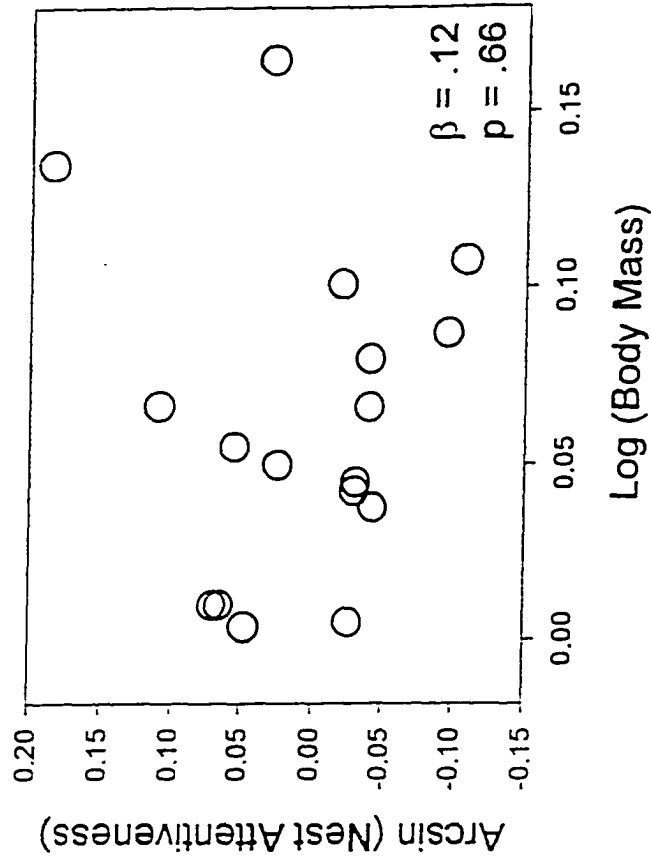
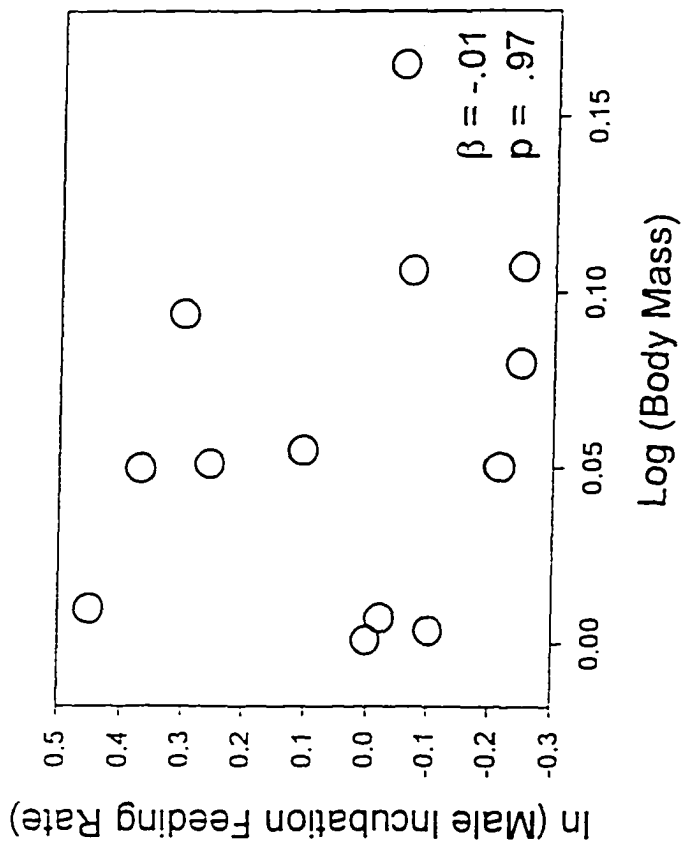
Body Size

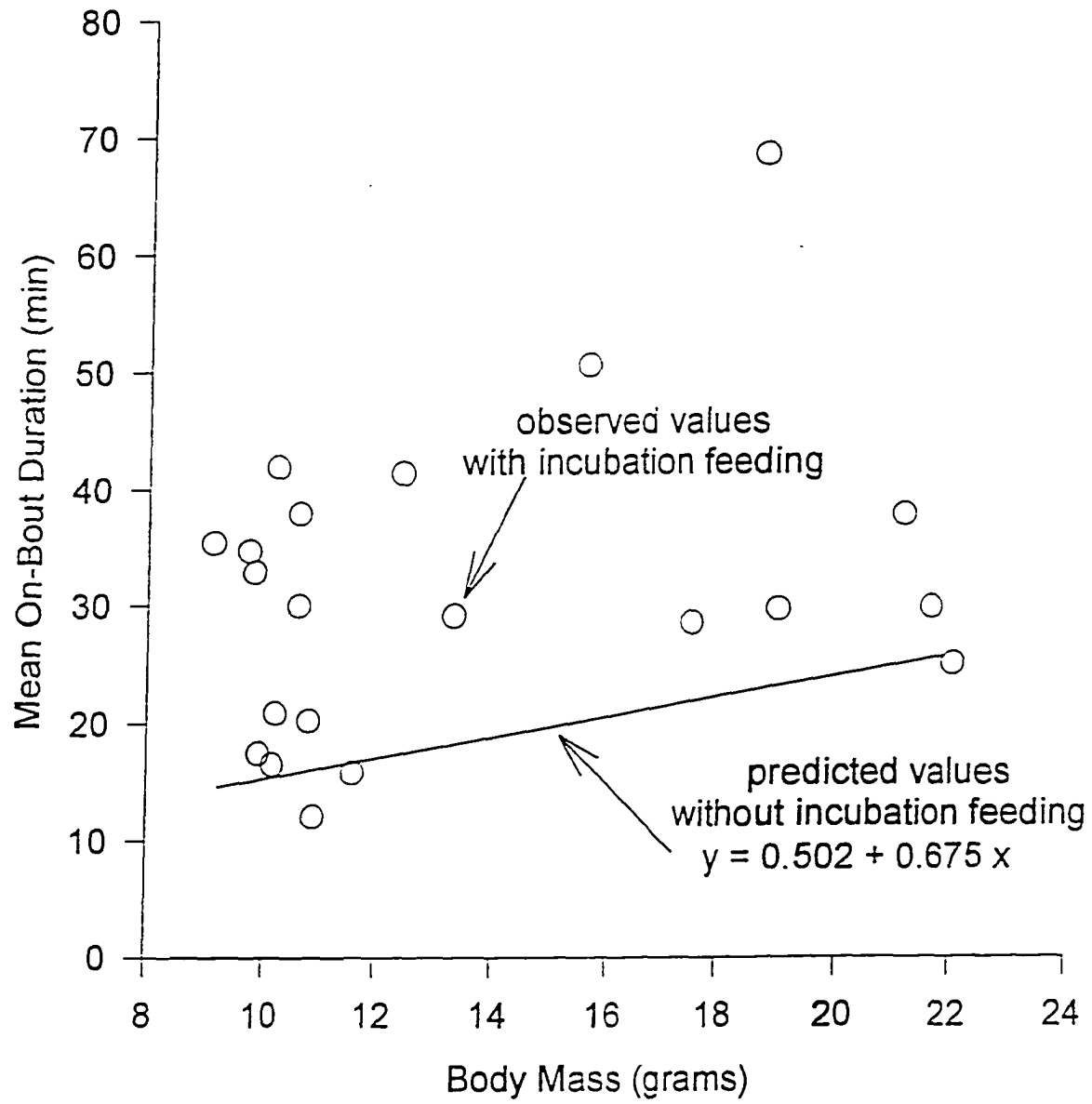


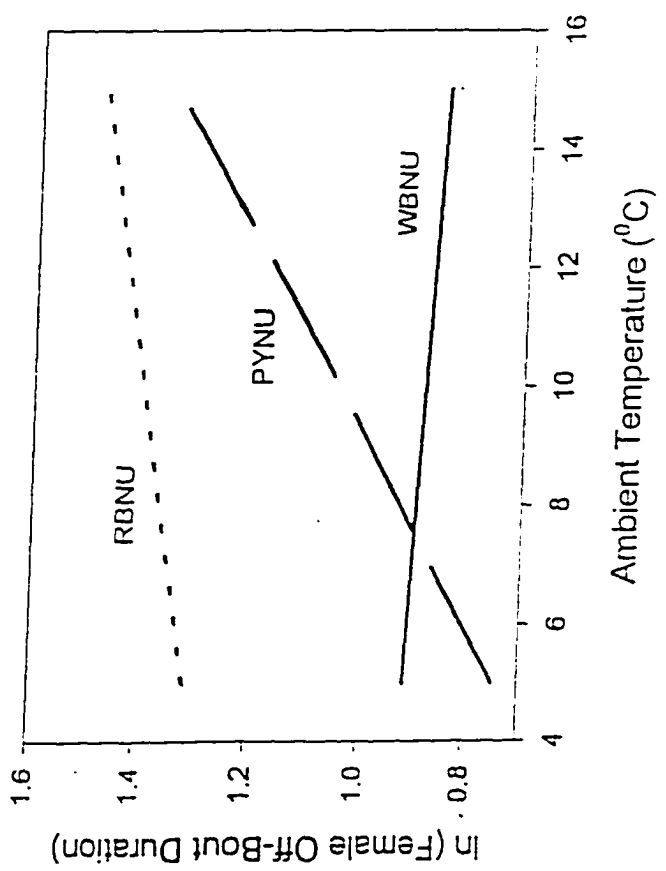
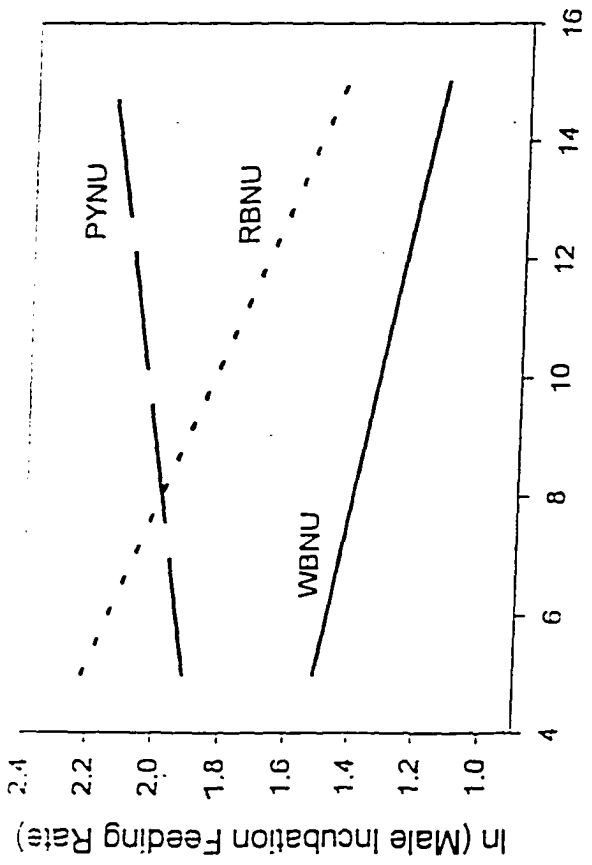
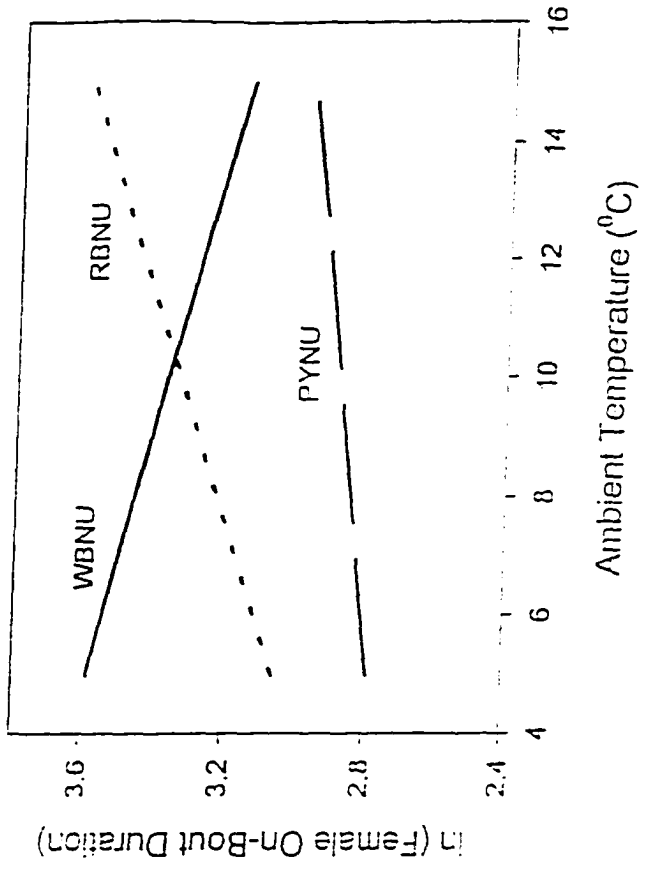
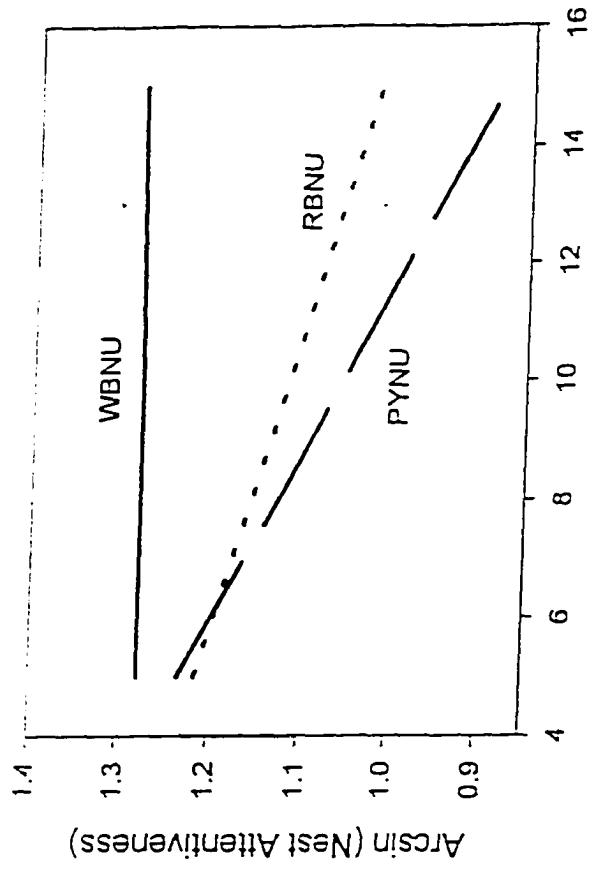
Egg Size

