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The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine

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Abstract Organisms are expected to balance energy allocation in such a way that fitness is maximized. While much research has focussed on allocation strategies of reproducing parents, in particular birds, relatively little attention has been paid to how nestlings allocate energy while in the nest. Nestling birds are faced with a trade-off between devoting energy to growth or to thermoregulation, and in altricial species it is likely that the thermal environment of the nest site influences the nature of this trade-off. Here, we experimentally investigate how altering the microclimate of nests affects the growth, size and survival, as well as cell-mediated immune (CMI) response, of nestling tree swallows (*Tachycineta bicolor*) in a temperate environment. We place air-activated heating pads in nests of swallows when young were between 4 days and 16 days of age, and compared performance of offspring to control nests. Our manipulation raised temperatures of heated nests by approximately 5°C compared to control nests. Offspring in heated nests had enhanced survival while in the nest, and we also found that they were heavier and had longer ninth primary feathers at 16 days of age. In addition, heating nest boxes resulted in significantly faster growth of primaries, and there was a trend for growth rates of mass to also be higher in heated nests. There were no significant differences between heated and control nests in growth rate or size of tarsus at age 16 days, and we speculate that this lack of response to elevated nest temperatures may be due to growth of skeletal structures being limited by other factors such as calcium availability. We also found no difference between heated and

control nests in CMI response. Nonetheless, our results show overall that increasing temperatures of nests has significant benefits that enhance the fitness of offspring. As provisioning rates to offspring did not differ between heated and control nests, we suspect that the beneficial effects of heating were not the consequence of changes in parental behaviour. Our results provide insight into factors, other than food supply, that have important consequences in determining reproductive success of birds breeding in temperate environments.

Keywords Reproductive success · *Tachycineta bicolor* · Temperature · Trade-offs · Tree swallows

Introduction

Life-history theory suggests that organisms maximize fitness by resolving a series of trade-offs (Stearns 1992). These trade-offs arise because resources such as time and energy are limited, and an individual cannot allocate resources to one life-history trait without decreasing allocation to other traits that are competing for the same resource (Williams 1966; Stearns 1989). Much research on the evolution of life-history strategies has focussed on the cost of reproduction, where investing in current reproduction is thought to reduce future survival and fecundity (reviews in Lindén and Møller 1989; Dijkstra et al. 1990; Golet et al. 1998). Less attention has been given to trade-offs occurring at stages of an organism's life cycle other than when they are reproducing, despite the fact that the amount of resources that an individual is able to acquire, and how they are allocated, can vary not only among individuals, but also throughout an individual's lifetime (Stearns 1992).

For altricial birds, one of the most energetically costly periods in their life cycle occurs when young are in the nest. While the nestling period is costly for parents because they need to provision offspring (Drent and Daan 1980), the young also face energy limitations

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because of their rapid growth and development (Ricklefs 1983). In particular, after young begin to thermoregulate on their own and are no longer brooded by parents, they need to allocate their available resources to both tissue growth and maintenance activities such as sustaining elevated body temperature (Schew and Ricklefs 1998). Undoubtedly, the thermal environment of the nest is crucial in determining the allocation strategy of offspring. For example, cooler nest microclimates may require offspring to invest more energy in thermoregulation, at the expense of other processes such as growth or mounting an immune response. Alternatively, warm nest environments may reduce costs of maintaining homeothermy and so promote more rapid growth (see Visser 1998). Here, we experimentally investigate how variation in microclimates of nest sites influences the growth and survival, as well as cell-mediated immune (CMI) response, of nestling tree swallows (*Tachycineta bicolor*) in a temperate environment. By artificially heating nest boxes throughout the brood-rearing period, we provide insight into the trade-off between thermoregulation, and nestling development and survival.

Materials and methods

We studied tree swallows breeding in artificial nest boxes from May to August 2003 in the vicinity of Prince George BC, Canada (53°N, 123°W), in two different areas. The two areas ("Steward" and "Hydro" sites) were approximately 35 km apart and both consisted of open agricultural areas mixed with small patches of coniferous and deciduous trees, and small wetlands. The study was originally intended to be conducted on the Steward site; however, additional nests from the Hydro area had to be added to the sample after a large number of nests on the Steward site were depredated soon after hatching. Tree swallows arrived on both sites in early to mid-May and began laying eggs in late-May and early June. Swallows bred in nest boxes mounted on fence posts at the Steward site, whereas at the Hydro site nest boxes were mounted 3 m above the ground on electrical poles. Nest boxes at the Steward site were placed approximately 30 m apart, whereas at the Hydro site they were about 800 m apart. As a result, the breeding population at the Hydro site was much more dispersed than at the Steward site (average distance to nearest occupied box: Hydro site = $1,244 \pm 187$ m (SE); Steward site = 68 ± 13 m (SE); $F_{1,37} = 37.03$, $P < 0.0001$). In addition, the nest boxes at the two sites differed in size, with those at the Hydro site having a floor area of approximately 475 cm² while those at the Steward site were approximately 230 cm².

