EFFECTS OF TEMPERATURE AND FOOD ON AVIAN INCUBATION BEHAVIOR

By

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TABLE OF CONTENTS

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
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Avian incubation behavior is thought to be influenced mainly by ambient temperature and food availability. Field studies, however, have generated contradictory results and no general agreement about the relative importance of food and temperature influence and on how different components of incubation behavior are affected by each. Therefore, we experimentally increased both food availability and ambient temperature during incubation in the Northern Mockingbird (*Mimus polyglottos*). Our results demonstrated that both food availability and temperature influence incubation behavior. Increasing food availability enabled females to spend more time on the nest and in self-maintenance activities when off the nest. Increasing heat caused females to spend less time on the nest and to make more trips to and from the nest. When both food and temperature were increased, their effects on incubation time offset each other. These changes in incubation patterns had little effect on fitness, although embryo mass was lowest in the treatment in which only heat was increased, suggesting that heat may stress embryos, but not when extra food is also provided. Perhaps the reason why previous studies present contradictory results is because food and temperature offset each other in complex ways that could obscure their effects on incubation behavior.

CHAPTER 1
INTRODUCTION

Embryonic development in birds is unique among vertebrates because it typically requires direct transfer of body heat from incubating adults (Deeming, 2002a; Turner, 2002). The energetic costs of incubation have been generally overlooked because they are thought to be far lower than the more obvious costs of feeding young. Recent studies, however, suggest that incubation is energetically costly (Williams, 1996; Thomson et al., 1998; Tinbergen and Williams, 2002) and that incubation behavior influences the probability of predators finding the nest (Martin et al., 2000; Muchai and Plessis, 2005; Rastogi et al., 2006). Because time and energy invested in incubation means less time and energy for energy intake (foraging) and self maintenance, incubating birds face a trade-off between parental and self care (Williams, 1996; Tinbergen and Williams, 2002; Turner, 2002).

Elucidating this life history trade-off requires understanding what influences incubation rhythms (Martin, 2004), defined as the length and temporal pattern of incubation bouts. Two factors that play important roles in incubation rhythms are ambient temperature and food availability (Skutch, 1962; Lack, 1968; Grant, 1982; Martin, 1987; Weathers and Sullivan, 1989; Conway and Martin, 2000a; Conway and Martin, 2000b; Deeming, 2002b; Eikenaar et al., 2003; Lloyd and Martin, 2004; Martin, 2004; Nagy and Holmes, 2005; Zimmerling and Ankney, 2005). Ambient temperature influences energy expenditure during incubation and embryonic growth during recesses from incubation (Baerand, 1959; Weeden, 1966; Drent, 1970; Vleck, 1981a; Zebra and Morton, 1983; Reid et al., 1999; Conway and Martin, 2000a; Tinbergen and Williams, 2002; Cresswell et al., 2004). In contrast, food availability controls the rate of energy acquisition and hence the times off the nest and the time available for other self-maintenance activities (Skutch, 1962; Martin, 1987; Weathers and Sullivan, 1989; Nilsson, 1994; Sanz, 1996;

Cucco and Malacarne, 1997; Eikenaar et al., 2003; Zimmerling and Ankney, 2005; Rastogi et al., 2006; Chalfoun and Martin, 2007). Conway and Martin (2000a) concluded that incubation rhythm depended on ambient temperature rather than food. The effects of temperature, however, were non-linear and explained only a small proportion of variation in incubation rhythm among species. The same authors proposed that food does not explain variation in incubation rhythm, at least among species (Conway and Martin, 2000b). Within species, however, food can affect incubation rhythm (Conway and Martin, 2000a; Zimmerling and Ankney, 2005; Rastogi et al., 2006). Therefore, there are contradictory results and no general agreement about the relative contributions of food and temperature on avian incubation behavior.

We suggest that much of the confusion about the roles of food and temperature stems from the assumption that these two factors act independently or the belief that one factor overwhelms the effects of the other. Yet the relative importance and potential interaction of food and temperature are impossible to judge in the absence of experiments that manipulate both factors simultaneously (Martin, 1987; Conway and Martin, 2000a; Wiebe and Martin, 2000; Martin, 2004). We are not aware of any studies designed in such a way. Also, most studies of incubation focus on quantifying when birds are on or off the nest and generally do not attempt to describe behaviors when off the nest. Because behaviors that occur off the nest likely influence behaviors on the nest, both should be considered part of incubation behavior -- both can have a strong influence on nest survival and adult fitness (Franks, 1967; Vleck, 1981a; Davis et al., 1984; Cucco and Malacarne, 1997; Nagy and Holmes, 2005; Zimmerling and Ankney, 2005).

Our primary objective was to evaluate experimentally the interaction and relative importance of food availability and temperature on avian behavior during incubation. We hypothesized that both food and temperature affect incubation behavior. We tested three

8

predictions: **Prediction 1:** Females on territories with high food availability will spend more time on the nest and more time doing other potentially fitness-enhancing behaviors such as preening or defending the nest because hunger levels and foraging times will be reduced.

