



## Effects of temperature and food on incubation behaviour of the northern mockingbird, *Mimus polyglottos*

GUSTAVO A. LONDOÑO\*†, DOUGLAS J. LEVEY\* & SCOTT K. ROBINSON†

\*Department of Zoology, University of Florida

†Florida Museum of Natural History, University of Florida

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Avian incubation behaviour is thought to be influenced mainly by ambient temperature and food availability. Field studies, however, have generated contradictory results; there is little agreement about the relative importance of food and temperature and how different components of incubation behaviour are affected by them. To date, no studies have manipulated both food availability and nest temperature in a controlled experiment, making it impossible to assess any potential interaction between food and temperature. We experimentally increased both food availability and ambient temperature during incubation in the northern mockingbird. Our results show that both food availability and temperature influence incubation behaviour. Increasing food availability enabled females to spend more time on the nest and in self-maintenance activities when off the nest. Increasing nest temperature caused females to spend less time incubating 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 previous studies have yielded contradictory results is that food and temperature offset each other in complex ways that could obscure their individual effects. Indeed, our experiment shows that food and temperature both affect avian incubation behaviour, but that different trade-offs apply to each environmental factor.

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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 & Williams 2002) and that incubation behaviour influences the probability of predators finding the nest (Martin et al. 2000; Muchai & Plessis 2005; Duncan-Rastogi et al.

2006). Because time and energy invested in incubation translate to less time and energy for energy intake (foraging) and self-maintenance, incubating birds face a trade-off between parental care and self-care (Williams 1996; Tinbergen & 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; Haftorn 1978; Grant 1982; Martin 1987; Weathers & Sullivan 1989; Conway & Martin 2000a, b; Deeming 2002b; Eikenaar et al. 2003; Lloyd & Martin 2004; Martin 2004; Nagy & Holmes 2005; Zimmerling & Ankney 2005). Ambient temperature influences energy expenditure during incubation and embryonic growth during recesses from incubation (Baernands 1959; Weeden 1966; Drent 1970; Vleck 1981a; Zebra & Morton

Correspondence: D. Levey, Department of Zoology, 223 Bartram Hall, University of Florida, P.O. Box 118525, Gainesville, FL 32611, U.S.A. (email: [dlevey@zoo.ufl.edu](mailto:dlevey@zoo.ufl.edu)). S. Robinson is at the Florida Museum of Natural History, Dickinson Hall, University of Florida, Gainesville, FL 32611, U.S.A.

1983; Haftorn & Reinertsen 1985; Reid et al. 1999; Conway & Martin 2000a; Tinbergen & 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 & Sullivan 1989; Nilsson 1994; Sanz 1996; Cucco & Malacarne 1997; Eike-naar et al. 2003; Zimmerling & Ankney 2005; Duncan-Rastogi et al. 2006; Chalfoun & Martin 2007). Conway & Martin (2000a) concluded that incubation rhythm depends more on ambient temperature than on food. None the less, the effects of temperature were nonlinear and explained only a small proportion of total variation in incubation rhythm. The same authors proposed that food does not explain variation in incubation rhythm, at least among species (Conway & Martin 2000b). Within species, however, food can affect incubation rhythm (Conway & Martin 2000a; Zimmerling & Ankney 2005; Duncan-Rastogi et al. 2006). Therefore, there are contradictory results and no general agreement about how food and temperature influence avian incubation behaviour.

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 & Martin 2000a; Wiebe & Martin 2000; Martin 2004). We are not aware of any studies designed in such a way. Also, most studies on incubation focus on quantifying when birds are on or off the nest and generally do not attempt to describe behaviours when off the nest. Because behaviours that occur during incubation recess are likely to influence behaviours on the nest, both should be considered part of incubation behaviour—both can have a strong influence on nest survival and adult fitness (Franks 1967; Vleck 1981a; Davis et al. 1984; Cucco & Malacarne 1997; Nagy & Holmes 2005; Zimmerling & Ankney 2005).