We visited nests every 1–3 days beginning in mid-May and subsequently documented the date that the first egg was laid, clutch size, and date of hatching. Once all eggs in a nest had hatched, we captured adult swallows using a swing-door trap. Each adult was banded

with a standard aluminum leg band and weighed with a spring balance (nearest 0.25 g). Nests at each site were paired according to hatching date and brood size, with one nest from each pair allocated randomly to the heat treatment while the other acted as a control. When young were 4 days of age, we placed a small heating pad underneath the nesting material in the bottom of treatment nest boxes. These pads contained a mixture of charcoal, iron powder, vermiculite, salt, sawdust and moisture, and when exposed to the air produced elevated temperatures for 2 days due to the oxidation of the iron powder. We replaced heat pads with new ones every second day at treatment nests, with the last heat pad installed when young were 14 days old. Therefore, heated nest boxes continually had elevated temperatures when young were between 4 days and 16 days of age. Control boxes were treated in a similar manner, except we installed pads in which all iron powder had already been oxidized, and so did not produce any heat. At most heated and control nests, we used data loggers to document the temperature of the nest directly above the heat pads, but below the nesting material. Temperature readings were recorded every 2 min during the period when nestlings were between 4 days and 16 days old, and these values were averaged for each nest to provide an indication of the temperature regimes experienced by nestlings.

Each nestling was measured every 2 days, and most were measured from ages 4 days to 16 days, although measurements were taken at several nests only between 6 days to 16 days of age. We determined mass using a spring balance (nearest 0.25 g), length of ninth primary flight feather with a ruler (nearest 0.5 mm), and length of tarsus with digital calipers (nearest 0.01 mm). Length of tarsus was measured four times per nestling during each visit, and we subsequently used the mean values in analyses. When nestlings were 12 days old, we assessed their T-cell mediated immune response (CMI) by injecting 30 µl of 1 mg/ml phytohaemagglutinin-P (Sigma) in phosphate buffered saline (PBS) intradermally in the right wing web. We measured the thickness of the wing web with a thickness gauge (nearest 0.01 mm) four times just prior to and 24 h (± 1.5 min SE) after injection, and the means were subsequently used in analyses. CMI was the difference in the thickness of the wing web before and 24 h after injection of the mitogen (Smits et al. 1999, 2001).

To investigate whether manipulating microclimate of nests had consequences for growth of offspring, we calculated growth curves for mass, ninth primary and tarsus. Preliminary analyses were aimed at finding the growth model that best described the patterns seen in the entire data sets for each variable. We first calculated the means by nest for mass and length of tarsus at each age from 4 days to 16 days; for length of ninth primary we calculated means per nest from ages 8 days to 16 days because ninth primaries of most birds do not begin to grow until after 6 days of age. For each data set, we used iterative least-squares non-linear curve fitting procedures

to fit logistic, Gompertz and Richard's models using the Levenberg-Marquardt estimation method; for ninth primary we also fit a linear model. To distinguish among models, we used Akaike's information criterion (AIC) corrected for small sample size (AICc):

$$\text{AICc} = \left(N \times \ln \left(\frac{\text{SS}}{N} \right) \right) + 2K + \left[\frac{2K(K+1)}{N-K-1} \right]$$

where N = number of data points, SS = sums of squares of the vertical distances of the data points from the curve, and K = the number of parameters estimated by the model + 1. This approach is a compromise between model fit and parsimony, and deems models with the lowest AICc to best describe the data (see Burnham and Anderson 2002).