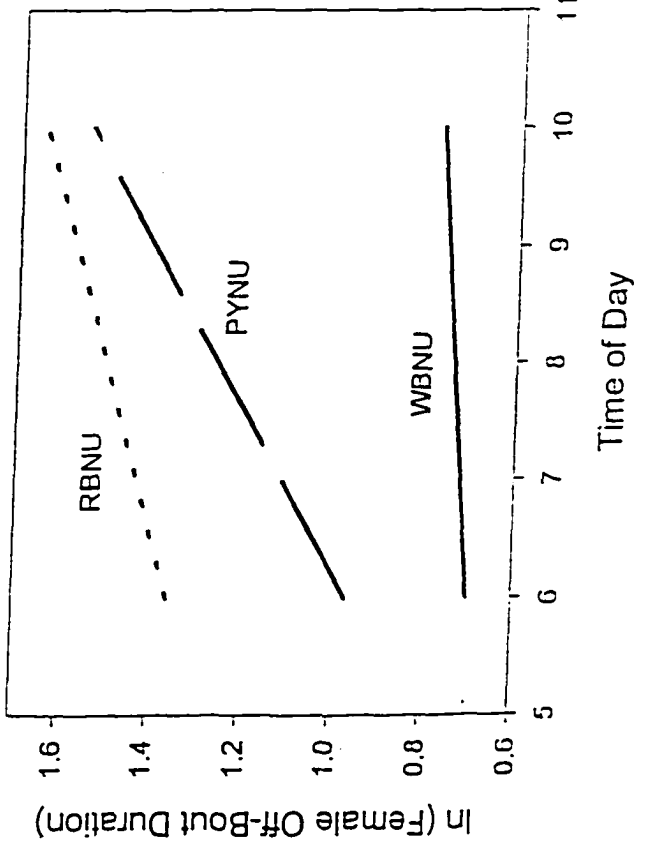
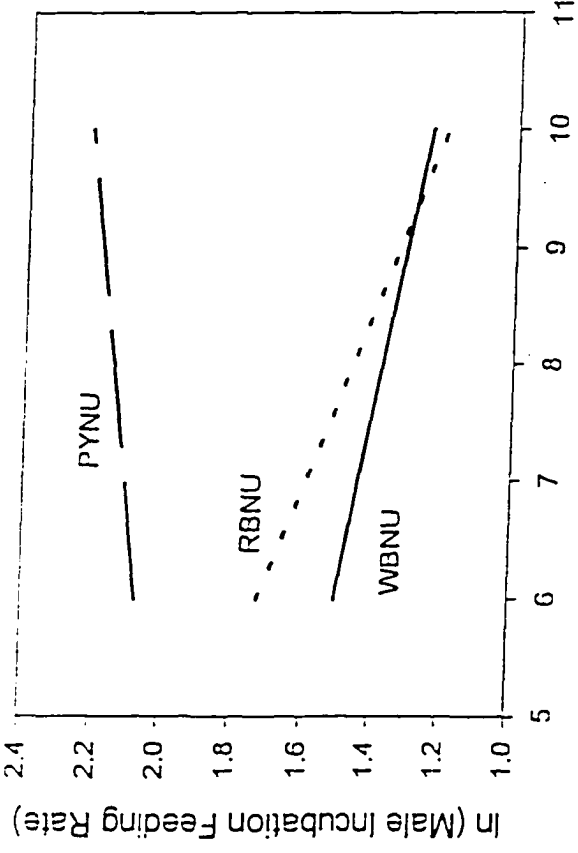
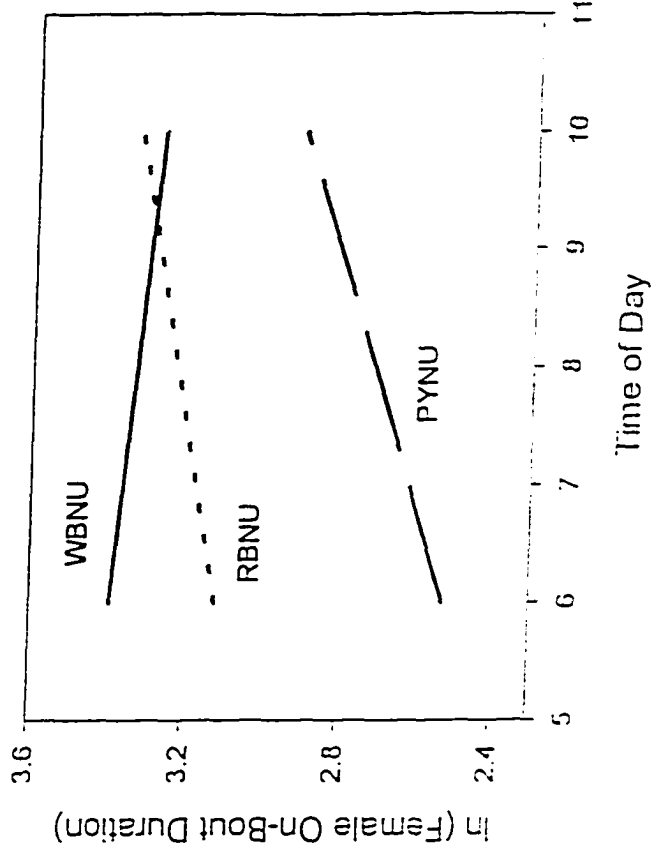
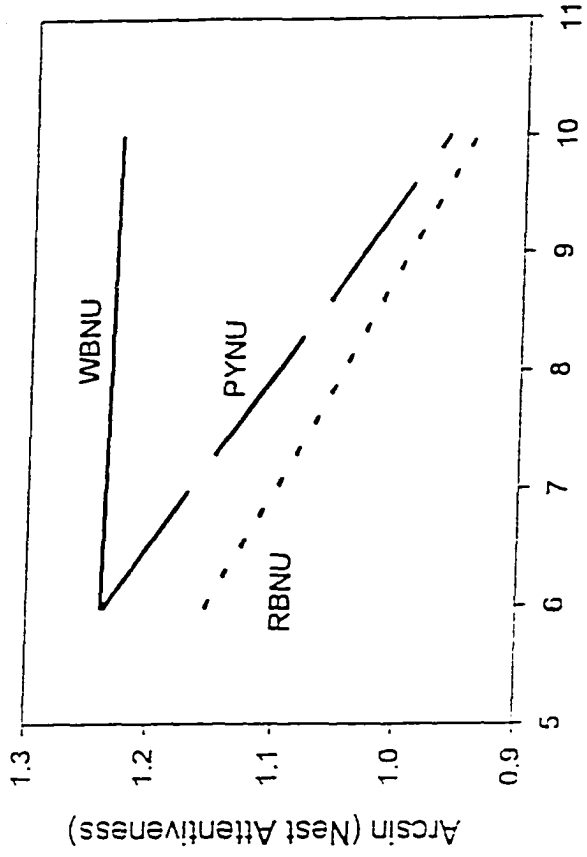
Nest Predation Risk











CHAPTER H

**RISK OF NEST PREDATION CONSTRAINS MALES FEEDING FEMALES:
COMPARATIVE FIELD EXPERIMENTS WITH INCUBATING NUTHATCHES**

INTRODUCTION

Differences in age-specific mortality are commonly thought to drive variation in life history strategies (e.g. Law 1979; Lynch 1980; Curio 1988; Reznick et al. 1990; Roff 1992; Stearns 1992; Martin 1995; Martin and Clobert 1996). Among species that provide parental care, risk of mortality to parents and young can influence how parents resolve trade-offs between allocating time and energy between the needs of their offspring and themselves (e.g. Williams 1966; Winkler 1987; Montgomerie and Weatherhead 1988; Partridge 1989; Clutton-Brock 1991; Martin 1992). For example, increased predation risk to young and eggs often is correlated with increased parental care among many invertebrates, fish, amphibians, and reptiles (reviewed in Clutton-Brock 1991). Yet, the influence of predation risk on parental care trade-offs in birds has gone largely untested, even though nest predation is often the primary source of nesting mortality and may strongly influence various life-history traits (Ricklefs 1969, 1984; Slagsvold 1982; Martin 1993, 1995; Bosque and Bosque 1995; Martin and Clobert 1996). Here, we test the importance of nest predation risk for the evolution of different incubation tactics in birds.

Incubation is a fundamental form of parental care in birds where parents must resolve trade-offs in allocation of time and energy between themselves and their young. In many bird species only females incubate and must choose between spending time on the nest providing heat for embryonic development and protection against predators versus spending time off the nest foraging to meet their own nutritional needs (see Ghalambor and Martin *in review*). Males can help ameliorate this trade-off by feeding females on the nest during incubation (i.e. incubation feeding) providing an indirect form of parental care that increases female nest attentiveness and overall reproductive success (Lyon and Montgomerie 1985, 1987; Lifjeld and Slagsvold 1986; Nilsson and Smith 1988). However, even closely related species can differ dramatically in female incubation rhythms

and male incubation feeding rates (Lack 1940; Kendeigh 1952; Skutch 1957, 1962). Past studies of avian incubation have focused primarily on causes of variation within species. Studies of responses within a single species, however, are limited only to proximate responses of individuals and may not reflect the underlying factors that drive the evolution of different tactics across species (Reznick 1985, 1992; van Noordwijk and de Jong 1986; Martin 1995). Thus, field studies comparing species that differ in their incubation behaviors can provide greater insight into the mechanisms for this interspecific variation in birds.

Comparative studies of incubation behavior are rare, and the potential role of nest predation in driving differences in incubation strategies across species has been neglected. Recently, we tested the hypothesis that visual nest predators constrain parental activity at the nest because this activity provides a cue for predators to locate nests (Skutch 1949, 1962, Lyon and Montgomerie 1987; Martin 1992, 1996; Ghalambor and Martin in review). We found risk of nest predation was strongly negatively correlated with male incubation feeding rate among 19 species of birds where only females incubate (Martin and Ghalambor in review). This strong correlation suggests that nest predation plays an important role in constraining parental care at the nest, yet there is no evidence that incubating birds modify incubation behavior in the presence of predators. Here, we examine this pattern experimentally to test whether incubating birds modify incubation feeding in response to increased predation risk.

Three sympatric congeners in Arizona, the White-breasted (*Sitta carolinensis*), Red-breasted (*Sitta canadensis*), and Pygmy (*Sitta pygmaea*) nuthatch, provide a model system to test the consequences of variation in nest predation risk on the evolution of incubation behaviors. These three species are phylogenetically and ecologically very similar, yet, they differ in their risk of nest predation (Table 1). All three species nest in

tree cavities, with only females incubating and males exhibiting frequent incubation feeding (Ghalambor and Martin in review). Nest microclimate does not differ among these three species, but nest predation varies and is correlated with lower incubation feeding rates (Table 1, Ghalambor and Martin in review). Our experiments modify perceived risk of nest predation and test predictions at proximate and ultimate levels. Proximate responses within each of the three species is measured as the amount of behavioral plasticity in response to increased perceived risk. If nest predation has been an ultimate selection pressure during the evolution of incubation tactics, then the magnitude of proximate responses to the experiment should differ across species and reflect differences in the probability of nest predation risk over evolutionary time.

METHODS

Study Sites and Experimental Design

Study sites were high-elevation (2600m) snow melt drainages on the Mogollon Rim, Arizona, USA containing an overstory dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*), and an understory dominated by canyon maple (*Acer grandidentatum*) and New Mexican locust (*Robinia neomexicana*) (see Martin 1998 for a detailed description of the study area). Study sites were searched for nests from May through late June, 1994 through 1996.

Experimental presentations of predators were made at nests of the three nuthatch species to examine the behavioral responses of females and males. The experimental design consisted of paired comparisons between days when a predator model was presented near the nest on one day versus control model presentations on a second day. During each observation day, the nest was watched for three consecutive time blocks that

included: (1) an initial control period before presentations, followed by (2) the presentation of either a control or predator model, and ended with (3) a second control period after the presentations. In 1994, time blocks were one hour long, but in 1995 and 1996, time blocks were extended to one and a half hours to increase the number of observations. For each individual nuthatch, observations were started at the same time on different days to control for time-of-day effects, and all observations were made from a blind at least 15m from the base of the nest tree. We focused on three behavioral metrics during our observations: (1) the number of incubation feeding trips to the nest by the male; (2) the amount of time spent vigilant by the male during each incubation feeding trip, measured as the number of seconds scanning within a 40-cm radius around the nest entrance; and (3) female nest attentiveness, measured as the number of minutes females spent on the nest during each time block.

Red squirrels (Tamiasciurus hudsonicus) are common nest predators at these sites, and will depredate nests of all three species of nuthatch (Martin 1988, 1993; Martin and Li 1992); therefore, we used a taxidermic mount of a red squirrel as a predator model. Predator presentations consisted of attaching the taxidermic mount to the end of a maple or aspen sapling (depending on the prevailing understory) prior to beginning experiments. Following the initial control period, the sapling was raised and leaned against either the nest tree or an adjacent tree, such that the squirrel was within 6 - 7m of the nest. In order to simulate the movements of a real squirrel, a thin twine was attached to the base of the sapling and used to sway the sapling, thus giving the impression that the squirrel was moving. Additionally, squirrel vocalizations recorded at the study site were played from a cassette recorder placed at the base of the sapling during predator presentations. The overall intention was not to illicit nest defense behavior per se, but rather to increase the perceived risk of having a predator in the vicinity of the nest, and in fact these

presentations did not result in any nest defense responses (C. Ghalambor, personal observation).

Control presentations followed the same order of observations as with predator presentations (i.e. initial control, presentation of model, control after presentation). In 1994 and 1995, control presentations consisted of only using the swaying sapling in an identical manner to the predator presentations but with the squirrel removed and vocalizations turned off. In 1996, to test the appropriateness of control presentations, we attached a taxidermic mount of a Dark-eyed Junco (Junco hyemalis) to saplings. Dark-eyed Juncos are a common bird species on these study sites that pose no predation threat to nuthatches. For all three nuthatch species, the response to the swaying sapling alone or with the Dark-eyed Junco did not differ, therefore results from both control presentations were combined. For each individual in the study, the order of control and predator presentations was randomized.

Predictions and Analyses

We tested for effects of experiments both within (proximate response) and across (ultimate response) species. First, proximate changes in behavior within each species were calculated by subtracting behavioral measures (i.e. vigilance time, incubation feeding rate, nest attentiveness) during predator presentations from responses during the pre-presentation period (before) and the post-presentation period (after). Behaviors during predator presentations may differ from pre- and post-presentation control periods simply due to normal time of day effects in behavior (see Ghalambor and Martin in review). As a result, we compared before and after changes in behavior between days with predators (squirrel) versus control (juncos) presentations. If before and after changes in behavior are simply due to time of day effects, then predator and control days will show the same

magnitude and direction of changes. However, if birds are modifying these behaviors in response to the predator, then the magnitude and direction of changes before and after will differ on predator days compared with control days. Differences between control and predator days were tested using paired samples t - tests and signed ranks tests.

Comparisons of behavior among different species can be confounded by the fact that the same behavior does not necessarily represent an equivalent effect across species. For example, species-specific differences in energy metabolism, or in the nutritional value of food brought to the nest by the male, may bias comparisons of changes in incubation feeding rates. Therefore, we make the following assumptions in testing for differences across species. First, we assume that because the three coexisting species are phylogenetically and ecologically similar (i.e. congeners with the same nest type, socially monogamous, same repertoire of parental behaviors, and exposure to the same predators) relative changes in male and female behavior should be comparable across species. Behaviors were made comparable by converting absolute changes in each behavior to percent changes between the before period and the predator presentation period. Therefore, a decrease in incubation feeding rate from 10 feeds/period to 5 feeds/period in one species is equivalent to a reduction from 4 feeds/period to 2 feeds/period in another species. Absolute changes in incubation behaviors were converted to percentages, and differences across species were tested using one-way ANOVA or Kruskal-Wallis tests, with species as the fixed main effect, and total behavioral response as the dependent variable (SPSS 8.0 1998). Contrasts were set up to test the a priori prediction that the magnitude of behavioral responses to the predator model reflects differences in observed nest predation risk in natural nests across species (i.e. White-breasted = Red-breasted > Pygmy, table 1).

RESULTS

Proximate Responses Within Species

Our prediction was that all three species would modify their incubation behavior in the presence of the squirrel model. Species showed a consistent response to the predator model both in vigilance time and incubation feeding rate, but not in nest attentiveness; vigilance increased and incubation feeding significantly decreased during the predator presentation for White-breasted and Red-breasted nuthatches (Tables 2, 3). These responses were clearly proximate responses to the presence of the predator because behaviors reverted to baseline levels when the stimulus was removed (Tables 2, 3). Significant changes in behavior were observed both within and between days in response to the predator model, but not in response to the control model (Tables 2, 3, 4). In contrast to the other two species, male Pygmy Nuthatches only significantly increased the time spent vigilant when feeding females (Table 4). In no species did females significantly modify nest attentiveness in response to the predator model (Tables 2, 3, 4). Note that a significant difference between predator and control presentations in the Pygmy Nuthatch occurs because incubation feeding increased during control presentations, not because of a significant decrease during predator presentations (Table 4).