Our primary objective was to evaluate experimentally the interaction and relative importance of food availability and temperature on incubation behaviour. We hypothesized that both food and temperature affect incubation behaviour and tested three predictions: (1) Females on territories with high food availability will spend more time on the nest and when off the nest will spend more time doing other potentially fitness-enhancing behaviours such as preening or defending the nest, because hunger levels and foraging times will be reduced. (2) Females on nests in hotter microclimates will decrease time on nest and increase the total number of trips to the nest per day, as predicted by Conway & Martin (2000a). Furthermore, females in hotter microclimates, when on the nest, should spend more time regulating nest temperature through behavioural responses such as panting (Franks 1967; Vleck 1981a; Davis et al. 1984). (3) Females that experience both hot microclimates and high food availability should spend an intermediate amount of time on the nest. The reasoning behind this 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 & Ankney 2005; Duncan-Rastogi et al. 2006) and heat increasing on- and off-bouts, which decrease time on the nest (Conway & Martin 2000a).

We tested these predictions by experimentally manipulating food availability and nest microclimate of northern mockingbirds, a species in which only females incubate and males do not provide food to incubating females (Derrickson & Breitwisch 1992; G. Londono, personal observation). In addition to testing the predictions, we looked for possible mechanisms underlying any responses by measuring several metrics of body condition and reproductive success: female body mass, ectoparasite load, embryonic development, and nest predation.

## METHODS

We conducted this study between 1 April and 15 July in 2005 and 2006 on the University of Florida campus in Gainesville, Florida, U.S.A. (N29°38'267"; W082°21'984"). The campus has ideal mockingbird habitat: large expanses of mowed grass for foraging and scattered shrubs for nesting.

### Nest Searching and Experimental Protocol

We divided the study area in six sections. Once per week, we searched all shrubs and trees within each section for nests. We randomly assigned each new nest, either under construction or with an incomplete clutch (one or two eggs), to one of four experimental treatments in a 2 × 2 factorial design: food increase (food+), heat increase (heat+), food and heat increase (food+/heat+) and neither food nor heat increase (control). We placed a feeder within 2 to 5 m of food+ nests. 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 17 g) in each feeder every day. Feeders were used exclusively by the pair of mockingbirds at the nearest nest, except in a few cases in which juveniles from a pair's previous clutch also used the feeder. In those cases, we placed an extra 8 g/day of mealworms in the feeder. Because high temperatures can kill mealworms in the feeders and because mockingbirds usually do not eat dead mealworms, we placed half of the mealworms in the feeders before sunrise and the remaining half 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-W bulb in a 47 × 32 mm (length × diameter) cylindrical aluminium tube on the day the third egg was laid, when the likelihood of nest abandonment was low. We placed the bulb and cylinder directly under the nest, touching nest material, approximately 30 mm from the eggs. After the clutch was complete and incubation had started, we turned the bulb on shortly before sunrise (0600 hours) and it remained on until the battery was drained, approximately 8 h 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. Ambient temperature ranged from 17.0 to 37.1 °C (average  $\pm$  SD = 26.6  $\pm$  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  $\times$  7 mm), one internal and one external, connected to an H8 4-channel Hobo data logger (Onset Computer Corporation). We placed the sensors in the nests the day the third egg was laid and recorded the temperature every minute. The internal sensor was attached to the nest wall just above the eggs, with a metal wire to avoid sensor movements during incubation. It provided two types of information: nest microclimate and the time at which the incubating bird left or returned to the nest, as 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 and with the same metal wire as the internal sensor. It was shielded from the heater and provided data on ambient temperature in the immediate vicinity of the nest.

All treatments lasted 10 days, when we collected all eggs for examination of embryo development (see below). We colour-banded all nesting females and used each only once in the experiment (i.e. for a single treatment). Across the 2 years of study, the numbers of nests in each treatment group were similar. Due to predation events and data logger malfunction, the numbers of nests per treatment varied among treatments:  $N = 12$  control,  $N = 11$  for food+,  $N = 18$  for heat+ and  $N = 10$  for food+/heat+.