For growth of mass and tarsus, AICc suggested that either Gompertz or logistic models fit the data sets equally well (differences between AICc values < 0.1 in both cases). To facilitate comparison of growth rates of mass from the present study to published values (e.g., McCarty 2001; see Discussion), we chose to use the logistic model, which has the form:

$$M(x) = \frac{a}{1 + be^{-cx}}$$

where $M(x)$ is the mass at age x , a is asymptotic mass, b is the inflection point, and c is the growth rate constant. To describe growth of the tarsus, we used the Gompertz model which takes the form:

$$T(x) = ae^{-e^{bc-x}}$$

where $T(x)$ is length of tarsus at age x , a is asymptotic length, b is the inflection point, and c is the growth rate constant. Growth of ninth primaries was best described by a linear equation. After deducing the appropriate models for each variable, we subsequently fit growth curves to each individual nestling, and then calculated the average growth rate constant for each variable on a per-nest basis. Nests for which we did not have complete growth data (i.e., ages 4–16 days for mass and tarsus; ages 8–16 for ninth primary) were excluded from these analyses.

If heating nests boxes had significant effects on growth and survival of offspring, such effects may be due to nestlings being able to devote less of their available energy to thermoregulation, or because parents altered their provisioning behaviour (see Discussion). While measuring metabolic rates of nestlings was beyond the scope of this study, we did investigate whether heating nest boxes changed parental provisioning behaviour. When offspring were 12 days old, we placed a digital recorder with a small microphone into a subsample of nest boxes and recorded begging of nestlings. Recordings were a minimum of 1 h (mean 1.32 ± 0.07 h (SE), $n = 18$ nests), which is sufficient to obtain estimates of provisioning rates that are not biased by the length of the sampling period (E.L. O'Brien, unpublished results). From each recording, we

quantified the number of bouts of begging, which accurately reflects the number of trips parents make to a nest box (E.L. O'Brien, unpublished results). McCarty (2002) has shown that the number of trips by parent tree swallows to the nest box is an accurate measure of the food delivery to nestlings.

Statistical analysis

We used analysis of variance (ANOVA) to test whether there were differences among treatments (heat vs. control) or areas (Steward vs. Hydro sites) prior to our manipulation. The variables examined in these analyses were clutch initiation date, clutch size, hatching date, number hatched, and mass of male and female parents. We also tested whether mean mass or tarsus length of nestlings, and brood size, differed among treatments and areas on the day our experiment commenced (nestling age 4 days).

To test whether our heat manipulation had the desired effect, we used ANOVA to examine whether the mean temperature of heated boxes differed from control boxes; this analysis also considered whether temperatures of nest boxes differed between areas (Steward vs. Hydro sites). Overall nest success was compared between heated and control nests using a Fisher's Exact test, where those nests fledging at least one young were considered successful while those fledging no young were unsuccessful. We also used a Fisher's Exact test to examine whether there were differences between heated and control nests in the proportion of nests that experienced brood reduction during the period of time from when our manipulation commenced (nestling age 4 days) until fledging. For each nest, we calculated the proportion of young that fledged (brood size at fledging/brood size at age 4 days) and compared these values between treatments and areas using analysis of covariance (ANCOVA). For the above analyses, we included only those nests that did not fail or lose young due to predators; therefore sample sizes differ among analyses. We used ANCOVA to test whether heating nests had consequences for average growth rates, size of offspring at 16 days, and CMI of offspring at 12 days. These analyses used mean values for each nest. In addition to testing for differences between heated and control nests in the above analyses, we also included area as a main effect, brood size and hatching date as potential covariates, plus all first-order interactions. A backwards stepwise procedure was then employed to remove terms and interactions that did not approach significance ($P > 0.10$). A similar ANCOVA was also used to test for differences in provisioning rates by parents between heated and control nests, and this analysis also included time of day that provisioning was quantified as an additional covariate.

Analysis were performed using SPSS (Norušis 2000) and SAS (SAS Institute 1990) software. Means \pm 1

standard error (SE) for control and heated nests are presented after controlling for any significant variables in models (see Results). We considered results significant at the 0.05 level.

Results

Our initial sample size in this study was 49 nests; however, a number of these nests were lost to a predator early in the brood-rearing period such that our final sample sizes consisted of 19 nests where temperature was manipulated (nine on the Steward site, ten on the Hydro site), while 20 nests acted as controls (ten on each site). One of these control nests was later lost to a predator just prior to fledging. There were no pre-existing biases in the sample because we could detect no differences between control and treatment nests in clutch initiation date, clutch size, hatching date, number hatched, and mass of male and female parents. Similarly, there were no differences between heated and control nests in mean mass and tarsus length of nestlings, or brood size at 4 days of age, when our manipulation commenced (all *P*s NS). However, birds breeding at the Hydro site had larger clutch sizes than those breeding at the Steward site (6.35 ± 0.27 vs. 5.43 ± 0.27 ; $F_{1,36} = 5.90$, $P = 0.02$), and as a consequence parents at the Hydro site hatched more eggs (6.20 ± 0.31 vs. 4.56 ± 0.32 ; $F_{1,35} = 13.59$, $P < 0.01$) and had larger brood sizes at age 4 days than did parents at the Steward site (6.15 ± 0.29 vs. 4.39 ± 0.30 ; $F_{1,35} = 18.03$, $P < 0.001$). In addition, we found that nestlings at age 4 days on the Hydro site were heavier ($F_{1,29} = 8.81$, $P < 0.01$) and had longer tarsi than birds on the Steward site ($F_{1,25} = 11.04$, $P < 0.01$).