Prediction 2: Females on nests in hotter microclimates will decrease time on nest and increase the total number of trips to the nest per day because metabolic needs increase at high temperatures, as predicted by Conway and Martin (2000a). Furthermore, females in hotter microclimates, when on the nest, should spend more time regulating nest temperature through behavioral responses such as panting or egg shading (Franks, 1967; Vleck, 1981a; Davis et al., 1984). **Prediction 3:** Females that experience both hot microclimates and high food abundance should spend an intermediate amount of time on the nest. The reasoning behind this last prediction is that food and heat influence time on the nest in opposite directions (predictions 1 and 2), with food increasing time on the nest (Zimmerling and Ankney, 2005; Rastogi et al., 2006) and heat (high temperatures) increasing on and off-bouts, which decreases time on the nest (Conway and Martin, 2000a).

We tested these predictions by experimentally manipulating food availability and nest microclimate of Northern Mockingbirds (*Mimus polyglottos*), a species in which only females incubate and males do not provide food to incubating females.

CHAPTER 2
STUDY SITE AND METHODS

This study was conducted between April 1 and July 15 in 2005 and 2006 on the University of Florida campus in Gainesville, Florida (N29º 38' 267"; W 082º 21' 984"). The campus has ideal mockingbird habitat: large expanses of mowed grass for foraging and scattered shrubs for nesting.

The study area was divided in six sections and, once per week, all shrubs and trees within each section were searched for nests. Each new nest, either under construction or with an incomplete clutch (1-2 eggs), was randomly assigned to one of four experimental treatments in a 2 x 2 factorial design: Food increase (food+), heat increase (heat+), food and heat increase (food+/heat+), and neither food nor heat increase (control). Food+ nests had a feeder placed within 2 to 5 m. Feeders consisted of a plastic food storage container mounted 1.5 m above the ground on a PVC pipe. They were placed when nests were first found and supplied daily with mealworms (*Tenibrio molitor*). Based on preliminary observations of the number of mealworms consumed by a pair of mockingbirds, we placed 160 mealworms (approximately 17g) in each feeder every day. Mealworms have an energetic value of 11.6 kJ/g and birds can metabolize a minimum of 71% of the energy available in an average insect (Bell 1990); our provision of 160 mealworms therefore would provide the mockingbird pair with about 5.83 kJ/h of additional energy. Female mockingbirds consumed 7.5±0.68 (se) mealworms per hour. We calculated the BMR (basal metabolic rate) for an insectivorous bird of 48g (eq. 6; McNab, 2005) to be 1.83 kJ/h. Thus, assuming that energetic requirements during incubation are three times higher than the BMR (Williams, 1993; Piersma and Morrison, 1994), we estimated that female mockingbirds spent 5.49 Kj/h during the incubation period. So, mealworms provided approximately 53% of the daily energy expended by the female during incubation.

Feeders were used exclusively by the pair of mockingbirds at the nearest nest, except in a few cases when juveniles from a pair's previous clutch also used the feeder. In those cases, an extra 8g of mealworms were placed in the feeder. Because high temperatures can kill mealworms in the feeders and because mockingbirds usually do not eat dead mealworms, half of the mealworms were placed in the feeders before sunrise and the remaining half were placed in the early afternoon. Typically, most or all of the mealworms had been consumed by the time more were added.

Heat+ nests received an 18 watt bulb in a 47 x 32.2mm (length x diameter) cylindrical aluminum tube on the day the third egg was laid, when the likelihood of nest abandonment was low. The bulb and cylinder were placed directly under the nest, touching nest material, approximately 30mm from the eggs. After the clutch was complete and incubation had started, the bulb was turned on shortly before sunrise (0600) and remained on until the battery was drained, approximately 8 hours later. When the bulb was on, the nest chamber experienced a temperature of approximately 35°C, which corresponds to the daytime high temperature at the study site in late summer, when most mockingbirds stop breeding. Ambient temperature ranged from 17.0 to 37.1 ^{o}C (average: 26.6; Std. Dev. = 1.2) during the study period. Nests that did not receive a heater (food+, and control nests) received a sham heater. Food+/Heat+ nests received both a feeder and a heater; control nests received neither.

All nests had two thermal sensors (39.5x7.1mm), one internal and one external, connected to a H8 4-Channel Hobo data logger (Onset Computer Corporation). Sensors were placed in nests the day the third egg was laid and recorded temperature every minute. The internal sensor was attached to the nest wall just above the eggs. It provided two types of information: incubation temperature and the time at which the incubating bird left or returned to the next, as

11

detected by rapid temperature shifts of at least 1.5°C (see below). The external sensor was attached to the outside nest wall at the same height as the internal sensor, and shielded from the heater. It provided data on ambient temperature in the immediate vicinity of the nest.

All treatments lasted ten days, when all eggs were collected for examination of embryo development (see below). All nesting pairs of mockingbirds were used only once and for a single treatment. Due to predation events and data logger malfunction, the number of nests per treatment varied among treatments: n = 11 for food+, n = 18 for heat+, n = 10 for food+/heat+, and n = 12 for control.