Comparisons Across Species

We predicted that the response across species should reflect evolutionary differences in risk of nest predation. Results are consistent with predictions for incubation feeding (Fig. 1). The percent change in incubation feeding to the predator models mirrors differences in nest predation risk among these species; the two species with the higher nest predation risk, White-breasted and Red-breasted nuthatches, exhibited larger decreases in response to the predator model compared with the Pygmy Nuthatch, the species with

lowest nest predation risk (Fig. 1).

The percent change in time spent vigilant in response to the predator model also was highest in White-breasted Nuthatch as predicted (Fig. 2) but did not significantly differ between Red-breasted and Pygmy nuthatches (Fig. 2). Indeed, White-breasted Nuthatch vigilance increased by almost 1,000 percent in the presence of the predator model (Fig. 2, see also Table 2) compared with increases of 150 and 90 percent in Pygmy and Red-breasted nuthatches respectively (Fig. 2). Despite reduced male incubation feeding in the presence of the predator, female nest attentiveness did not change from control levels for any of the species (Fig. 3).

DISCUSSION

The optimal parental care strategy is the one that maximizes fitness given the costs and benefits associated with providing care. Tests of evolutionary influences on parental care tactics often are limited to examining the adaptive nature of care within a single species (Clutton-Brock 1991). Yet, such single-species studies can only test proximate responses that by themselves may not reflect evolutionary effects responsible for differences across species. Comparative approaches such as those used in this study can provide insight into ultimate constraints underlying variation in proximate responses among species.

Past studies investigating variation in female nest attentiveness and male incubation feeding have focused primarily on the effects of proximate energetic costs associated with regulating egg temperatures under varying nest microclimates, whereas the ecological and evolutionary effects of nest predation risk have gone largely untested (Ghalambor and Martin *in review*; Martin and Ghalambor *in review*). Our results suggest that incubating birds are responding to nest predation risk in a proximate manner that reflects ultimate

constraints. We show a proximate response in all three coexisting nuthatch species, where incubation feeding rates decreased and time spent vigilant increased in response to a predator model, and subsequently showed the opposite pattern when the predator was removed (Tables 2, 3, 4). Reduced male incubation feeding has been shown to decrease female nest attentiveness within (e.g. von Haartman 1958; Lyon and Montgomerie 1985) and among species (Martin and Ghalambor in review). However, in no species did female attentiveness change in the presence of the predator model (tables 2, 3, 4; fig. 3). The lack of an observed response in females likely is due to predator presentations being of a relatively short duration (i.e. 90 min.), and because after predator presentations ended, males resumed incubation feeding at rates similar to pre-presentation levels (Tables 2, 3).

The responses to predator presentation we observed within each species is typical of other experimental studies investigating a wide range of parental behaviors that document adaptive changes in behavior (see reviews in Montgomerie and Weatherhead 1988, Lima and Dill 1990, Martin 1992). However, the comparative context of our study provides additional insight into the role of nest predation as an evolutionary constraint on incubation behaviors. Across species, the change in incubation feeding rates and vigilance time in response to the predator presentation corresponded closely to differences in nest-predation risk among these species (Figs. 1, 2). Furthermore, these results provide experimental evidence in support of a broader pattern across 19 different species that show decreasing incubation feeding rates with increased risk of nest predation (Martin and Ghalambor in review). Therefore, our results suggest that nest predation is both an ecological factor responsible for proximate changes in incubation behavior within species, and an ultimate evolutionary constraint on these same proximate changes across species.

Ecological versus Evolutionary Effects on Incubation

Ecological and evolutionary influences represent processes operating at two distinct levels on parental care tactics, including incubation behaviors. For example, prior research has focused on the proximate effects of nest microclimate on incubation behaviors (see Williams 1996). In an ecological context, colder nest microclimates require increased female nest attentiveness to keep eggs warm, which in turn reduces female foraging time and leads to increased male incubation feeding rates (see Martin and Ghalambor *in review*). Indeed, single-species studies of temperate nesting passerines often show a negative correlation between female nest attentiveness and male incubation feeding rates with ambient temperature (von Haartman 1958; White and Kinney 1974; Haftorn 1979, 1984; Nilsson and Smith 1988; Weathers and Sullivan 1989; Cowie and Novack 1990; Halupka 1994). However, if the proximate effects of nest microclimate on variation in incubation behavior are phenotypic in origin, then assuming that microclimate drives variation across species may be inappropriate. For example, the absence of incubation feeding within some species often is interpreted as an indication that females are able to resolve any energetic constraints imposed on them without male assistance (Moreno 1989; Weathers and Sullivan 1989; Williams 1990; Johnson and Kermott 1992). Yet, if other factors such as nest predation constrain incubation feeding in an evolutionary context, then proximate energetic constraints may play little role in understanding variation across species. This point is illustrated in a comparative study by Thompson and Raveling (1987), who dismissed energetic constraints as an underlying mechanism for different patterns of nest attentiveness in arctic-nesting geese, and instead concluded that the interaction of nest predation risk with the ability to defend the nest were more likely explanations for interspecific differences. Clearly, more comparative field studies that use experimental approaches are needed in order to distinguish between ecological and

evolutionary determinants of incubation behaviors. In particular, future studies should test if the proximate response to changes in temperature is smaller for species with higher nest predation risk compared to species with lower predation risk in order to gain insight into how proximate energetic constraints interact with evolutionary constraints.

Predation Risk, Parental Care, and Life History

Although our results are consistent with the prediction that risk of nest predation can help explain differences in incubation tactics among the species we studied, other factors may also contribute to variation in incubation feeding tactics. For example, differences in life-history traits such as reproductive effort and annual adult survival may constrain how parents allocate time and energy between their own needs and those of their offspring. Among the species in this study, White-breasted Nuthatches are unique in that they rely exclusively on existing cavities for nest sites, and they may be more limited in their breeding opportunities than either Red-breasted or Pygmy nuthatches (Martin 1993, unpublished data). Limited breeding opportunities in non-excavating cavity nesting birds is highly correlated with increased annual reproductive effort and lower annual adult survival (see Beissinger and Waltman 1991, Martin 1993, 1995). Therefore, independent of predation risk across species, White-breasted Nuthatch parents should be less willing to put their broods at risk because of their increased reproductive value. Indeed, White-breasted Nuthatches were least willing to visit the nest and significantly elevated their vigilance in the presence of a nest predator compared with either Red-breasted or Pygmy nuthatches (Fig. 1, 2). Thus, life-history theory can be used as a framework to understand evolutionary constraints on incubation strategies in much the same way that it has been applied to understanding parental investment and nest defense (Montgomerie and Weatherhead 1988; Forbes et al. 1994; Dale et al. 1996).

In short, proximate changes in behavior may be constrained by evolutionary history and when considered in a comparative context, proximate behavioral responses can provide insight into ultimate constraints. We show nest predation risk to be acting as both an ecological factor that changes behavioral decisions during incubation, and an evolutionary constraint on incubation feeding rates across species. Future studies of the evolution of parental care that examine closely related species should consider the use of comparative field experiments as a method to test evolutionary hypotheses.

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Table 1. Comparative data for three species of nuthatches on the Mogollon Rim, Arizona 1994-95. Shown are estimated marginal means (\pm se). Nest failure rate represents nests lost only during the incubation period over a 10 year period.

	White-breasted	Red-breasted	Pygmy
Nest failure (%) ¹	5.10	5.20	2.90
Incubation Feeding Rate (#/hr) ²	3.60 (.36)	4.20 (.36)	6.38 (.42)
% Nest Attentiveness (min/hr) ²	0.91 (.02)	0.90 (.01)	0.86 (.01)
Off-Bout Duration (min) ²	3.85 (.36)	4.86 (.31)	4.88 (.39)

¹ Data from Martin and Ghalambor ([in review](#)).

² Data from Ghalambor and Martin ([in review](#)).

Table 2. Mean (\pm se) changes in behavior for predator (squirrel) and control (junco) presentations for White-breasted Nuthatches ($n=11$ nests). Changes were calculated as control minus experimental presentations, describing the difference in response when the model was presented compared with pre-presentation (before \rightarrow presentation) and post-presentation (after \rightarrow presentation) control periods.

	Type of Presentation ¹			Paired Samples Test ²
	Predator Model	Control Models		
Incubation feeding rate (#)				
before \rightarrow presentation	-6.36 (1.09)*	-2.00 (1.22)		$t = 2.88, p < 0.05^{**}$
after \rightarrow presentation	-6.73 (1.01)*	2.55 (1.19)		$t = -8.52, p < 0.05^{**}$
Mean time spent vigilant per visit (sec)				
before \rightarrow presentation	20.77 (6.92)*	-1.92 (1.07)		$Z = -2.93, p < 0.00^{**}$
after \rightarrow presentation	20.37 (6.79)*	-0.29 (0.24)		$Z = -2.93, p < 0.00^{**}$
Mean nest attentiveness (min/period)				
before \rightarrow presentation	-0.01 (0.01)	-0.03 (0.02)		$t = -1.54, p = 0.31$
after \rightarrow presentation	0.01 (0.02)	0.02 (0.02)		$t = -0.31, p = 0.38$

¹ Change within a day was tested with a one-sample test for differences from zero. Significance after correcting for multiple tests using sequential Bonferroni correction denoted by * (Rice 1989).

² Tests are one-tailed paired t-tests, except for time spent vigilant which is a one-tailed Wilcoxon signed rank test with the critical value estimated based on a Z distribution (SPSS 8.0, 1997). Significance after correcting for multiple tests denoted by ** (Rice 1989).

Table 3. Mean (+/- se) changes in behavior for predator (squirrel) and control (junco) presentations for Red-breasted Nuthatches (n= 11 nests). Changes were calculated as control minus experimental presentations, describing the difference in response when the model was presented compared with pre-presentation (before → presentation) and post-presentation (after → presentation) control periods.

	Type of Presentation ¹			Paired Samples Test ²
	Predator Model	Control Models		
Incubation feeding rate (#)				
before → presentation	-3.09 (1.13)	0.09 (1.05)		t = 2.07, p < 0.05
after → presentation	-1.36 (0.98)	1.27 (0.94)		t = -2.07, p < 0.05
Mean time spent vigilant per visit (sec)				
before → presentation	1.94 (0.77)*	-0.42 (0.35)		Z = -2.29, p < 0.01**
after → presentation	3.46 (1.85)*	0.89 (1.25)		Z = -2.80, p < 0.00**
Mean nest attentiveness (min/period)				
before → presentation	0.01 (0.02)	-0.00 (0.03)		t = -0.87, p = 0.81
after → presentation	0.02 (0.03)	0.03 (0.0)		t = -0.81, p = 0.87

¹ Change within a day was tested with a one-sample test for differences from zero. Significance after correcting for multiple tests using sequential Bonferroni correction denoted by * (Rice 1989).

² Tests are one-tailed paired t-tests, except for time spent vigilant which is a one-tailed Wilcoxon signed rank test with the critical value estimated based on a Z distribution (SPSS 8.0, 1997). Significance after correcting for multiple tests denoted by ** (Rice 1989).

Table 4. Mean (+/- se) changes in behavior for predator (squirrel) and control (junco) presentations for Pygmy Nuthatches (n= 8 nests). Changes were calculated as control minus experimental presentations, describing the difference in response when the model was presented compared with pre-presentation (before → presentation) and post-presentation (after → presentation) control periods.

	Type of Presentation ¹		Paired Samples Test ²
	Predator Model	Control Models	
Incubation feeding rate (# /period)			
before → presentation	-1.75 (1.18)	3.88 (1.61)	t = 2.19, p < 0.05
after → presentation	1.50 (1.52)	4.38 (1.10)*	t = -1.29, p = 0.12
Mean time spent vigilant per visit (sec)			
before → presentation	3.05 (1.05)*	-2.03 (1.67)	t = -2.24, p = 0.01
after → presentation	5.16 (2.27)	0.07 (0.99)	t = -1.68, p < 0.05
Mean nest attentiveness (min/period)			
before → presentation	0.01 (0.02)	0.03 (0.04)	t = 0.35, p = 0.37
after → presentation	0.02 (0.02)	0.02 (0.04)	t = 0.08, p = 0.47

¹ Change within a day was tested with a one-sample test for differences from zero. Significance after correcting for multiple tests using sequential Bonferroni correction denoted by * (Rice 1989).

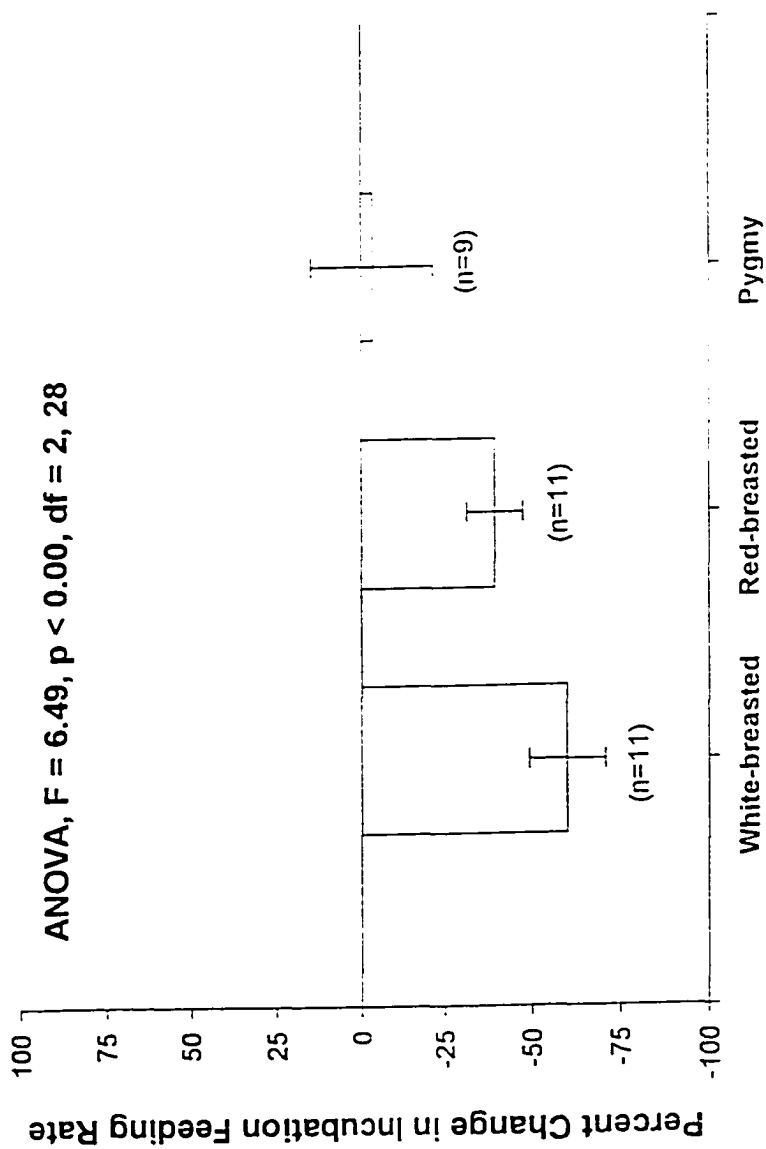
² Tests are one-tailed paired t-tests, except for time spent vigilant which is a one-tailed Wilcoxon signed rank test with the critical value estimated based on a Z distribution (SPSS 8.0, 1997). Significance after correcting for multiple tests denoted by ** (Rice 1989).