## Behaviour

Between days 4 and 9 of treatments, we observed each female for a total of 8 h, distributed in 2-h blocks between sunrise and 1400 hours over 4 days. During these 2-h blocks, we continuously recorded the time spent by the female in the following behaviours: incubating, foraging, preening, panting on the nest (cooling the eggs), being still (no obvious behaviour) and 'other' (singing, territorial defence, flying etc.). If a female conducted one of these behaviours for more than 30 s, we recorded the time spent on the behaviour; otherwise we did not. Most behaviours 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 the female 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 behaviour during the day. We conducted behavioural observations on 65 nests ( $N = 16$  for control,  $N = 16$  for food+,  $N = 19$  for heat+,  $N = 14$  for food+/heat+).

## Other Measurements

### *Female body mass*

On day 10 of the incubation period, we captured as many females as possible (control 12; food+ 9; heat+ 16; food+/heat+ 8) and weighed them to the nearest gram.

### *Nest predation*

For each treatment, we recorded the day on which any nest was lost to predation before the completion of the experiment (10 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 ( $N = 21$  for control,  $N = 17$  for food+,  $N = 24$  for heat+,  $N = 18$  for food+/heat+).

### *Embryo development*

On day 10 after sunset, we collected the eggs from all nests to measure treatment effects on embryonic development. We measured egg mass to the nearest 0.05 g and egg length and width to the nearest 0.1 mm. We opened each egg, removed all membranes, weighed the embryo to the nearest 0.05 g (wet mass), and recorded the length and width to the nearest 0.1 mm. We also recorded the number of undeveloped 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, 27 embryos from 12 heat+ nests and 19 embryos from 7 food+/heat+ nests.

### *Ectoparasites*

In 2006, we collected ectoparasites by the "dust-ruffling" technique (Jackson 1985; Walther & Clayton 1997). We lightly dusted females with pyrethrin powder, except for the head. We worked the pyrethrum into the feathers with fingers, waited 5 min, and ruffled the feathers over a tray lined with coloured paper, against which the ectoparasites were easily visible. We placed ectoparasites in microcentrifuge tubes with 99% ethanol. Because the dust-ruffling technique works best for lice (Walther & Clayton 1997), we quantified only the number of feather lice, which we counted under a stereomicroscope. We sampled a total of 28 females: 5 from control nests, 6 from food+ nests, 11 from heat+ nests, 6 from food+/heat+ nests.

## Data Analysis

We obtained the temporal pattern of incubation for each nest from temperature fluctuations detected by each nest's internal sensor and analysed it following the protocol suggested by Cooper & Miles (2005). In brief, we converted temperature readings from the data loggers into a text file, which we then transformed into a sound file, using Rhythm software (Cooper & Miles 2005). An algorithm detected all intervals in which temperatures decreased monotonically. It 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, the start 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. The start 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.

We analysed data on incubation behaviour with a repeated-measures ANOVA (mixed-model procedure of SAS, version 9.1; SAS Institute 2003), with food, heat, year and all two-way interactions included in the model. Response variables, each analysed separately, were total minutes of incubation time during daylight for each of the 10 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. Total time on the nest, trip duration and number of trips were dependent variables, food and heat were fixed factors and nest was a random factor. We report adjusted means (least-squares means) and standard errors, except where indicated.

We analysed differences in female and embryo mass with a two-way ANOVA, with mass as a dependent variable, food and heat as fixed factors and nest as a random factor. We compared the numbers of nests lost to predation in each treatment with a chi-square test. We estimated daily predation rates among treatments using Shaffer's logistic regression model (SAS Institute 2003; Shaffer 2004). For post hoc tests we used the Tukey–Kramer honestly significant difference, which is relatively unlikely to result in a type 1 error (Hilton & Armstrong 2006).