Only female mockingbirds incubate. Between days four and nine of treatments, we observed each female for a total of eight hours, distributed in two-hour blocks between sunrise and 14:00 over four days. During these two-hour blocks, we continuously recorded the time spent doing the following behaviors: incubating, foraging, preening, being still, panting on the nest (cooling the eggs) and "other" (singing, territorial defense, flying, etc.). Most behaviors were mutually exclusive – birds could not engage in two simultaneously. Panting and incubation were exceptions, because incubating birds often panted. In that situation, we recorded the exact time intervals during which females panted. Females spent all night on the nests, arriving at sunset and departing at sunrise. Therefore, any differences in incubation among treatments are due to differences in incubation behavior during the day. Behavioral observation were conducted on 65 nests (food+ = 16; food+/heat+ = 14; heat+ = 19; control = 16).

On day ten of the incubation period, we captured as many females as possible (food+ = 9 females; food+/heat+ = 8; heat+ = 16; control = 12) and weighed them to the nearest gram.

For each treatment, we recorded the day on which any nest was lost to predation before the completion of the experiment (ten days). We used two metrics of nest predation for each

treatment: the total number of nests lost to predation and the average daily survival rate. For this analysis we used 80 nests, 17 in food+, 21 in control, 18 in food+/heat+ and 24 in heat+.

On day ten after sunset, we collected the eggs from all nests to measure treatment effects on embryonic development. Egg mass was measured to the nearest 0.05g and egg length and width were measured to the nearest 0.1mm. We opened each egg, removed all membranes, weighed the embryo to the nearest 0.05g, and recorded the length and width to the nearest 0.1mm. We also quantified the number of non-developed embryos, which we define as eggs that contained minute embryos that were too small to weigh or remove from the yolk without damage. We measured 111 embryos from 42 nests: 38 embryos from 13 control nests; 27 embryos from 10 food+ nests; 19 embryos from 7 food+/heat+ nests, and 27 embryos from 12 heat+ nests.

In 2006, we collected ectoparasites by the "dust-ruffling" technique (Jackson, 1985; Walther and Clayton, 1997). Females were lightly dusted with pyrethrin powder, except for the head. We worked the pyrethrum into the feathers with fingers, waited 5 minutes, and ruffled the feathers over a tray lined with colored paper, against which the ectoparasites were easily visible. We placed ectoparasites in micro-centrifuge tubes with 99% ethanol. Because the dust-ruffling technique works best for lice (Walther and Clayton, 1997), we only quantified the number of feather lice, which we counted under a stereo microscope. We sampled a total of 28 females; five from control nests, six from food+ nests, six from food+/heat+ nests, and 11 from heat+ nests.

The temporal pattern of incubation for each nest was obtained from temperature fluctuations detected by each nest's internal sensor and analyzed following the protocol suggested by Cooper and Mills (2005). In brief, temperature readings from the data loggers were converted into a text file, which was then transformed into a sound file, using Rhythm software

(Cooper and Mills, 2005). An algorithm detected all intervals in which temperatures decreased monotonically and retrieved three quantities for each such interval: duration, total drop in temperature, and initial rate of temperature decrease. Based on preliminary analyses coupled with direct observations of when females arrived and left nests, detection of an off-bout (end of an incubation period) was triggered when nest temperature decreased monotonically for at least 1 min and dropped at least 2°C at an initial rate of at least 0.5°C/min. Detection of an on-bout (beginning of an incubation period), was triggered when temperature increased monotonically for at least 1 min at an initial rate of at least 0.5°C/min.

Data on incubation behavior were analyzed with a repeated-measures ANOVA (General Linear Model procedure of SAS, version 9.1), with food, heat, year, and all two-way interactions included in the model. Response variables, each analyzed separately, were total minutes of incubation time during daylight for each of the ten days of a treatment (i.e., sum of all on-bout times for each day), number of trips from the nest for each day (i.e., total number of off-bouts), and total duration of trips from the nest for each day. Differences in female and embryo mass were analyzed with a two-way ANOVA, with mass as a dependent variable, food and heat as fixed factors and nest as a random factor. The numbers of nests lost to predation in each treatment were compared with a chi-square test. We also estimated daily predation rates among categories, using Shaffer's logistic regression model (Shaffer, 2004; SAS, 9.1). For post hoc tests we used the Tukey-Kramer honestly significant difference (Tukey-Kramer HSD), which is relatively unlikely to result in a Type 1 error (Hilton and Armstrong, 2006).

CHAPTER 3
RESULTS

Inner nest temperatures were always hotter than ambient temperatures, with differences fluctuating between 3 and 7ºC depending on the treatment. By day, when heaters were turned on, nest temperatures differed significantly among treatments ($F_{3,407} = 27.37$, p < 0.001). Nests in both heat treatments (heat+ and food+/heat+) had higher temperatures (2-3ºC; *p*'s < 0.001), than non-heated treatments (food+ and control). Nest temperatures did not differ significantly among heat treatments (*p*'s = 0.97). In contrast, daily nest temperatures differed between food+ and control treatments (*p*'s < 0.007), with higher nest temperatures (0.9ºC) in food+ treatments.