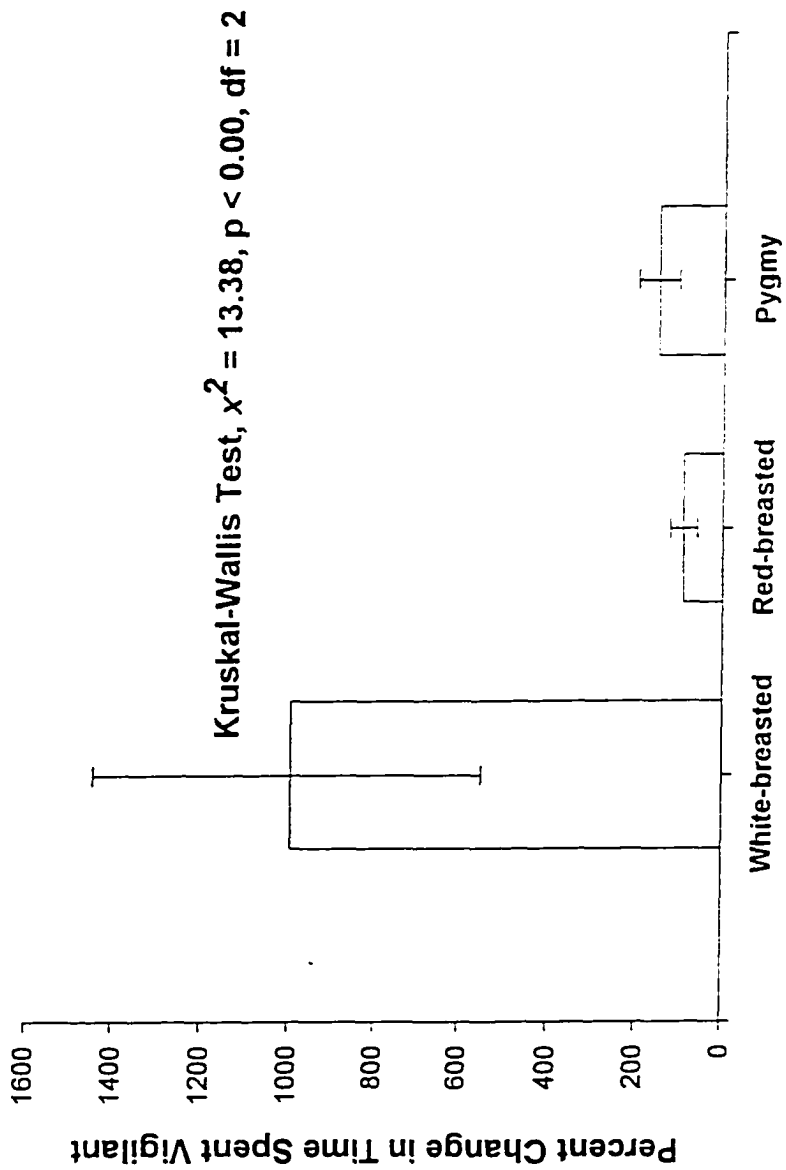
FIGURE LEGENDS

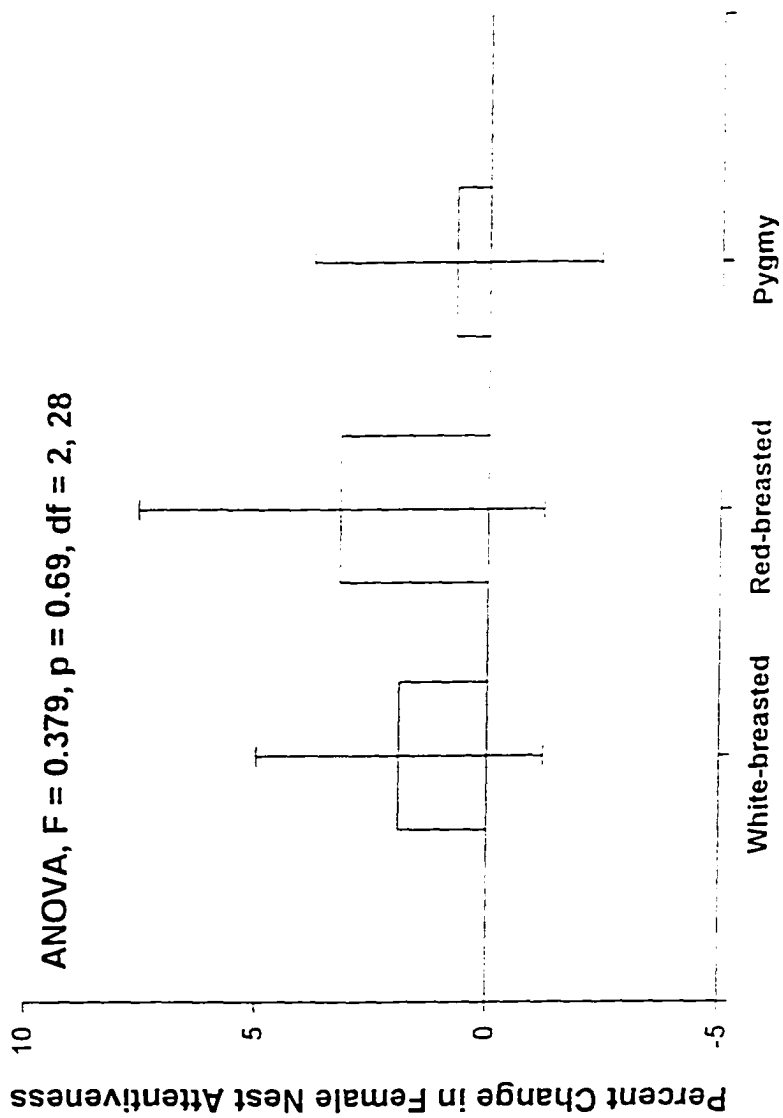
Figure 1. Percent change in male incubation feeding rate in response to predator presentations near the nest. White-breasted and Pygmy nuthatches significantly differ from each other (Contrast = -0.54, $t = -2.89$, $df = 27$, $p < 0.00$), and Red-breasted and Pygmy nuthatches significantly differ from each other (Contrast = -0.33, $t = -1.79$, $df = 27$, $p = 0.04$).

Figure 2. Percent change in male vigilance time in response to predator presentations near the nest. White-breasted and Pygmy Nuthatches significantly differ from each other (Contrast = 10.41, $t = 2.49$, $df = 27$, $p < 0.00$), but there is no significant difference between Red-breasted and Pygmy Nuthatches (Fig. 2, Contrast = 1.73, $t = 0.42$, $df = 27$, $p = 0.68$).

Figure 3. Percent change in female nest attentiveness in response to predator presentations near the nest. White-breasted and Pygmy Nuthatches are not significantly different from each other (Contrast = -0.005, $t = 0.19$, $df = 27$, $p = 0.85$), and Red-breasted and Pygmy Nuthatches are not significantly different from each other (Contrast = 0.016, $t = 0.61$, $df = 27$, $p = 0.55$).







CHAPTER III

**CONSTRAINTS ON BEHAVIORAL PLASTICITY: WHY SHOULD INCUBATING
BIRDS RESPOND DIFFERENTLY TO EXPERIMENTAL CHANGES IN
TEMPERATURE ?**

INTRODUCTION

Understanding the evolution of different behavioral strategies requires knowledge of the selective pressures acting on individuals within species, and how the relative importance of these selection pressures in turn can lead to variation in behavior among populations or species (e.g. Arnold 1981a, b). However, identifying the suite of selection pressures acting on specific behaviors and the nature of constraints limiting the ability of these behaviors to change remains a primary challenge to explaining the evolution of different behaviors (see Brooks and McLennan 1991; Harvey and Pagel 1991; Boake 1994). Avian incubation provides a model system in which to test the consequences of different selection pressures on the evolution of different behavioral tactics. Incubation is an integral form of parental care, in which parents must resolve a trade-off between spending time on the nest caring for eggs and time off the nest foraging to meet their own nutritional needs (Chapter 1). This trade-off is particularly pronounced in species where only the female incubates, because energetic constraints may limit the amount of time females can spend on the nest caring for eggs (see Williams 1990, 1996). Maintenance of egg temperatures within the range of temperatures at which embryonic development is possible is thought to be the primary selection pressure acting on the amount of time females spend on and off the nest (Webb 1987; Haftorn 1988). In particular, cooler nest temperatures may result in rapid cooling of unattended eggs, constraining the amount of time females can spend off the nest foraging, which in turn may lead to males feeding females on the nest (e.g. White and Kinney 1974; Drent 1975; Carey 1980; Lyon and Montgomerie 1987; Nilsson and Smith 1988; Moreno 1989; Smith et al. 1989; Martin and

Ghalambor in review). Indeed, empirical studies of intraspecific variation in incubation behavior have found that cooler ambient temperatures are correlated with higher female nest attentiveness (i.e. percent time females spend on the nest) and increased male incubation feeding (i.e. males feeding females on the nest). However, incubating birds may be subject to selection pressures other than those associated with the challenges of regulating egg temperature. For example, in a comparison of 19 different bird species, we found that variation in the risk of nest predation was strongly correlated with male incubation feeding rates and females nest attentiveness (Martin and Ghalambor in review). In contrast, we found no evidence that different nest temperatures were responsible for interspecific differences. These results, as well as experimental manipulations of the perceived risk of nest predation within species, suggest that visual nest predators may be an important selection pressure acting to create differences in male and female incubation behaviors among species, whereas the effects of nest temperature may be more limited to variation within species (Chapter 1, 2). One species which is an outlier to the pattern is the White-breasted Nuthatch (*Sitta carolinensis*). Nest attentiveness in White-breasted Nuthatches is higher and more constant than expected given their risk of nest predation and frequency of male incubation feeding (Martin and Ghalambor in review, Chapter 1). Furthermore, in response to predator presentations, White-breasted Nuthatches exhibited a disproportionately strong response in terms of their vigilance and decrease in incubation feeding rates relative to either Red-breasted Nuthatches (*S. canadensis*) or Pygmy Nuthatches (*S. pygmaea*) (Chapter 2). We hypothesized that White-breasted Nuthatches are subject to different selection pressures during incubation, because they are a non-excavating cavity nester (Chapter 1; Chapter 2; Martin and Ghalambor in review).

Numerous studies have documented that non-excavating species are limited in their breeding opportunities and subject to strong competition for obtaining and retaining nest sites (Nilsson 1984; Brawn et al. 1987; Balda and Brawn 1988; Beissinger and Waltman 1991; Bock et al. 1992, Martin and Li 1991; Martin 1992, 1993, *unpublished*). We suggest that nest site limitation is a strong selection pressure for females to maintain high nest attentiveness in non-excavating species because the fitness cost of losing a nest to a predator or competitor is magnified by the reduced opportunities for re-nesting. Therefore, we predict that non-excavating species may be less “willing” to leave eggs unattended during incubation even under more benign temperature regimes and low nest predation risk.

Here, we contrast the behavioral response to experimental changes in nest temperature in two coexisting and congeneric species, the White-breasted Nuthatch and Red-breasted Nuthatch. These two species provide a model system in which to test the constraints of limited breeding opportunities on incubation behavior because (1) they are closely related species, such that phylogenetic effects are reduced; (2) they have similar behavioral repertoires during incubation; (3) they experience similar nest temperatures and predation risks during the incubation period (Chapter 1, 2, Martin and Ghalambor in review), and (4) they represent two ends of a continuum in terms of their excavation ability within this genus (Martin 1993). Red-breasted Nuthatches regularly excavate multiple nest cavities each breeding season and place over 76% of their nests in freshly excavated cavities (Ghalambor and Martin in press). In contrast, White-breasted Nuthatches never excavate nests and rely completely on existing cavities for breeding (Pravosudov and Grubb 1993). Thus, for the same risk of nest predation, White-breasted

Nuthatches are expected to be under stronger selection to retain nest sites compared with Red-breasted Nuthatches because following nest failure the probability of acquiring a cavity for re-nesting is lower. We test this prediction by experimentally increasing and decreasing nest temperatures of incubating White-breasted and Red-breasted nuthatches in order to test the importance of excavation ability as a constraint on the behavioral response of females and males to changes in nest temperature.

METHODS

Study Sites and Experimental Design

Study sites were high-elevation (2500m) snow melt drainages on the Mogollon Rim, Arizona, USA containing an overstory dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*), and an understory dominated by canyon maple (*Acer grandidentatum*) and New Mexican locust (*Robinia neomexicana*) (see Martin 1998 for a detailed description of the study area). Study sites were searched for nests of White-breasted and Red-breasted nuthatches from May through late June of 1995 through 1997. Nest microclimate was manipulated at nests of incubating nuthatches to examine the behavioral response of females and males to changes in nest temperatures. We focused on two behavioral metrics during observations of nests, (1) the number of incubation feeding trips to the nest by the male; and (2) female nest attentiveness, measured as the number of minutes females spent on the nest during each time block. To manipulate nest temperature, two small holes were drilled into the cavity approximately 2 and 4cm above the incubating female using a cordless drill. We used an optical fiberscope to estimate the height of the holes drilled above the incubating female. A small thermistor was inserted

through the lower hole and connected to a data logger where air temperature in the nest was recorded every one minute, and a section of copper tubing with the top half bent into a hanger shape was inserted into the upper hole then connected to 25m of aquarium tubing. The shape of the copper tubing allowed only the top half of the tube to enter the hole, while the rest of the tubing was flush with the side of the nest tree. The copper tubing was tightly wrapped with Nichrome wire and insulated with electrical tape, and a 25m-long electrical cord was soldered to the Nichrome wire. The aquarium tubing and electrical cord were taped together, affixed to the tree, and led to an observation area at least 15m from the base of the nest tree. At the observation area a tank of compressed air attached to an air flow meter was connected to the aquarium tubing. The air flow meter allowed us to regulate the flow of air that entered the cavity. This setup allowed us to blow air from the observation area through the aquarium tubing and into the nest cavity, with the effect that air temperature in the cavity decreased. To warm the nest cavity, the electric cord was connected to a car battery that heated the Nichrome wire and the copper tubing and in turn heated the air as it entered the nest. Finally, to ensure that the two holes drilled into the nest cavity did not change air convection within the cavity, we used wood putty to seal up the space around the two holes we drilled into the nest. Previous experimental work on incubation behaviors suggest that incubating females adjust their nest attentiveness in response to egg temperatures independently of air temperature (e.g. White and Kinney 1974; Davis et al. 1984). Therefore, we assumed that any changes in behavior in response to changing air temperatures were made with regard to the effects on egg temperature (i.e rate of egg cooling). However, we acknowledge that changes in nest temperature may also influence energy expenditure in females (see Discussion).

The experimental design consisted of comparisons between days when (1) heated air was blown into the cavity, (2) cool air was blown into the cavity, and (3) no air was blown into the cavity. During each observation day, the nest was watched for two consecutive 90-min blocks beginning at 6:00 AM. On days when heated air was blown into the cavity the air was turned on during the first time block (6:00-7:30) and followed by a control period (7:30-9:00). On days when cool air was blown into the cavity the air was turned on during the second time block (7:30-9:00) and was preceded by a control time block (6:00-7:30). On control days no air was turned on during the two time blocks, but observations of behavior were made as during the air manipulation days. We chose this experimental design because incubation feeding and nest attentiveness tend to be highest when ambient temperature is at its coolest early in the morning (Chapter 1). Therefore, to exaggerate the effects of the manipulation we blew warm air during the first time block when ambient temperature were coolest (i.e. 6:00-7:30), and cool air during the second time block when ambient temperatures were warmest (i.e. 7:30-9:00). Under this design, we were able to compare the effects of days when warm or cool air was blown into to the nest to a control day when no air was blown (Fig. 1). Each individual in the study was observed on three separate days (warm air, cool air, and control) and all observations were made from a blind at least 15m from the base of the nest tree. For each individual in the study, the order of warm, cool, and control manipulations was randomized.