## RESULTS

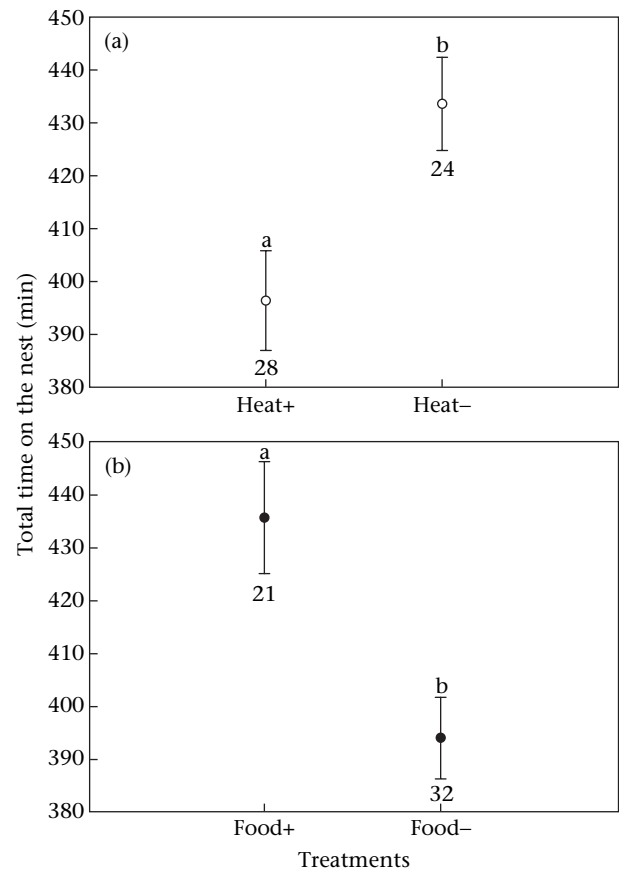
Internal nest temperatures were always hotter than external (ambient) temperatures, with differences fluctuating between 3 and 7 °C depending on the treatment. By day, when heaters were turned on, nest temperatures differed significantly among treatments ( $F_{3,407} = 27.37$ ,  $P < 0.001$ ). Nests in both heat treatments (heat+ and food+/heat+) had significantly higher temperatures, by 2–3 °C, than nonheated treatments (food+ and control; Tukey:  $P < 0.001$ ). Nest temperatures did not differ significantly between the two heat treatments (Tukey:  $P = 0.97$ ) but did differ between food+ and control treatments (Tukey:  $P < 0.007$ ), with higher nest temperatures (0.9 °C) in the food+ treatments.

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 a mockingbird pair with about 5.83 kJ/h of additional energy. Female mockingbirds consumed  $7.5 \pm 0.68$  ( $\bar{X} \pm \text{SE}$ ) mealworms per hour. We calculated basal metabolic rate (BMR) for a 48-g insectivorous bird to be 1.83 kJ/h (McNab 2005). Thus, assuming that energetic requirements during incubation are three-fold higher than the BMR (Williams 1993; Piersma & Morrison 1994), we estimated that female mockingbirds spent 5.49 kJ/h during the incubation period. Accordingly, we estimate that mealworms provided approximately 53% of the daily energy expended by the female during incubation.