Incubation time. Females in the four groups spent from 52.2% (heat+) to 64.4% (food+) of daylight hours incubating. There was no year effect on total daily incubation time ($F_{1,45} = 0.00$, p = 0.98). Food+ and heat+ treatments affected total incubation time, although their influences were only marginally significant ($F_{1,45} = 4.1$, p = 0.04; $F_{1,45} = 3.9$, p = 0.05, food+ and heat+, respectively). All interaction terms were non-significant. Total incubation time for females over the entire 10-day period on food+ nests was 12.2% greater than those on heat+ nests (p's < 0.04, Tukey's; Fig. 1). Total incubation time on control and food+/heat+ was intermediate (56.1-56.6%, respectively), and not significantly different from food+ or heat+ nests (p's = 0.31 and 0.45, Tukey's, respectively; Fig. 1). The average number of trips off the nest each hour was significantly affected by heat+ ($F_{1,45} = 5.56$, p = 0.02), with females on heat+ nests averaging 21.9%, 18.8%, and 13.9% more trips per hour than on food+, control, and food+/heat+ nests, respectively (Fig. 2a). There were marginally significant differences in number of trips per hour on food+ and heat+ nests (p's = 0.06, Tukey's). Trip length (Fig. 2b) was not significantly affected by food+ ($F_{1,45} = 2.65$, p = 0.11) or heat+ treatments ($F_{1,45} = 2.67$, p = 0.11). Females in the food+ treatment tended to make shorter trips, approximately 21% less than females in the

other treatments, but no pair-wise posthoc comparisons were significant ($0.08 < p\text{'s} < 0.15$

Tukey's, Fig. 2b). During incubation, females differed in the percentage of time spent panting

($F_{3,64} = 4.86$, p = 0.04), with females on heat+ and food+/heat+ nests spending 19% and 17%

(respectively) of incubation time panting, compared to 3% of time for females on both food+ and

control nests.

Behaviors: Female behavior off the nest differed among treatments (Fig. 3). Foraging

behavior was significantly influenced by food+ ($F_{1,64} = 148.23$, p <0.0001) and not by heat+

($F_{1,64} = 0.24$, p = 0.20). Time spent preening was greatly influenced by additional food (food+;

$F_{1,64} = 60.12$, p <0.0001) but not by additional heat (heat+; $F_{1,64} = 0.002$, p = 0.967). Time spent

being still was affected by food+ ($F_{1,64} = 4.04$, p = 0.04) and not by heat+ ($F_{1,64} = 1.68$, p = 0.20).

Time spent on "other" activities was not influenced by either food+ ($F_{1,64} = 2.63$, p = 0.11) or

heat+ ($F_{1,64} = 0.001$, p = 0.976) treatments.

Other measurements: Body mass on the last day of trials (day ten) was not affected either

by food ($F_{1,46} = 0.68$, $p = 0.42$) or heat ($F_{1,46} = 0.97$, $p = 0.33$). The total number of nests lost to

predators did not differ among groups ($X^2_{0.05} = 0.43$, df = 3, $p = 0.94$). Daily nest survival rates

ranged from 97.8% and 98.2% and did not differ among treatments. Frequency of ectoparasites

was very low. We found lice on only two of 45 females that were examined. One was in the

heat+ treatment and the other was from the control group.

Embryo mass was significantly affected by our treatments ($F_{1,40} = 6.44$, $p < 0.001$, Fig. 4).

Embryo mass in the heat+ treatment was between 26% and 28% lighter than any other treatment.

Embryo mass was similar among control, food+ and food+/heat+ treatments. There were no