We tested for effects of manipulations both within (proximate response) and across (ultimate response) species. First, proximate changes in behavior within each species were calculated by subtracting the behavior of each individual (i.e. incubation feeding rate and

nest attentiveness) between the two time blocks for each day of observation. To control for differences in individual quality, we converted absolute changes in behavior to percent change, therefore a reduction in incubation feeding from 10 feeds to 5 feeds in one individual would be equivalent to a reduction from 8 to 4 feeds in another. We compared the percent change in behavior between the two time blocks on the control day to changes in behavior during the same time blocks on temperature manipulation days (Fig. 1). We predicted that in response to a heated nest microclimate during the first time block, females should decrease nest attentiveness because egg-cooling rates will be slowed, and in turn lead to a reduction in male incubation feeding (Fig 1). In response to cooling the nest cavity during the second time block, we predicted that female nest attentiveness should increase because egg cooling rate is increased, leading to an increase in incubation feeding rates (Fig. 1). If changes in behavior are simply due to time of day effects, then heated and cooled treatment days will show the same magnitude and direction of changes as control days. However, if birds are modifying these behaviors in response to changes in temperature, then the magnitude and direction of changes will differ in temperature manipulation days compared with control days. We assume that effects of different ambient temperatures among days for the same individual are small and have previously shown that this is a reasonable assumption (Chapter 1). Differences between control and warm air days and control and cold air days were tested using paired samples T - tests.

Comparisons of behavior among different species can be confounded by the fact that the same behavior does not necessarily represent an equivalent effect across species. Therefore, we make the following assumptions in testing for differences across species. First, we assume that because the two coexisting species are similar phylogenetically and

ecologically (i.e. congeners with the same nest type, socially monogamous, same repertoire of parental behaviors, and exposure to the same predators) relative changes in male and female behavior should be comparable between species. Furthermore, because behaviors are converted from absolute to percent change, a relative measure of change among species is achieved.

RESULTS

Experimental Changes in Nest Temperature

We conducted experiments on a total of 11 nests (5 White-breasted; 6 Red-breasted). However, temperature measurements were only collected at 5 Red-breasted Nuthatch nests because a data logger failed to record temperature at one nest. Mean nest temperatures experienced by the two species did not significantly differ on control days (nested ANOVA; $F = 0.215$, $df = 1, 8$, $p = 0.655$), cooled treatment days (nested ANOVA; $F = 1.249$, $df = 1, 8$, $p = 0.296$) or heated treatment days (nested ANOVA; $F = 0.121$, $df = 1, 8$, $p = 0.737$). Mean nest temperatures for both species combined were 14.65 °C (0.08) on control days, 13.91 °C (0.08) on cooled days, and 13.57 °C (0.05) on heated days.

The method of pumping heated and non-heated compressed air into nest cavities was effective in changing nest temperatures. When comparing changes in temperature from the first time block (6:00 to 7:30) to the second time block (7:30 to 9:00) for Red-breasted Nuthatch, mean temperature in the nest cavity significantly decreased during the cool air treatment days (mean change = -1.42 °C) compared with control days (mean change = 3.63 °C; $t = 8.18$, $df = 4$, $p < 0.01$). This difference in temperatures comes about

because temperatures are warming up between the first and second time block on control days, and cooling down during cool air treatment days. A significant change in temperature was also observed when comparing these same time blocks on days when the heated air was pumped into the nest cavity (mean change = -2.99°C) compared with control days (mean change = 3.63°C ; $t = 6.70$, $df = 4$, $p < 0.01$). In this case, the difference in temperature is observed because the warm air is effective in heating the nest cavity during the first time block, leading to a reduction in temperature between the first and second time blocks.

Experiments were similarly effective in changing nest temperature for White-breasted Nuthatches during control days where temperature increased between the first and second time blocks (mean change = 3.75°C) and significantly decreased on days when temperature was cooled (mean change = -1.96°C ; $t = 2.88$, $df = 4$, $p < 0.01$), and on days when nests were heated (mean change = -2.55 ; $t = 3.01$, $df = 4$, $p < 0.01$). There was no significant difference between the two species in the magnitude of change for temperatures on control ($F = 0.004$, $df = 1,8$, $p = 0.953$), cooled ($F = 0.811$, $df = 1,8$, $p = 0.394$), or warmed days ($F = 0.173$, $df = 1,8$, $p = 0.689$).

Behavioral Response to Changes in Nest Temperature

Female and male Red-breasted Nuthatches responded to the cool air treatment as predicted (Fig. 2). In comparison with control days, female Red-breasted Nuthatches increased nest attentiveness in the predicted direction in response to experimentally cooler nest temperatures by 2.5 %, although this increase was not significant at the 0.05 level, whereas males did significantly increased their incubation feeding rates by 68% (Fig. 2).

In contrast, female and male White-breasted Nuthatches did not show any significant changes in behavior in response to the cool air treatment, and in neither case were changes in the predicted direction (Fig. 3). Female and male Red-breasted Nuthatches also responded to the warm air treatment (Fig. 4). In comparison with control days, female Red-breasted Nuthatches decreased nest attentiveness by 4.3% in response to warmer nest temperatures, males decreased incubation feeding rates by 103% (Fig. 4). Female and male White-breasted Nuthatches, however did not exhibit any statistically significant responses to the warm air treatment (Fig. 5). Opposite to predictions, there was a non-significant trend for female White-breasted Nuthatches to spend more time on rather than off the nest when the nest was heated, but there was no concomitant increase in male incubation feeding rates (Fig. 5).

DISCUSSION

Response to Temperature within Species

Female Red-breasted Nuthatches increased nest attentiveness and males increased incubation feeding rates relative to controls in response to cooler nest temperatures (Fig. 2). We were unable to measure actual egg-cooling rates in response to temperature manipulations, but our results are consistent with other studies that showed incubating females increased nest attentiveness and decreased time off the nest when temperatures were low and egg-cooling rates were high (e.g. Haftorn 1982, 1988; Davis et al. 1984; Moreno 1989). Increased female nest attentiveness in response to cooler nest temperatures, however, reduces the time available for foraging, and cooler nest temperatures may also increase female energy expenditure, which in turn explains the

increase in male incubation feeding rates (Fig. 2). Indeed, the frequency of male incubation feeding has been shown to increase in response to the nutritional needs of the incubating female (e.g. Lifjeld et al. 1987; Smith et al. 1988; Lifjeld and Slagsvold 1989). Female nutritional need may be detected by males through the loudness of begging calls females give when they are fed by males (Ghalambor and Martin *in press*). Future studies should investigate whether the food solicitation calls given by females change in response to different nutritional states.

In response to heated nest temperatures the opposite pattern was observed. female Red-breasted Nuthatches decreased time on the nest and males decreased the frequency in which they fed females on the nest (Fig. 3). In this case, females spend more time off the nest foraging presumably because the cooling rate of unattended eggs slows due to warmer nest temperatures. Spending more time off the nest in response to warmer nest temperatures again supports previous studies showing females make proximate adjustments in attentiveness in response to egg-cooling rates (e.g. Davis et al. 1984). It is interesting to note that the percentage change in female nest attentiveness in response to cooling and heating of the nest relative to controls is much smaller compared with the percentage change in male incubation feeding rates (Figs. 2, 3). This difference between male and female response to changes in temperature may reflect greater behavioral plasticity in males compared to females, and the previous held contention that females are subject to a largely inflexible incubation rhythm (e.g. Davis et al. 1984; Haftorn 1988).

In contrast, White-breasted Nuthatches showed no significant changes in either female nest attentiveness or male incubation feeding rates in response to cooling and heating of the nest (Figs. 4, 5). A lack of response to cooler nest temperatures in female

White-breasted Nuthatches may be explained by a number of physiological factors. One possible explanation is that White-breasted Nuthatch eggs are more tolerant of colder temperatures compared with Red-breasted Nuthatch eggs, allowing females to maintain the same attentiveness at colder temperatures. We have no data on the thermal tolerance of the two species, however, it is important to note that female White-breasted Nuthatches under both natural and experimentally modified nest temperatures have extremely high nest attentiveness. Mean nest attentiveness on control days during the first time block was 94.2 % and increased to 94.8 % during the second time block, whereas on the cool air treatment days nest attentiveness was 97.6 % and 95.4% during the same respective time blocks. Indeed, we can find no published reports of any passerine species where only females incubate that has higher nest attentiveness than White-breasted Nuthatches even after controlling for time of day sampled (see Cowie and Novak 1990; Martin and Ghalambor in review). Thus, White-breasted Nuthatches have very little opportunity for adjusting attentiveness upwards. It is, however, far more difficult to explain why female White-breasted Nuthatches do not decrease attentiveness in response to heating of the nest (Fig. 5). White-breasted Nuthatches have larger eggs that should retain heat and cool more slowly compared with the smaller Red-breasted Nuthatch eggs (Chapter 1). Heating the nest should relax the constraint of sitting on the nest because slower egg cooling rates should allow for more time off the nest, yet opposite to predictions there is a non-significant trend for female White-breasted Nuthatches to spend more time on the nest (Fig. 5). Therefore, it seems unlikely that female White-breasted Nuthatches adjust attentiveness based on egg-cooling rates, but rather choose to maintain high nest attentiveness independent of changes in temperature (see also Chapter 1). Likewise, male

incubation feeding rates appear to be largely independent of changes in temperature, although males will decrease and increase incubation feeding rates in the presence and absence of a predator model, suggesting that there is some behavioral plasticity (Chapter 2, 4).

Differences Among Species in Response to Temperature

Although it is well documented that many species adjust attentiveness in response to changes in egg temperature (reviewed in Haftorn 1988), there is considerable variation among species in the degree to which adjustments are made. We found that Red-breasted and White-breasted nuthatches differed in the degree to which they adjust behavior to the same magnitude of change in nest temperatures. A similar result was found by Johnson and Cowan (1974) in a comparison of incubation behaviors in European Starlings (*Sturnus vulgaris*) and Crested Mynas (*Sturnus cristatellus*) nesting in British Columbia. Johnson and Cowan (1974) found that *S. vulgaris*, which is native to the temperate zone increases attentiveness in response to colder temperatures, whereas *S. cristatellus* which is native to the Asian subtropics does not increase attentiveness and as a result has significantly lower hatching success. Similarly, Davis et al. (1984) found that in response to experimentally heated and cooled eggs, female Savannah Sparrows (*Passerculus sandwichensis*) adjusted attentiveness, but only within certain limits. Both of these studies concluded that while there is some plasticity in female attentiveness, patterns of attentiveness appear to be controlled by a set internal rhythm. These results, in addition to the results presented here, indicate that the proximate effects of temperature on incubation behavior cannot be generalized across species. And, understanding proximate changes in incubation behaviors requires insight into possible evolutionary influences that may constrain the proximate

response to temperature. For example, it is likely that because *S. cristatellus* evolved in the subtropics there was never selection for plasticity to cope with large temperature fluctuations; as a result hatching success is much lower (61%) in British Columbia than in its native India (98 %) (Johnson and Cowan 1974). More comparative studies between tropical and temperate species are needed in order to test the evolutionary importance of climatic differences on the incubation tactics of birds.

In comparing White-breasted and Red-breasted nuthatches the question remains as to why White-breasted Nuthatches maintain such high levels of attentiveness that are invariant to changes in temperature. Both species are native to the temperate zone, and thus are unlikely to have evolved under drastically different climatic or temperature regimes. White-breasted Nuthatches differ from Red-breasted Nuthatches in two important ways, White-breasted's have a larger body size and they never excavate nest cavities (Chapter 1). As discussed above, body size alone seems insufficient in explaining why female White-breasted Nuthatches do not respond to changes in temperature, particularly at warmer nest temperatures when their larger egg size should allow for more time off the nest. Therefore, White-breasted Nuthatch egg temperatures are unlikely to cool to any lower critical levels. Rather, it appears that the primary cost to high nest attentiveness at warmer temperatures for White-breasted Nuthatches is a reduction in foraging time off the nest. Future studies should investigate the energetic consequences of high nest attentiveness in White-breasted Nuthatches under a range of different temperatures in order to quantify the female's energy budget. Also, the larger body size of White-breasted Nuthatches relative to Red-breasted Nuthatches may allow for more energy storage (Blem 1990), which in turn may allow for higher nest attentiveness.

Alternatively, the hypothesis that differences in excavation tendency explain the pattern of high and constant attentiveness is supported. Non-excavators are under strong selection to obtain and retain nest cavities which have been shown to be a limited resource (Nilsson 1984; Brawn et al. 1987; Balda and Brawn 1988; Beissinger and Waltman 1991; Bock et al. 1992, Martin and Li 1991; Martin 1992, 1993, *unpublished*). Indeed, based on 5 years of observation at more than 50 White-breasted Nuthatch nests, only a single confirmed case of re-nesting has been observed following failure (Ghalambor, *personal observation*). In contrast, Red-breasted Nuthatches readily re-nest following failure using either a cavity excavated earlier during the season or a freshly excavated cavity (Ghalambor and Martin *in press*). Furthermore, high nest attentiveness should be selected for during incubation, because White-breasted Nuthatches are effective at defending their cavities when challenged by either predators or competitors (Kilham 1968; *personal observation*). Thus, it appears that high nest attentiveness in White-breasted Nuthatches is not simply related to maintenance of egg temperatures, but may also serve as tactic to deter predators and competitors.

Limited-breeding Opportunities, Life-histories, and Incubation

In comparing the incubation tactics of Red-breasted and White-breasted nuthatches, it is important to acknowledge the contrast not only in excavation ability, but also in life-history strategies. Non-excavating bird species have life histories characterized by high reproductive effort and low annual adult survival, which is thought to be in response to limited breeding opportunities over evolutionary time (e.g. Martin 1993, 1995). Excavating species like Red-breasted Nuthatches have life histories that fall on the

other end of this continuum, with low reproductive effort and high annual adult survival (e.g. Martin 1993, 1995). According to life-history theory, non-excavators should incur more costs during the incubation period by investing more resources toward the defense and care of eggs relative to excavators because the probability of surviving and reproducing in the future is lower. Incubation is energetically costly form of parental care (Williams 1996), but these costs are often not considered in passerines as a mechanism by which survival and future reproduction may be compromised.

In short, selection pressures acting on incubating birds can differ among species, and these differences can lead to different proximate responses to changes in temperature. Future studies of incubation should consider these evolutionary constraints on the proximate responses of incubating birds to changes in temperature.