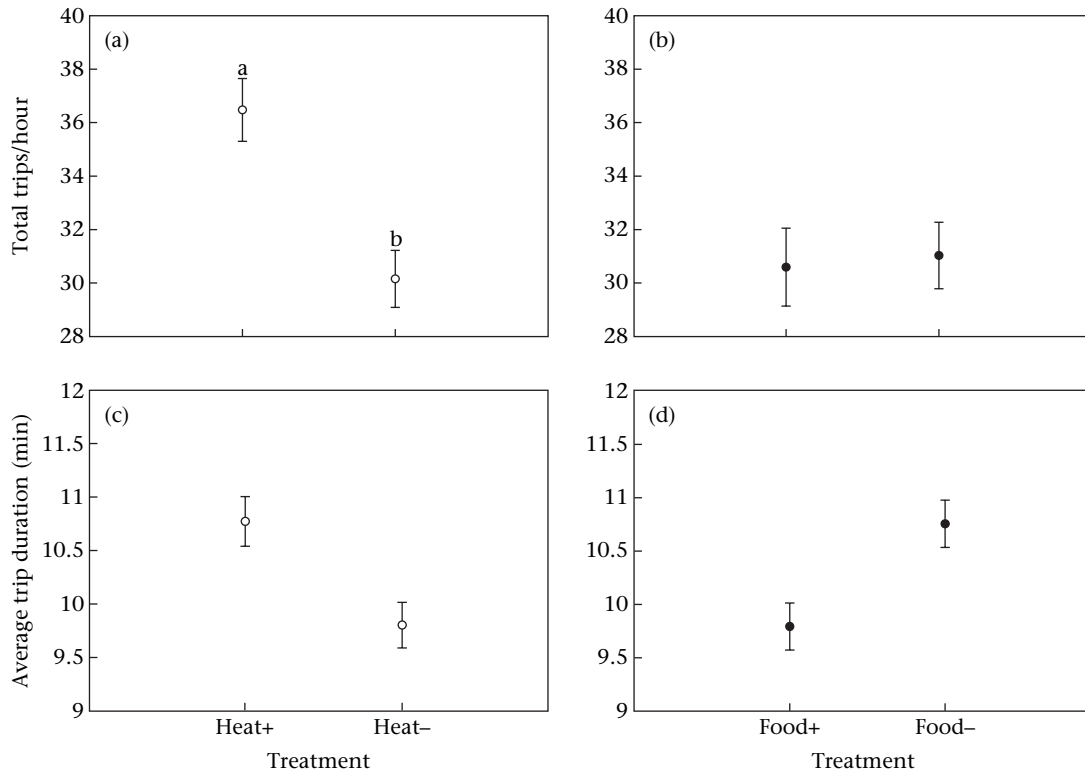
## Incubation Time

Females in the four treatments spent from 52.2% (heat+) to 64.4% (food+) of daylight hours incubating.

There was no year effect on total daily incubation time ( $F_{1,45} = 0.03$ ,  $P = 0.86$ ) and all interaction terms were non-significant. Food+ and heat+ treatments affected total incubation time ( $F_{1,45} = 4.55$ ,  $P = 0.03$ ;  $F_{1,45} = 4.36$ ,  $P = 0.04$ , food+ and heat+, respectively); controlling for heat, supplemental food increased total incubation time approximately 11%. Controlling for food, increased temperature decreased total incubation time by approximately 9% (Fig. 1a, b). The average number of trips off the nest each hour was significantly affected by heat+ ( $F_{1,45} = 5.50$ ,  $P = 0.02$ ), with females on heat+ nests averaging 22% more trips per hour than females on nests without heat (Fig. 2a). Supplemental food did not affect the number of trips (Fig. 2b) nor the length of trips (Fig. 2d). Length of trip was also not affected by temperature (Fig. 2c). 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,



**Figure 1.** Least-squares means of summed incubation times for each treatment over the 10 days of each trial. (a) Females on heat+ territories received heaters under their nests (heat+/food- and heat+/food+); those on heat- territories did not receive heaters under their nest (heat-/food+ and heat-/food-). (b) Females on food+ territories received supplemental food (food+/heat- and food+/heat+); those on food- territories did not receive supplemental food (food-/heat+ and food-/heat-). Bars represent standard errors, numbers below bars show sample sizes, and matching letters above bars indicate nonsignificant differences ( $P > 0.05$ ) between treatments.



**Figure 2.** (a, b) Mean number of trips and (c, d) mean trip length during the first 10 days of the incubation period for each treatment. Notation as in Fig. 1.

compared to 3% for females on both food+ and control nests (not illustrated).

### Behaviours during Recess from Incubation

Female behaviour off the nest differed among treatments (Fig. 3). Foraging time of females while off the nest was greatly reduced in food+ and food+/heat+ treatments ( $F_{1,64} = 148.23$ ,  $P < 0.0001$ ), whereas foraging time did not differ between heat+ and control treatments ( $F_{1,64} = 0.24$ ,  $P = 0.20$ ). Time spent preening was greatly increased by additional food ( $F_{1,64} = 60.12$ ,  $P < 0.0001$ ) but not by additional heat ( $F_{1,64} = 0.002$ ,  $P = 0.967$ ). Time spent being still was not affected by food+ ( $F_{1,64} = 1.45$ ,  $P = 0.23$ ) or 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 Fitness Measurements