difference in the number of undeveloped embryos among treatments ($X^2_{0.05} = 5.15$, df = 3, $p =$
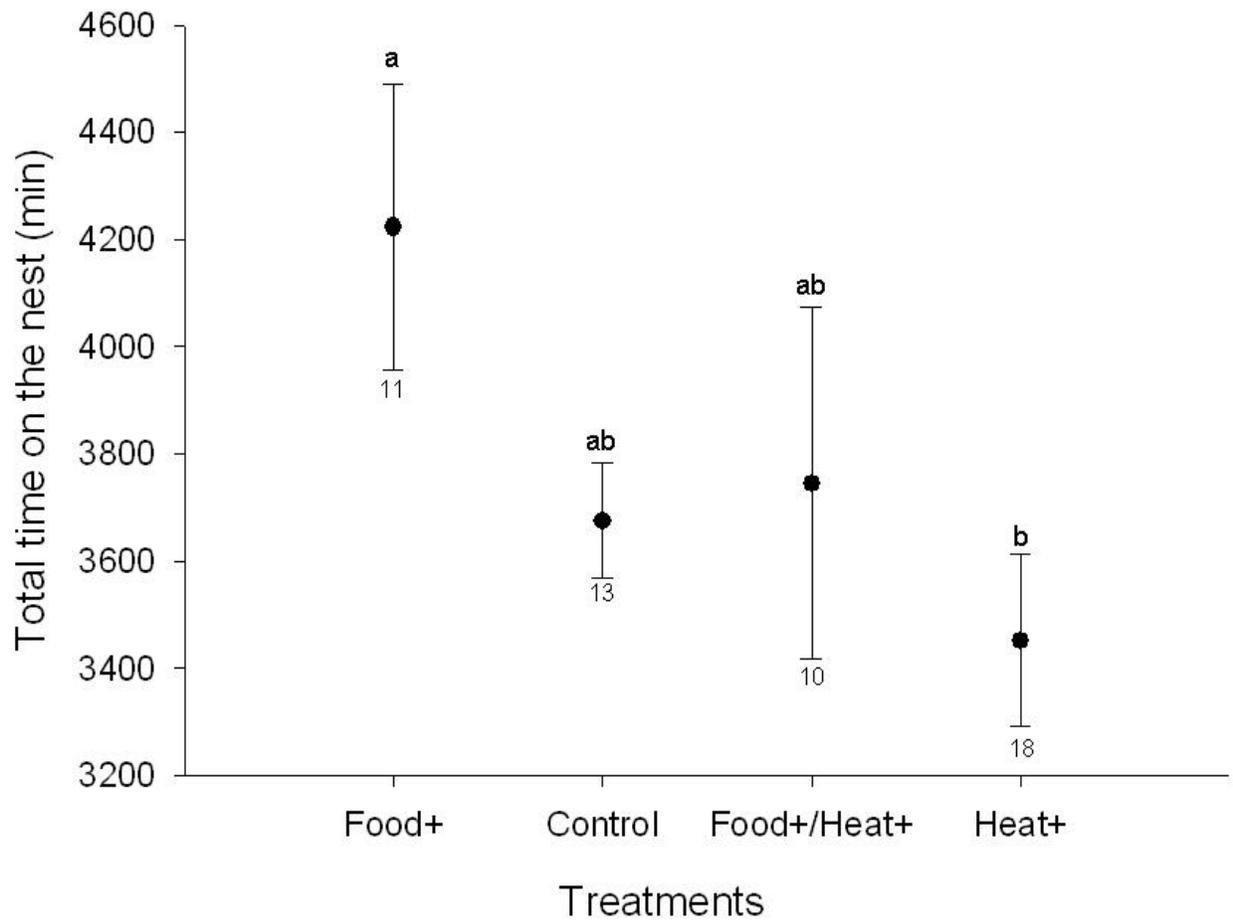
0.16).

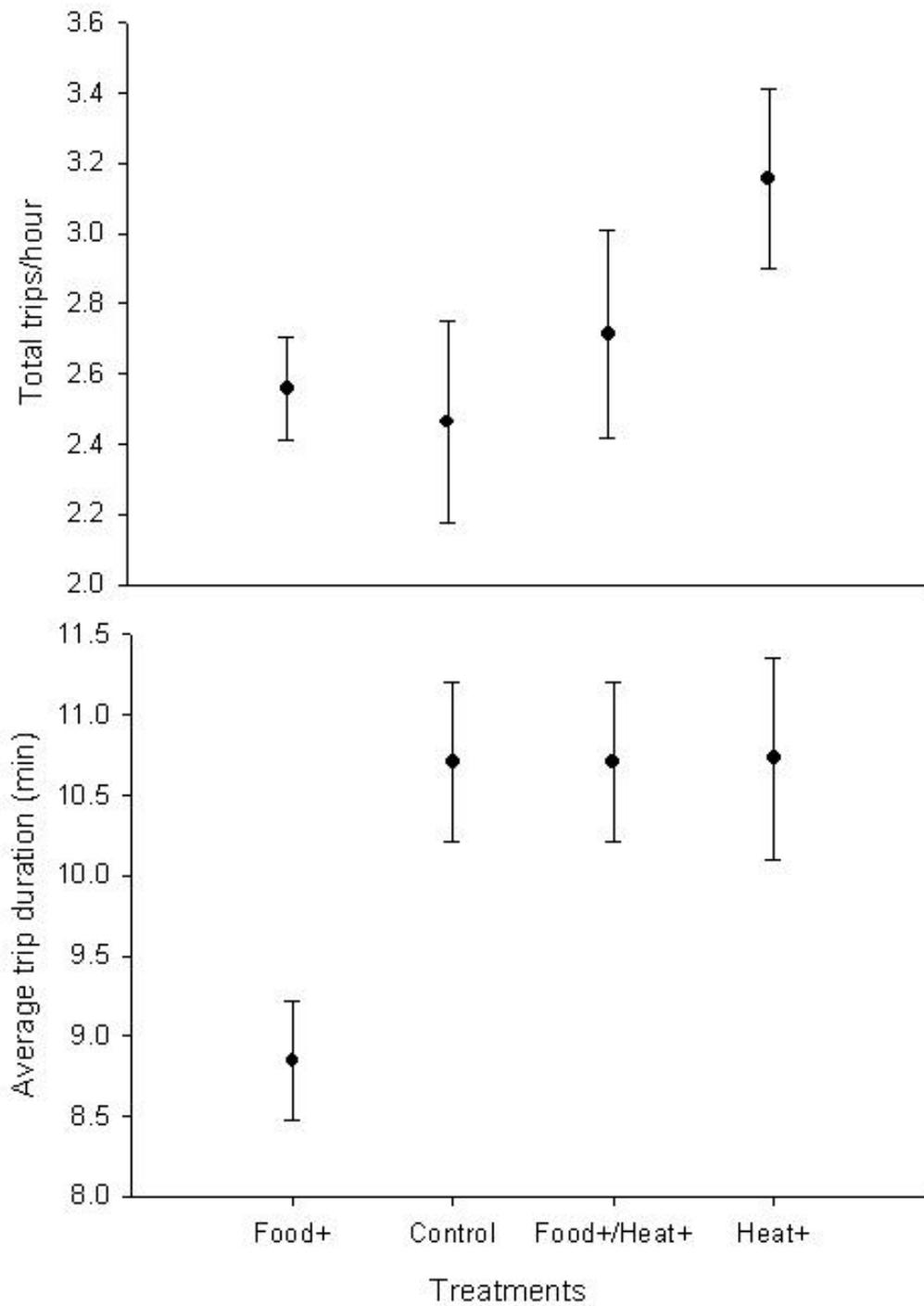Figure 3-1. Mean incubation times during ten days of the different experimental females.