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FIGURE LEGENDS

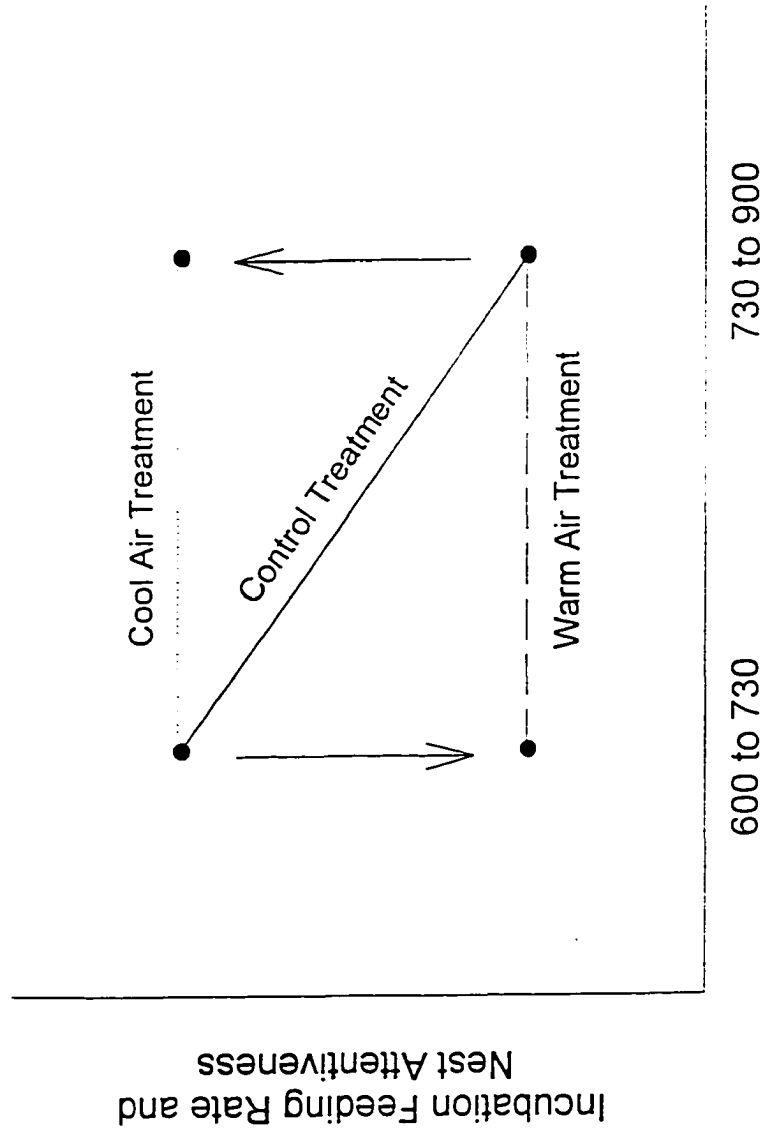
Figure 1. Experimental design used in testing for the effects of heated and cooled nest temperature on female nest attentiveness and male incubation feeding rate. See Methods for more details.

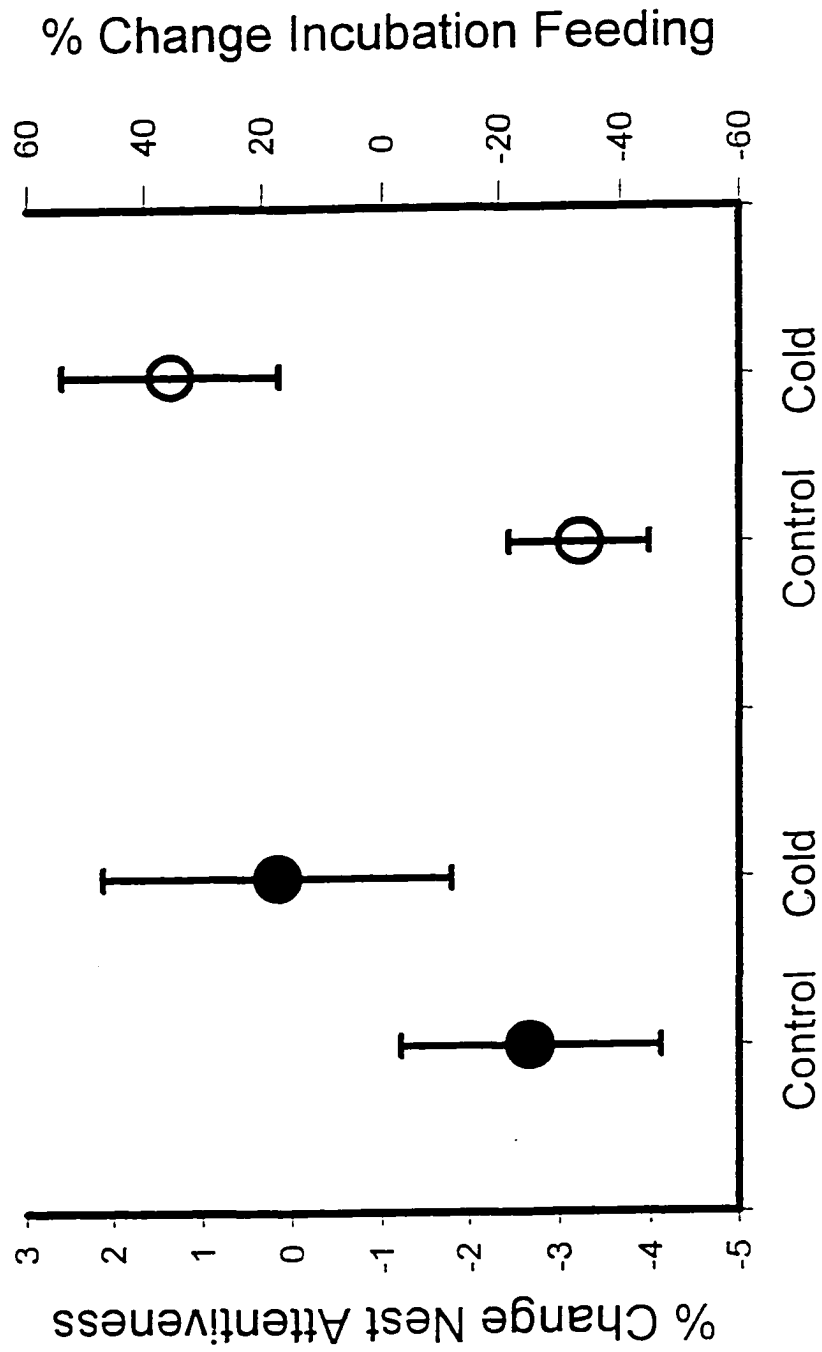
Figure 2. Percent change in response to cooler nest temperatures relative to control observations for Red-breasted Nuthatch female nest attentiveness (paired t-test; $t = -0.95$, $df = 5$, $p = 0.19$) and male incubation feeding rate (paired t-test; $t = -2.96$, $df = 5$, $p = 0.01$).

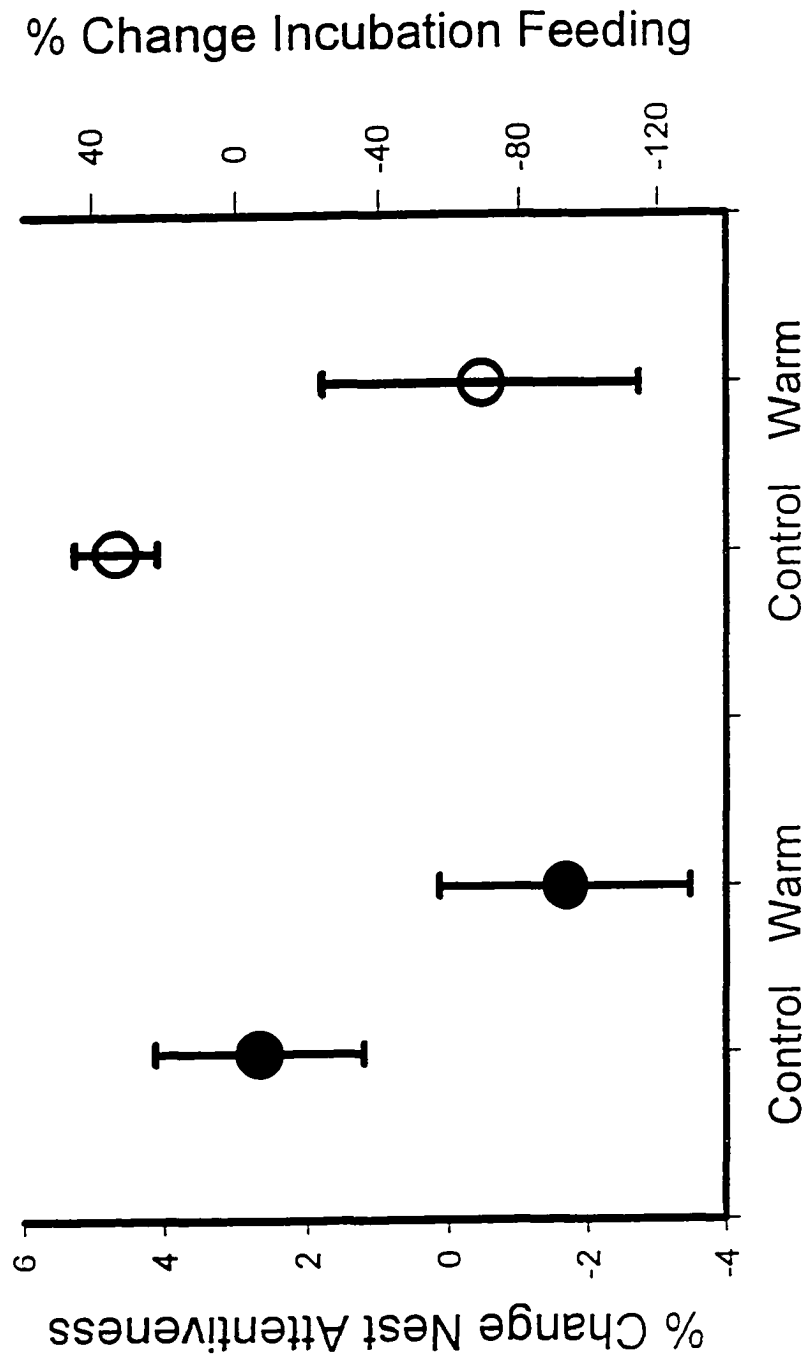
Figure 3. Percent change in response to warmer nest temperatures relative to control observations for Red-breasted Nuthatch female nest attentiveness (paired t-test; $t = -2.51$, $df = 5$, $p = 0.027$) and male incubation feeding rate (paired t-test; $t = -2.44$, $df = 5$, $p = 0.029$).

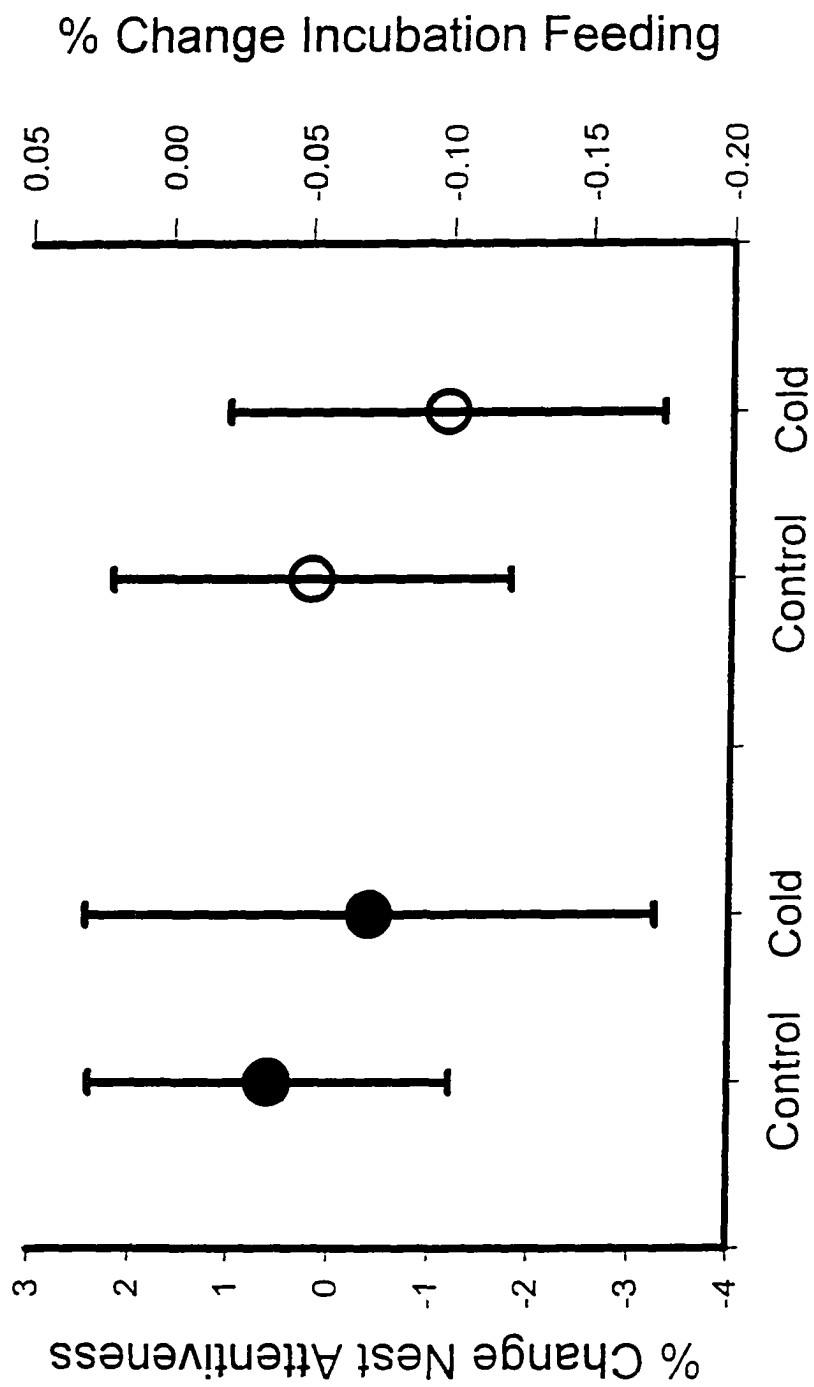
Figure 4. Percent change in response to cooler nest temperatures relative to control observations for White-breasted Nuthatch female nest attentiveness (paired t-test; $t = -0.39$, $df = 4$, $p = 0.71$) and male incubation feeding rate (paired t-test; $t = 0.34$, $df = 5$, $p = 0.75$).

Figure 5. Percent change in response to warmer nest temperatures relative to control observations for White-breasted Nuthatch female nest attentiveness (paired t-test; $t = -0.89$, $df = 4$, $p = 0.57$) and male incubation feeding rate (paired t-test; $t = -0.89$, $df = 4$, $p = 0.42$).