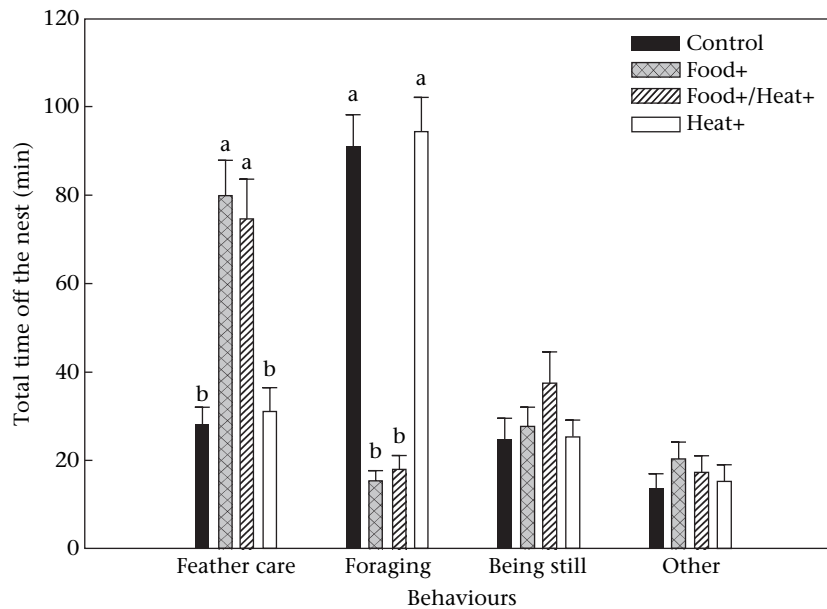
Body mass on the last day of trials (day 10) was not affected either by food+ ( $F_{1,46} = 0.68$ ,  $P = 0.42$ ) or by heat+ ( $F_{1,46} = 0.97$ ,  $P = 0.33$ ). The total number of nests lost to predators did not differ among treatments ( $\chi^2_3 = 0.43$ ,  $P = 0.94$ ). Daily nest survival rates ranged from 97.8 to 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% less than any other treatment. Embryo mass was similar among control, food+ and food+/heat+ treatments. There was no difference in the number of undeveloped embryos among treatments ( $\chi^2_3 = 5.15$ ,  $P = 0.16$ ).

### DISCUSSION

Our results show that both food availability and temperature influenced the pattern of avian 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 all three predictions. Changes in incubation patterns, however, had no immediate effect on fitness. Embryonic mass was reduced in the heat+ treatment, but this may simply reflect heat stress, which incubating females presumably reduced by panting. None of the other fitness-related metrics (ectoparasite loads, adult mass, nest predation) differed among treatments.

Perhaps the reason temperature explained only 17–47% of variation in incubation patterns in a previous study (Conway & Martin 2000a) is that the two factors food and temperature offset each other, obscuring their individual effects on incubation behaviour. In the remainder of this



**Figure 3.** Average amount of time females spent engaged in feather care, foraging, being still, and all other activities while off the nest over a total of 8 h. Females on food+ territories received supplemental food, those on heat+ territories received heaters under their nests, those on food+/heat+ territories received both supplemental food and heaters, and those on control territories received sham treatments. Bars represent standard errors and matching letters above bars indicate nonsignificant differences ( $P > 0.05$ ; Tukey's post hoc) between treatments.

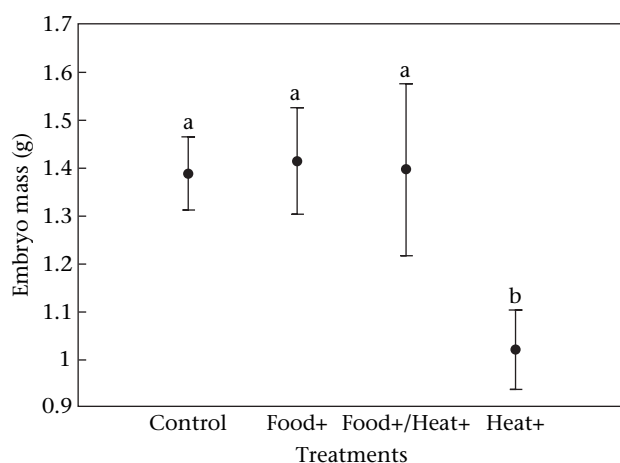
section, we first look at how each factor affects incubation separately and then discuss possible repercussions of their joint effect.