Figure 3-2. Mean number of trips and trip length during ten continuous day of incubation among treatments.
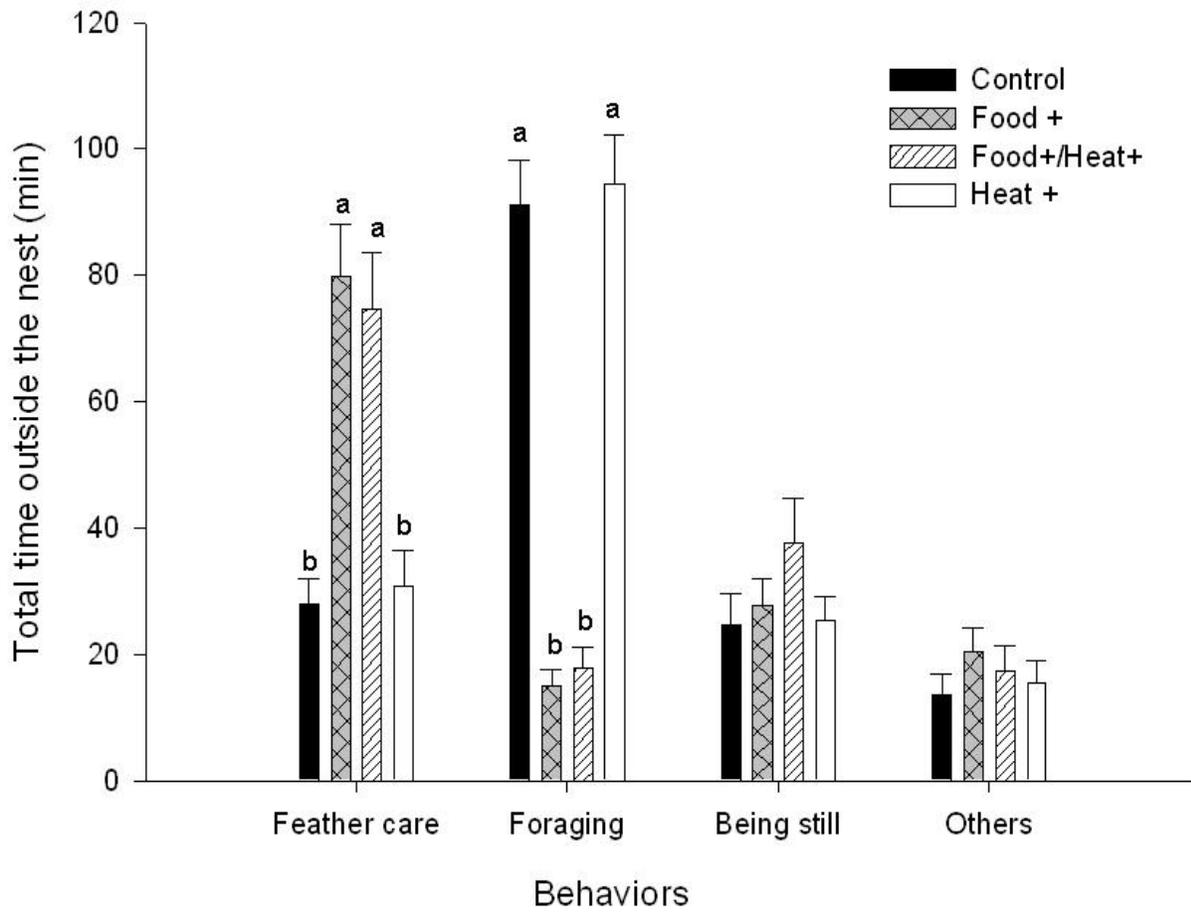
Figure 3-3. Average female time spent during incubation recesses, throughout eight hours of observation among treatments on different behaviors.
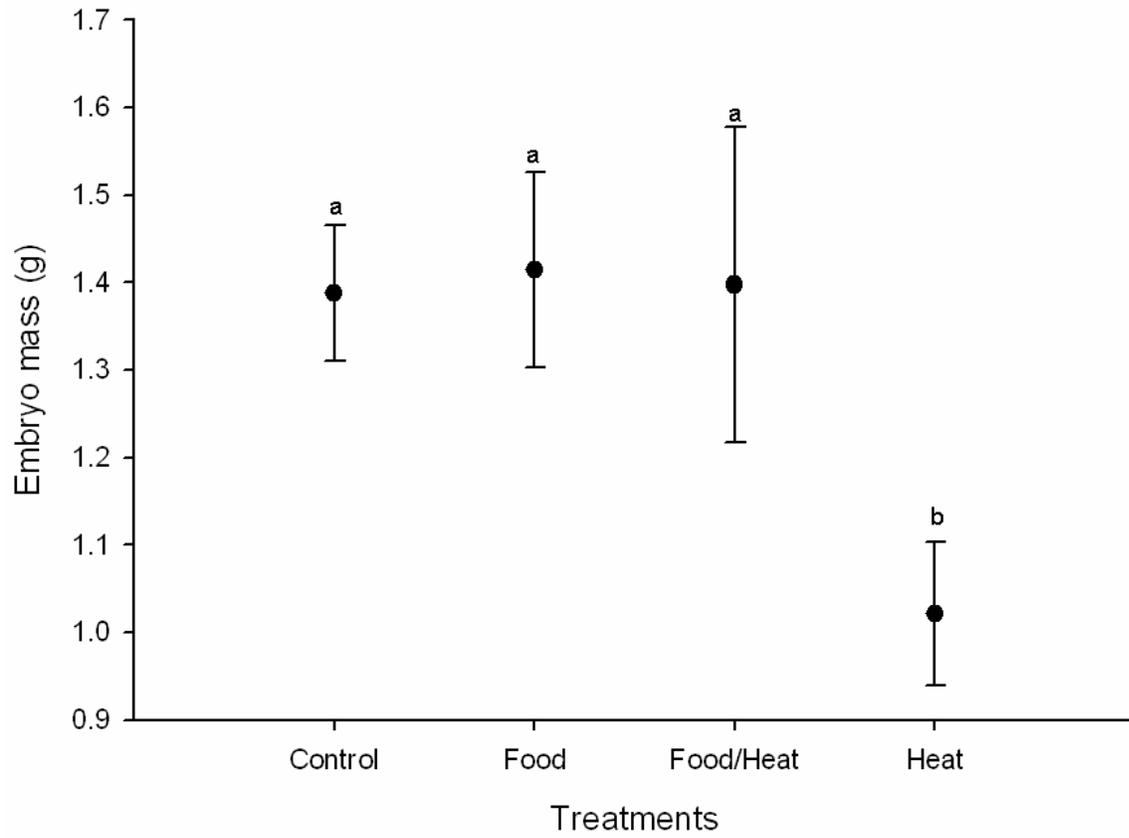
Figure 3-4. Embryo mass among treatments after ten days of continuous incubation.