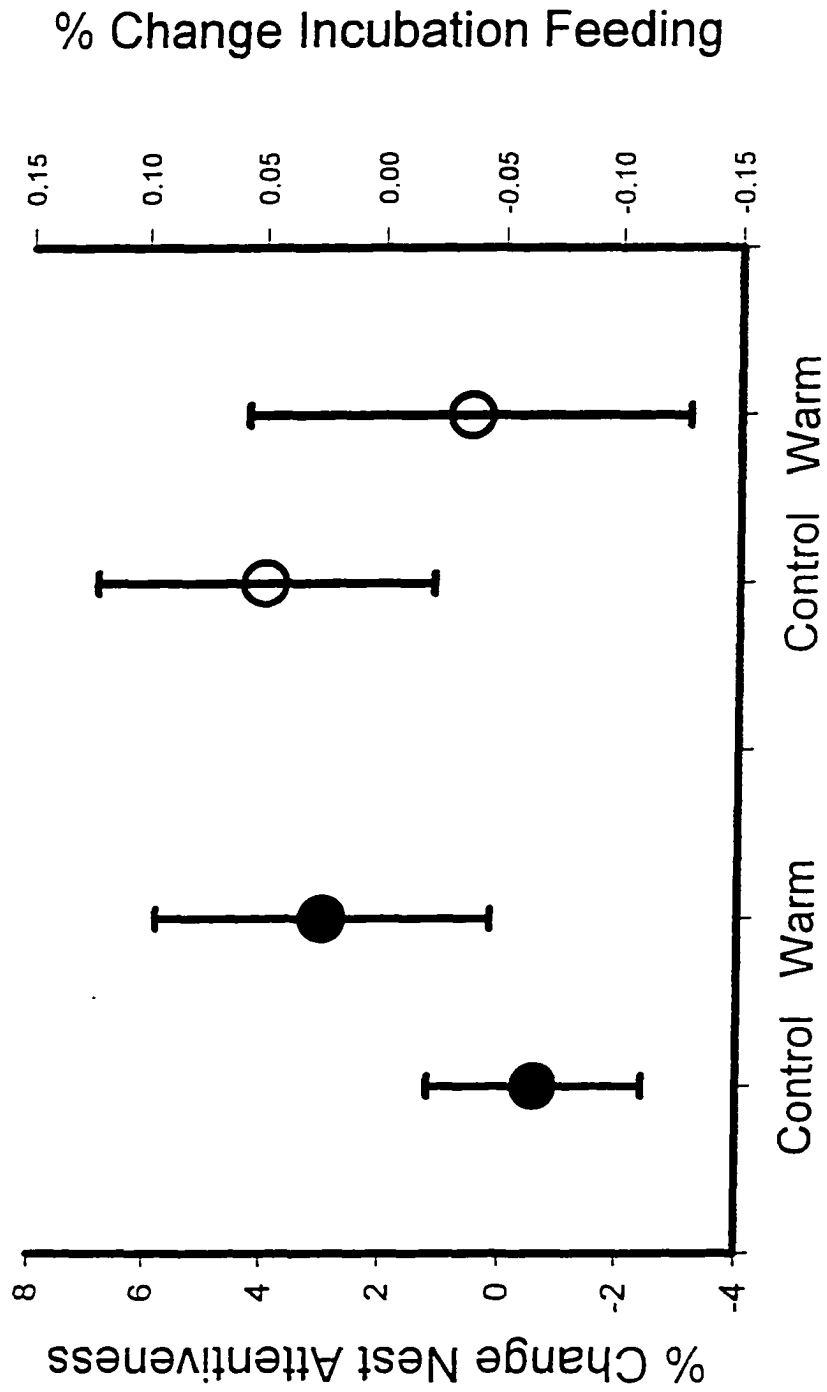




% Change Nest Attentiveness

3 2 1 0 1 2 3 4

Control Cold Control Control Cold Control



CHAPTER IV

**HOW MUCH ARE YOU AND YOUR EGGS WORTH? THE IMPORTANCE OF
LIFE-HISTORIES ON MALE RISK-TAKING BEHAVIOR**

INTRODUCTION

A central tenet of life-history theory is the trade-off between investment in current versus future reproduction (Williams 1966; Trivers 1972; Clutton-Brock 1991; Roff 1992; Stearns 1992). This trade-off predicts that parental investment decisions should maximize lifetime reproductive success by considering the reproductive value of the current brood versus residual reproductive value (i.e. the probability of surviving and breeding in the future) (Sargent and Gross 1985; Montgomerie and Weatherhead 1988). Thus, parents should invest more in current reproduction if the likelihood of future survival and reproduction is low, and withhold current investment if future prospects of survival and reproduction are high. Predation risk to parents and young is one important factor that may influence how parents decide to invest time and energy toward current versus future reproduction, and risk-taking behavior has been a common metric of parental investment used to develop and test theory (Montgomerie and Weatherhead 1988; Lima and Dill 1990; Clutton-Brock 1991; Martin 1992; Dale et al. 1996). Empirical studies of nest defense have shown that parents appear to adjust investment based on these expected current and future fitness costs (e.g. Greig-Smith 1980; Pugesek 1983; Coleman et al. 1985; Curio 1987; Weatherhead 1989; Wicklund 1990; Dale et al. 1996). Yet, most studies on risk-taking and parental investment have focused on decision making among individuals within a species, whereas comparisons among species have been rare (but see Ricklefs 1977; Forbes et al. 1994). The lack of interspecific comparisons is surprising, given that life-history theory clearly predicts that highly fecund and short-lived species should put themselves at greater risk than long-lived, less fecund species (Montgomerie and Weatherhead 1988).

Cavity-nesting birds provide a model system in which to test the effects of different life histories on risk-taking behavior. Cavity-nesting birds can be divided into two different groups, those which excavate their own nest cavities (excavators), and those that rely on existing cavities for nest sites (non-excavators). Studies of life-history strategies that control for phylogenetic effects show that excavators and non-excavators represent two of ends of a life-history continuum, with excavators being comprised of species with low annual fecundity and high annual adult survival, and non-excavators being comprised of species with high annual fecundity and low annual adult survival (Beissinger and Waltman 1991; Martin 1992, 1993, 1995; Martin and Li 1992). Differences in life histories among these two groups are thought to be caused by limited breeding opportunities over evolutionary time in non-excavators (see Newton 1994), which has selected for high reproductive effort at a cost to future survival and reproduction.

In this study, we examine risk-taking behavior in two closely related and coexisting nuthatches that differ in their life history strategies; the Red-breasted Nuthatch (*Sitta canadensis*) versus the White-breasted Nuthatch (*Sitta carolinensis*). Red-breasted Nuthatches have a mean clutch size of 5.74 (Ghalambor and Martin *in press*), and White-breasted Nuthatches have a mean clutch size of 7.3 (Pravosudov and Grubb 1993). Annual adult survivorship in White-breasted Nuthatches has been estimated at only 35% (Karr et al. 1990). Comparable adult survivorship in Red-breasted Nuthatches is currently unavailable, but is assumed to be higher given their smaller clutch size (Ekman and Askenmo 1986; Sutherland et al. 1986; Saether 1987; Bennett and Harvey 1988; Martin and Li 1992; Martin 1995).

We compare risk-taking in these two species during the incubation period in

relation to an egg predator and an adult predator. Given differences in life histories between the two species, we predicted that White-breasted Nuthatches would be more willing to place themselves at risk, and less willing to put their offspring at risk, because of their higher current reproductive investment and reduced residual reproductive value. In contrast, we predicted that Red-breasted Nuthatches would be less willing to put themselves at risk and more willing to put their young at risk, because the probability of adults surviving and reproducing in the future is higher.

METHODS

Study sites were high-elevation (2600m) snow melt drainages on the Mogollon Rim, Arizona, USA. See Martin (1998) for a detailed description of the vegetation on these study sites. Study sites were searched for nests from May through late June of 1996 and 1997. Nests were monitored and model presentations were made at nests of incubating White-breasted and Red-breasted Nuthatches. The goal of model presentations was to increase the perceived risk of predation near the nest, therefore we chose two common predators that naturally occur on these study sites; House wren (*Troglodytes aedon*) a potential predator of eggs for both species but of no threat to adults, and Sharp-shinned Hawk (*Accipiter striatus*) a potential predator of adults, but not of eggs. Response to predator models was compared to a control model of a Dark-eyed Junco (*Junco hyemalis*) which represents no known threat to adults or eggs. The experimental design consisted of paired comparisons for each individual between days when taxidermic mounts of an egg predator (*Troglodytes aedon*), an adult predator (*Accipiter striatus*), and a control (*Junco hyemalis*) were presented in a randomized order on three

consecutive days. To control for possible time-of-day effects, observations of each individual were started at the same time everyday. Models were attached to a small quaking aspen (*Populus tremuloides*) or canyon maple (*Acer grandidentatum*) sapling depending on the prevailing understory near the nest and the same location was used for each model. In addition, to increase the detectability of the models, we broadcast taped vocalizations for each model species from a cassette player placed at the base of the sapling where the model was perched. Model presentations were made between 6 and 8m from the nest tree.

We measured two response variables as an index of risk-taking. First, in both species of nuthatch males frequently feed females on the nest (i.e. incubation feeding); therefore, we focused specifically on the male's willingness to visit the nest and feed the female. Following the methodology of Dale et al. (1996), 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. This method is particularly effective in controlling for habituation to the model. 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 seconds. Nests were observed from a blind approximately 20m from the nest tree, and 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.

To test for differences in behavior in response to the different models, we

compared behavior of nuthatches in response to the two predator models with behavior in response to the control model with paired T-tests. Thus, we tested whether differences in response between the control and predators were significantly different from zero. We also compared the response to the two predators models against each other in order to test if there was a difference between species in response to an egg predator versus an adult predator.

RESULTS

A total of 19 nests in natural cavities were found for both species (9 White-breasted Nuthatches; 10 Red-breasted Nuthatches) and all experiments were carried out between days 6 and 10 of the incubation period. There was a significant effect of model type on the elapsed time between male nest visits following model presentations (Table 1) and on the number of aborted visits to the nest (Table 2) for both White-breasted and Red-breasted nuthatches. Both species took significantly longer to visit the nest in the presence of the wren and hawk models than in the presence of the junco (Fig. 1). However, male White-breasted Nuthatches responded more strongly to the wren than to the hawk (paired T-test; $t = 2.75$, $df = 8$, $p = 0.02$), whereas male Red-breasted Nuthatches responded more strongly to hawk compared to the wren ($t = -3.29$, $df = 9$, $p < 0.00$).

White-breasted Nuthatches aborted visits to the nest only in the presence of the wren (Table 2), and this difference was significant (Fig. 2). Red-breasted Nuthatches aborted visits in the presence of the wren and hawk, but compared with the control, only the response to the hawk was significant (Fig. 2). Red-breasted Nuthatches aborted more

visits in the presence of the hawk than to the wren (paired T-test; $t = -3.97$, $df = 9$, $p < 0.00$), and White-breasted Nuthatches aborted more visits in the presence of the wren than the hawk ($t = 2.53$, $df = 8$, $p = 0.03$).

DISCUSSION

Life-history theory assumes that reproduction entails a cost, leading to a trade-off in investment between current and future reproduction. Predation risk to parents and young can influence investment decisions when parents must choose between caring for their young or themselves. The results of this study suggest that differences in life history strategies among species influence the investment decisions of breeding birds. Relative to control models, both species of nuthatches took fewer risks in response to predator models as measured by the amount of time elapsed after models were presented and in the number of aborted visits to the nest (Fig. 1, 2). However, White-breasted Nuthatches took significantly more time before visiting the nest in the presence of an egg predator compared with an adult predator, whereas the reverse was true for Red-breasted Nuthatches (Tables 1, 2, Figs. 1, 2). It therefore appears that White-breasted Nuthatches place relatively greater value on their young, while Red-breasted Nuthatches place greater value on themselves when taking risks. An increase in the amount of time between visits to the nest in response to model presentations is thought to be a good indicator of the “willingness” of parents to put themselves or their offspring at risk (Dale et al. 1996). We assume, therefore, that in the presence of the hawk model, the males become hesitant to visit the nest because they are placing themselves at increased risk of predation, whereas in the presence of an egg predator males, become reluctant to visit the nest because visual

egg predators may cue in on their behavior to find nests (Skutch 1949; Lima 1987; Lyon and Montgomerie 1987; Martin 1992, 1996; Martin and Ghalambor in review). Similarly, aborted visits are an index of parental risk taking, as there appears to be a proximate change in decision to visit the nest. The number of aborted visits in the presence of the predator models reflected a similar pattern as with the elapsed time between nest visits, with White-breasted Nuthatches aborting more visits in the presence of an egg predator and Red-breasted Nuthatches aborting more visits in the presence of an adult predator. Thus consistent with life-history theory, the species with greater annual fecundity the White-breasted Nuthatch, was less willing to place its offspring at risk and more willing to put itself at risk in comparison to the species with reduced annual fecundity the Red-breasted Nuthatch, which was more willing to put its offspring at risk and less willing to put itself at risk. Clearly more comparative studies of risk-taking are needed among species that have different life-history strategies in order to better understand how species assess risk to themselves and offspring.

Interspecific comparisons of risk-taking behavior in birds are rare, however. Ricklefs' (1977) comparison of Panamanian birds, and Forbes et al. (1994) comparison of ducks suggest that such comparisons can be very useful. Both of these studies looked at parental nest defense in response to human disturbance, and found similar to our results that differences in life histories among species predict "risky" behavior, where shorter-lived, more fecund species are more willing to put themselves at risk. However, interspecific comparisons of nest defense and risk-taking have been criticized because species may differ in such traits as parental ability to defend against predators (Montgomerie and Weatherhead 1988). We acknowledge that certain interspecific

comparisons may be confounded by differences among species that cannot be experimentally controlled. However, in this study we avoid using nest defense as a measure of risk-taking and simply focus on the willingness of parents to expose themselves or their young to the risk of predation (see also Dale et al. 1996). Indeed, other studies have shown that breeding birds do recognize predators in the environment and will modify patterns of parental care when exposed to such threats (e.g. Martindale 1982; Marzluff 1985; Kalina 1989; Wheelwright and Dorsey 1991). Comparative studies that measure the proximate response of parents to adult versus egg predators using the approach outlined here, may provide an effective means of comparing risk-taking among species.

Finally, variation in age-specific mortality is generally assumed to underlie variation in life history strategies (Roff 1992; Stearns 1992; Martin 1995). Therefore, understanding the relationship between decision making “rules” when under risk of predation and age-specific mortality is a critical component of life history evolution. If decision making is related to life history strategies as the results here suggest, then future work should consider the degree to which such behaviors are genetically correlated with other life history traits. For example, Brodie (1989) used such an approach to show that the anti-predator behavior of snakes was genetically correlated with their color patterns, such that these traits showed a correlated response to selection. A similar approach could be applied to in studies of life history evolution, by investigating the degree to which behaviors such as decision making under the risk of predation evolve alongside changes in age-specific mortality.

ACKNOWLEDGMENTS

We would like to thank Chris Ormond for assistance in the field. We thank 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. Funding from the National Science Foundation (IBN-9701116) made this research possible.

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Table 1. Results from model presentation experiments for two species of incubating nuthatch on the Mogollon Rim, AZ, USA. Shown are mean elapsed times (min. \pm SE) until the nest was visited by males in the presence of three models.

	Control Model (<i>Junco hyemalis</i>)	Egg Predator Model (<i>Troglodytes aedon</i>)	Adult Predator Model (<i>Accipiter striatus</i>)	ANOVA ¹
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	5.00 (1.79)	20.55 (3.26)	10.22 (11.14)	F = 13.93, df = 2, 16, p < 0.00
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	4.05 (1.20)	8.40 (1.78)	20.05 (5.02)	F = 11.39, df = 2, 18, p < 0.00

¹ANOVA tests the main treatment effect of different model presentations on elapsed time until male visits the nest, while blocking on individuals within species to control for individual effects.

Table 2. Results from model presentation experiments for two species of incubating nuthatch on the Mogollon Rim, AZ, USA. Shown are mean number (\pm SE) of aborted visits to the nest by males in the presence of three models.