## Incubation Time

### Effects of supplemental food

As predicted, supplemental food increased time on the nest (Eikenaar et al. 2003; Zimmerling & Ankney 2005; Duncan-Rastogi et al. 2006; Chalfoun & Martin 2007). Females increased their time on the nest more by reducing the average duration of trips off the nest than by reducing the number of trips. Shorter trips not only ensure longer times of appropriate thermal condition for embryonic

development, they also reduce the cost of rewarming eggs, which do not cool down as much during short bouts off the nest as during long bouts (Vleck 1981a, b; Tinbergen & Williams 2002). Shorter trips off the nest were likely made possible by faster acquisition of energy in food+ territories (see below).



**Figure 4.** Embryo mass among treatments after 10 days of continuous incubation. Notation as in Fig. 3.

### Effects of increased temperature

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

The average nest temperatures during our experiment did not fall outside the normal temperature range faced by mockingbirds during the breeding season in northern

Florida, which suggests that overheating or excessive cooling during longer than average nest recesses was not a major problem. During the hottest time of the breeding season (late in the summer), ambient temperatures can reach 35 °C. Measurements taken during the 2007 breeding season showed that egg temperatures during incubation were on average 2 °C higher than ambient temperatures (G. Londoño, unpublished data), suggesting that it is unlikely that egg temperatures in the heat treatments would have been above 37 °C, which is below the lethal temperature for bird eggs (Grant 1982). Conversely, we know from 2007 data that egg temperatures never dropped below 30 °C (G. Londoño, unpublished data), which suggests that excessive cooling did not occur (Haforn 1978; Conway & Martin 2000a).

#### *Interactions of food and temperature*

As we predicted, females on food+/heat+ territories spent an intermediate amount of time on the nest, not significantly different from either heat+ or food+ females. This result suggests that increased food availability compensated for the high energy expenditure of cooling eggs under hot conditions, by allowing females to reduce the number of trips off the nest and thereby better regulate egg temperature. These differences in incubation patterns may explain why embryo mass was significantly reduced in heat+ treatments, but not in food+/heat+ treatments.

Our results may shed light on why neither food nor temperature explained much of the variance in incubation patterns in Conway & Martin's (2000b) interspecific analysis. Birds living in food-rich environments may be able to compensate for temperature-induced stresses (Dykstra & Karasov 1992; McWilliams et al. 1999). Conversely, birds living in colder climates may benefit more from increasing temperatures than did our mockingbirds, which breed mainly in a warm, subtropical climate. Thus, the effects of increased food and temperature on incubation behaviour can offset one another. By the same token, they can generate much variation in incubation behaviour in environments in which they vary and covary in different ways.

#### **Behaviours during Recess from Incubation**

The time freed from foraging by food+ females was allocated to maintenance behaviours. Maintenance behaviours have been shown to influence nest survival and fitness (Cucco & Malacarne 1997; Nagy & Holmes 2005; Duncan-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 behaviours (e.g. territorial defence) was not influenced by either food+ or heat+. One possible explanation is the lack of direct effects of these behaviours on current reproduction and adult survival. Cucco & Malacarne (1997) showed that individuals in

territories with supplemented food increased the time allocated to nest defence. However, female mockingbirds with high food availability did not increase territorial defence, probably because in this species, males defend territories and do not incubate.

#### **Nest Predation**

Despite significant differences in trips per hour among treatment groups, we found no difference in the numbers of nests lost to predators or in the average survival time of eggs in nests. This result contradicts those of several previous studies that report a positive association between the number of trips to a nest and nest predation (Martin et al. 2000; Muchai & Plessis 2005; Duncan-Rastogi et al. 2006). However, this association is clearly not universal; our results agree with those of Hans-Christian et al. (2005). 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, for example, nest predation rates may be most strongly predicted by the behaviour of males, who actively defend nests against predators (Derickson & 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 incubation sessions and modify their behaviour while incubating and while off the nest. Such changes in behaviour often entail trade-offs. 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 studies have argued that temperature is a more important determinant of incubation behaviour than is food availability (reviewed in Conway & Martin 2000a). Our results show the importance of both food and ambient temperature. Increasing food availability enabled birds to spend more time keeping eggs at presumably optimal temperatures and more time in self-maintenance activities, which may substantially reduce the costs of incubation. 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 behaviour, but that different trade-offs apply to each of these environmental factors.

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