CHAPTER 4
DISCUSSION

Results showed that both food availability and temperature influence the pattern of incubation. Increasing food availability enabled females to spend more time on the nest, and more time in self-maintenance activities when off the nest. Increasing heat caused females to spend less time on the nest and to make more trips to and from the nest. When both food and temperature were increased, their effects on incubation time offset each other. Thus our results provide support for our predictions. Changes in incubation patterns had little effect on fitness. Embryonic mass was reduced in the heat+ treatment, but this may simply reflect heat stress, which incubating females sometimes had to offset by panting. None of the other measurement of fitness (ectoparasite loads, adult mass, nest predation) differed among treatments

Perhaps the reason why temperature only explained 17-47% of the variation in incubation patterns (Conway and Martin, 2000a) is that the two factors, food and temperature, offset each other in complex ways that could obscure their effects on incubation behavior. In the remainder of this section, we first look at how each factor affects incubation separately, and then explore ways in which the two factors interact.

Incubation Time

Effects of supplement food: As predicted, supplemental food increased time on the nest (Eikenaar et al., 2003; Zimmerling and Ankney, 2005; Rastogi et al, 2006; Chalfoun and Martin, 2007). Females increased their time on the nest by reducing the average duration of trips off the nest, rather than by reducing the number of trips. Shorter trips not only assure longer times of appropriate thermal condition for adequate embryo development, they also reduce the cost of re-warming eggs, which do not cool down as much during short off bouts (Vleck, 1981a; Vleck,

1981b; Tinbergen and Williams, 2002). Shorter trips off the nest were likely made possible by faster acquisition of energy in food+ territories (see below).

Effects of supplement heat: As predicted by Conway and Martin (2000a), females with supplemental heat increased the number of trips without increasing the length of these trips. The result was a reduction in nest attentiveness. Temperatures outside the thermal neutral zone (region of physical regulation), such as those experienced by our heat+ females on the nest, can increase adult metabolic rate (McNab, 2002), which would in turn require an increase in food intake (McWilliams et al.,1999; Dykstra and Karasov, 1992). Moreover, adult thermoregulation during incubation can be costly and can account for 31% of daily energy expenditure (Piersma and Morrison, 1994). Thus, foraging activity might be predicted to increase among birds that incubate in high ambient temperatures (Bergstrom, 1989; Conway and Martin, 2000a; Conway and Martin, 2000b). We did not, however, find that females increased their foraging time in supplemental heat treatments. The lack of increase in food intake at high temperatures suggests that behavioral responses maybe more important in regulating body temperatures at high temperatures, above the thermal neutral zone (Ricklefs, 1987). Alternatively, we may not have increased temperatures enough to cause significant energetic stress in the adults.