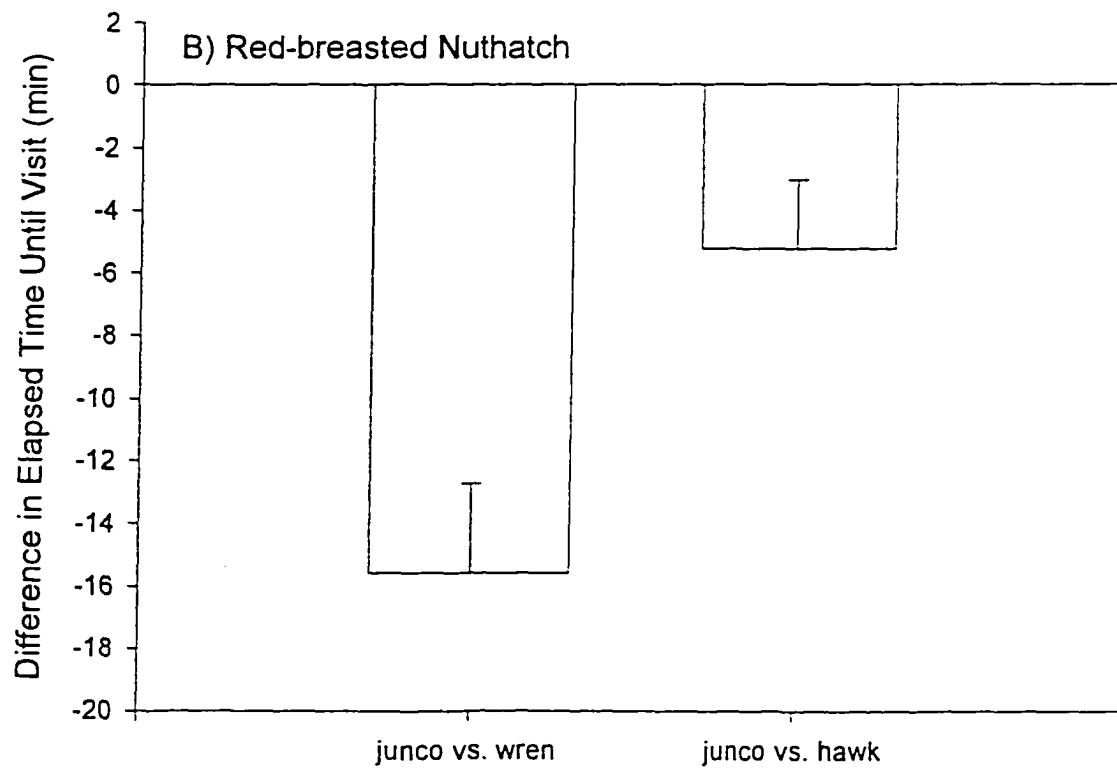
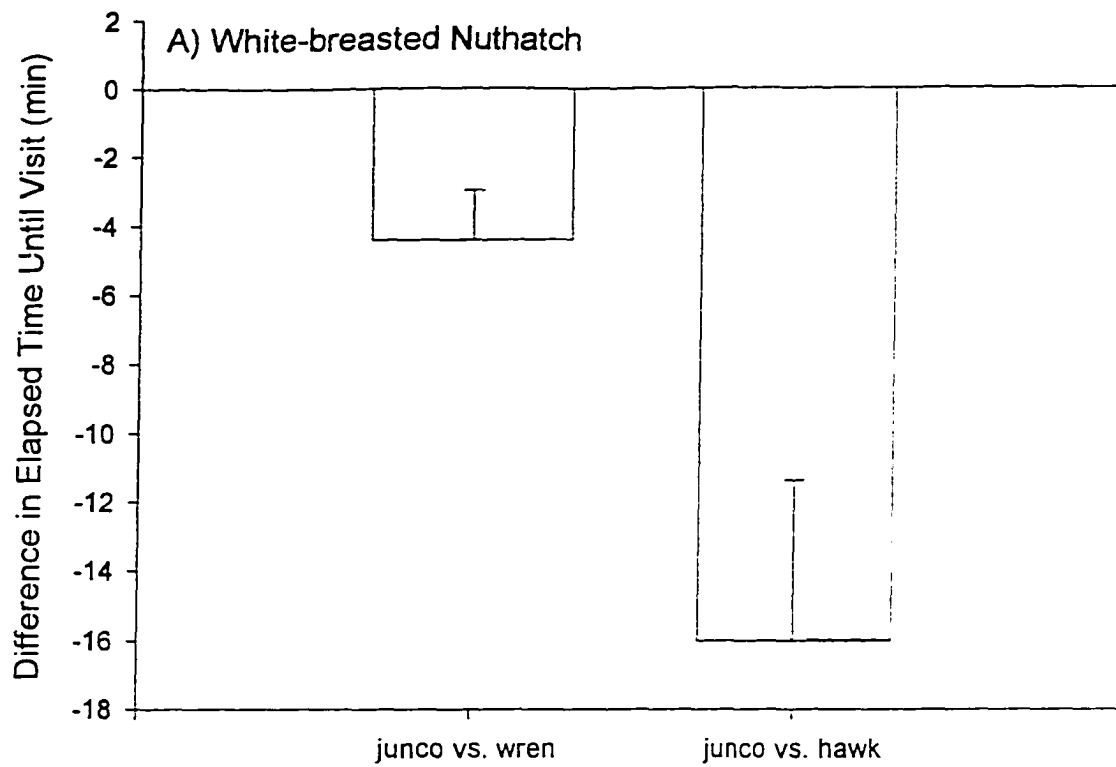
	Control Model (<i>Junco hyemalis</i>)	Egg Predator Model (<i>Troglodytes aedon</i>)	Adult Predator Model (<i>Accipiter striatus</i>)	ANOVA ¹
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0.00 (0.00)	1.11 (0.26)	0.00 (0.00)	F = 18.18, df=2, 16, p < 0.00
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	0.00 (0.00)	0.20 (0.13)	1.30 (0.30)	F = 15.94, df=2, 18, p < 0.00

¹ANOVA tests the main treatment effect of different model presentations on the number of aborted visits to the nest by males while blocking on individuals within species to control for individual effects.

FIGURE LEGENDS

Figure 1. A. Difference in amount of time elapsed after presentation of a control model (junco) versus an egg predator = wren (Paired t-test; $t = -5.49$, $df = 8$, $p < 0.00$) and adult predator = hawk (Paired t-test; $t = -2.36$, $df = 8$, $p < 0.00$) in White-breasted Nuthatches. B. Difference in amount of time elapsed after presentation of a control model (junco) and an egg predator = wren (Paired t-test; $t = -3.06$, $df = 9$, $p < 0.00$) and adult predator = hawk (Paired t-test; $t = -3.45$, $df = 9$, $p < 0.00$) in Red-breasted Nuthatches.

Figure 2. A. Difference in the number of aborted feeds in the presence of a control model (junco) versus an egg predator = wren (Paired t-test; $t = -3.46$, $df = 8$, $p < 0.00$) and adult predator = hawk (Paired t-test; $t = 1.00$, $df = 8$, $p = .38$) in White-breasted Nuthatches. B. Difference in the number of aborted feeds in the presence of a control model (junco) versus an egg predator = wren (Paired t-test; $t = 1.50$, $df = 9$, $p = 0.17$) and adult predator = hawk (Paired t-test; $t = 4.33$, $df = 9$, $p < 0.00$) in Red-breasted Nuthatches.



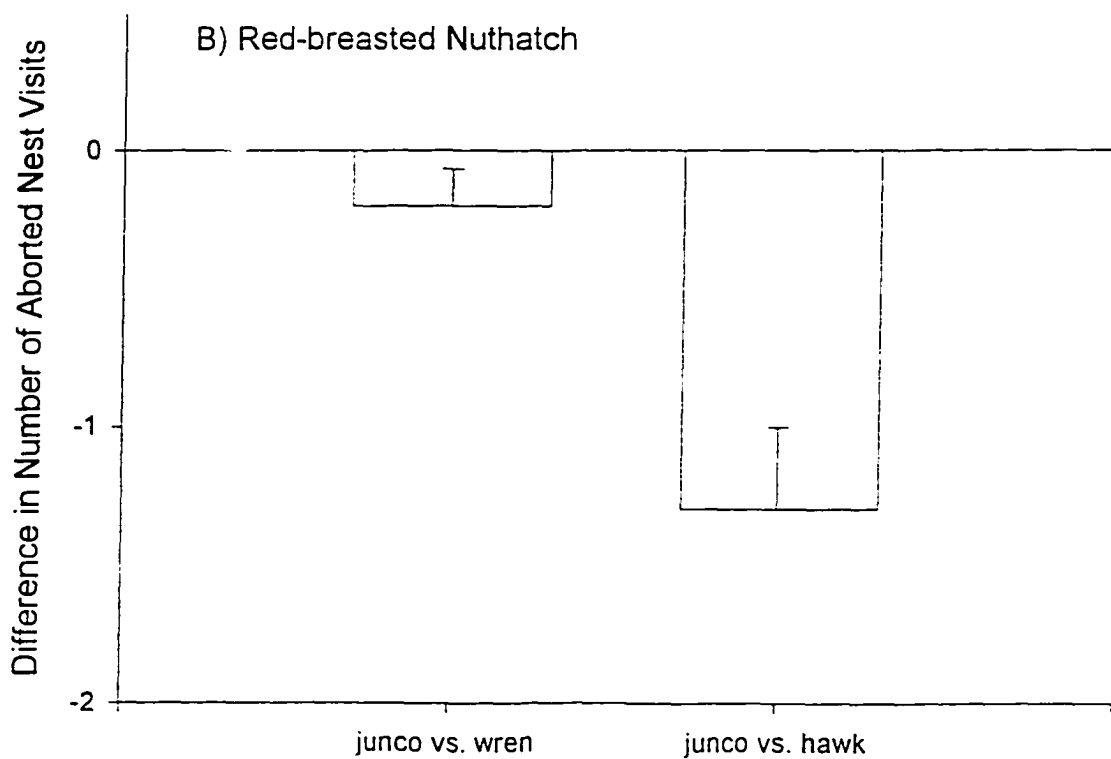
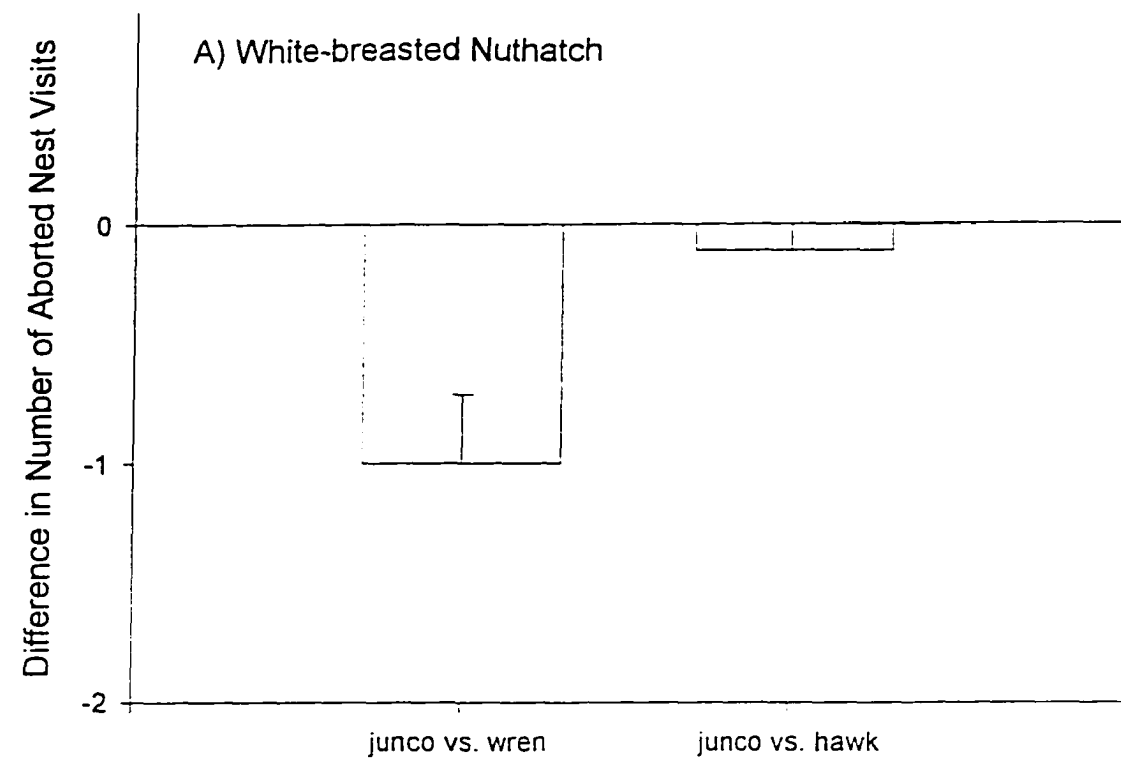
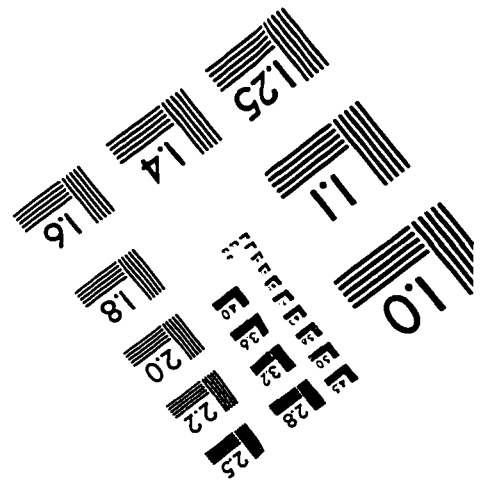
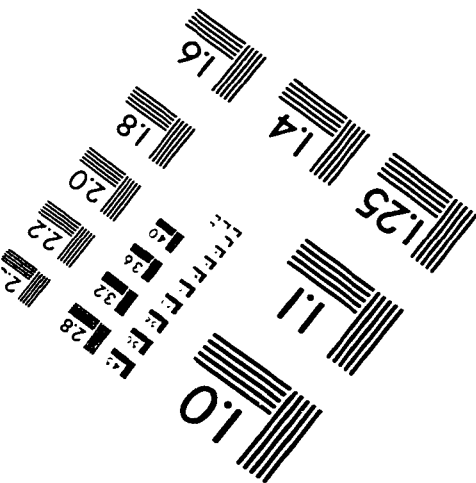
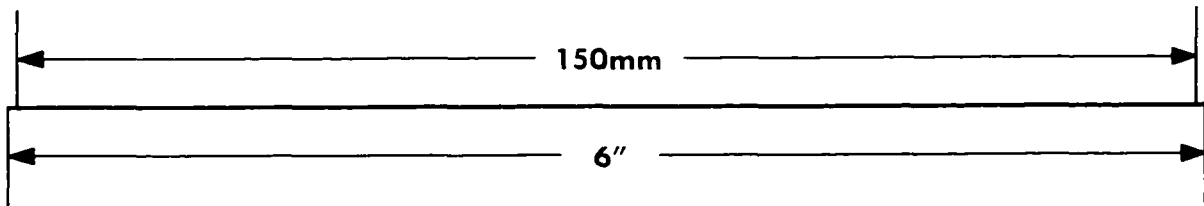
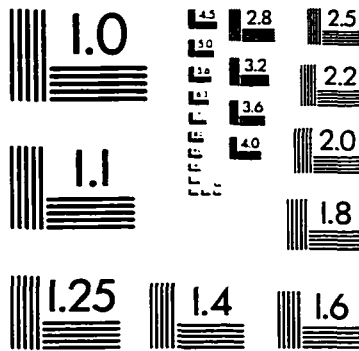
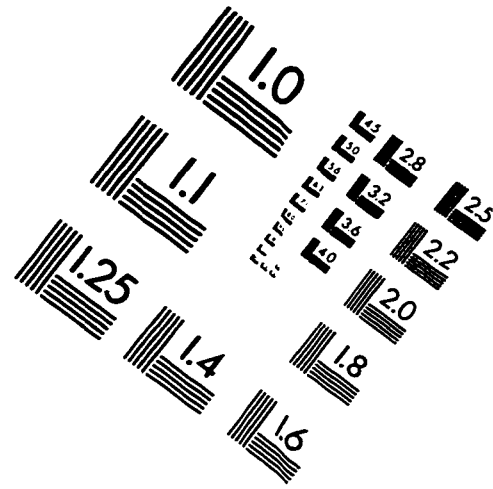
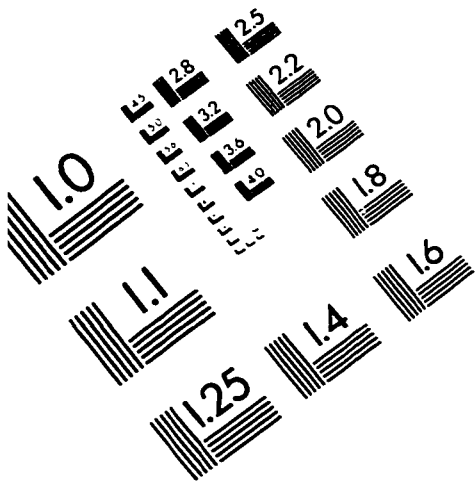


IMAGE EVALUATION TEST TARGET (QA-3)



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