Interactions food and temperature: As we predicted, females on control and food+/heat+ territories spent an intermediate amount of time on the nest, not significantly different than either heat+ or food+ females. These results suggest that increases in food availability compensate for the high energy expenditure of cooling eggs in hot conditions, by allowing females to reduce the number of trips off the nest and thereby better regulating egg temperature. This difference in incubation patterns may explain why embryo mass was significantly reduced in heat+ treatments,

but not in food+/heat+ treatments. We do not yet know how the extra food may enable females to provide better conditions for embryonic development.

Our results may shed light on why neither food nor temperature explained much of the variance in incubation patterns in Conway and Martin's (2000b) interspecific analysis. Birds living in food-rich environments may be able to compensate for temperature-induced stresses (McWilliams, et al., 1999; Dykstra and Karasov, 1992). Conversely, birds living in colder climates may benefit more from increasing temperatures than did our mockingbirds, which breed mainly in warmer, south temperature climates. Thus, the interactions of food and temperature can offset each other and likely vary greatly among environments that differ in ambient temperature and food availability.

Behaviors during Recess from Incubation

The time freed from foraging by food+ females was allocated to maintenance behaviors. Maintenance behaviors have been shown to influence nest survival and fitness (Cucco and Malacarne, 1997; Nagy and Holmes, 2005; Rastogi et al., 2006), but we found no evidence for reduced nest predation or adult condition. The lack of difference in body mass suggests that females with supplemental food did not store extra energy; rather they invested it in the current nesting attempt. Although our urban mockingbird population had few ectoparasites, reduction and removal of parasites by preening could result in higher fitness (Casida et al., 1995).

Time allocated to other behaviors (e.g., territoral defense, intra-specific interactions) was not consistent among treatments. Consequently, these behaviors were not influenced by either food+ or heat+. One possible explanation for this can be the lack of direct effects of these behaviors on current reproduction and adult survival. Cucco and Malacarne (1997) showed that individuals in territories with extra, supplemented food increased the time allocated to nest

defense. However, female Mockingbirds with high food availability did not increase territorial defense, probably because in this species, males do most territorial defense, but do not incubate.

Nest predation Despite significant differences in trips per hour among the four treatment groups, we found no differences in the number of nests lost to predators or in the average survival time of eggs in nests. This result contradicts those of several previous studies that found a positive association between trip number and nest predation (Martin et al., 2000; Muchai and Plessis, 2005; Rastrogi et al., 2006). However, this association is clearly not universal; our results agree with those of Hans-Christian (2005). Possibly, a 20% increase in trips per hour may not be enough to significantly affect nest predation rates. Alternatively, differences in nest predation observed among studies may be driven by factors correlated with visit frequency but not directly examined in any of the studies. In mockingbirds, nest predation rates may be constrained by the behavior of males, which actively defend nests against predators (Derrickson and Breitwisch, 1992).

Conclusions: For birds, incubation may be costly because eggs develop externally and often in environments with large fluctuations in temperature. To keep temperatures in the optimal range for development, birds can vary the frequency and duration of incubating sessions and modify their behavior while incubating and while off the nest. But, this involves life-history tradeoffs. Increasing the duration and frequency of incubation sessions requires less time spent on other fitness-enhancing activities such as foraging and self-maintenance. Consequently, temperature and food have long been hypothesized to be the primary constraints on the ability of birds to provide optimal conditions for incubating eggs. Several recent papers (reviewed in Conway and Martin, 2000a) have argued that temperature is a more important determinant of incubation behavior than food availability. Our results, however, point to the importance of both

24

food and ambient temperature. Increasing food availability enabled birds to spend more time keeping eggs at optimal temperatures and more time in self-maintenance activities, which may substantially reduce the costs of incubating for the adults themselves. Increasing temperatures, on the other hand, mainly influenced the frequency of visits to the nest except at very high temperatures when the birds were apparently forced to spend energy cooling their eggs to avoid potentially lethal effects. Thus, our experiment shows that food and temperature both affect avian incubation behavior, but that different tradeoffs apply to each environmental factor.

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BIOGRAPHICAL SKETCH

Gustavo Adolfo Londoño was born in 1976 in Cali, Colombia. The older of two children, he grew up mostly in Cali, Colombia, graduating from Gimnasio la Colina High School in 1993. After his high school graduation, he spent 1 year in Morton, Illinois, as an exchange student. In fall 1994 he enrolled the Universidad de los Andes, Bogota, Colombia, where he started his biology bachelor's degree. During his undergrad career Gustavo was involved in many field research programs that principally involved birds. After finishing his B.S. in biology in 2000, Gustavo was involved in bird field projects in different countries, Canada, Costa Rica, Perú and Colombia. In 2003 he participates in the Organization for Tropical Ecology field course in ecology and conservation in Costa Rica. Gustavo work with Wildlife Conservation Society Colombia program from 2002-2004, gathering data to develop conservation strategies for some endanger Andean birds in Colombia that affect incubation behavior of the Northern Mockingbird.

Upon completion of his master's program, Gustavo will begin working toward his Ph.D. At the Zoology Department, University of Florida under the advice of Douglas Levey and Scott Robinson where he will study factors that affect incubation behavior of high elevation tropical birds.