The installation of heat pads significantly increased the temperature in nest boxes of the heated group (average temperature from day 4 to 16 of brood rearing = $31.8^\circ\text{C} \pm 0.6$, $n = 17$ nests) compared to control nests ($21.7^\circ\text{C} \pm 0.6$, $n = 18$ nests; $F_{1,33} = 140.09$, $P < 0.0001$; see Fig. 1); therefore, our manipulation had the desired effect. It is important to recognize that the probes measured temperature directly on top of the heating pads, and not in the nest bowl; some of the heat produced would have dissipated through the walls and floor of the boxes, so the temperature differences in the nest bowl were probably less than that reported above. In fact, under controlled laboratory conditions, the temperature in the nest bowl of heated nests was elevated by 5.1°C (± 0.18 , $n = 6$ boxes) over ambient temperature.

The manipulation of microclimate did not significantly influence overall nest success, with heated parents fledging at least one young in 17 of 19 nests while control parents fledged young in 14 of 19 nests (Fisher's Exact test, $P = 0.41$). However, parents with heated nests were significantly less likely than control parents to have brood reduction occur (5 of 19 heated nests had brood reduction compared with 14 of 19 control nests; Fisher's Exact test, $P = 0.005$). Because our sample sizes were

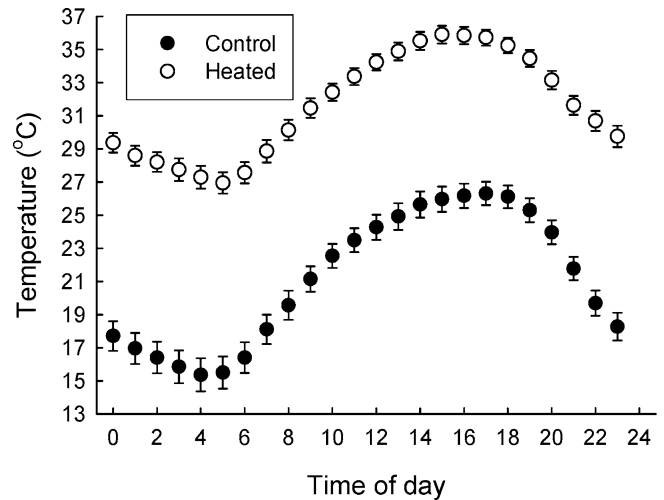


Fig. 1 Average temperature (\pm SE) according to time of day for control ($n = 18$) or artificially heated ($n = 17$) nests of tree swallows (*Tachycineta bicolor*). Average hourly temperature was first calculated separately for each nest when young were between 4 days and 16 days of age and then these values were subsequently used to calculate means for each treatment

relatively small, we did not analyze these data separately by area, but the patterns in the data were similar between areas. Heated nests also fledged a significantly higher proportion of their offspring ($F_{1,33} = 5.08$, $P = 0.03$; Fig. 2a), and average brood size at fledging was significantly larger in heated nests than control nests ($F_{1,33} = 4.91$, $P = 0.03$; Fig. 2b).

We included brood size, hatching date and area effects in analyses of growth rates, offspring size at 16 days of age, CMI response, and parental provisioning rates. Time of day was also included in analysis of provisioning rates. With several exceptions (see below), these terms and interactions did not contribute significantly to our models and so were eventually removed from analyses. There was a non-significant trend for growth rate constants for mass to be higher among heated nests ($F_{1,23} = 3.51$, $P = 0.07$), and nestlings on the Steward site also grew faster than did those on the Hydro site ($F_{1,23} = 15.20$, $P < 0.001$; Fig. 3a). Growth rates of ninth primaries were significantly higher in heated nests than control nests ($F_{1,30} = 5.57$, $P = 0.03$; Fig. 3b). We could detect no differences between treatment and control nests in growth rates of tarsi ($F_{1,20} = 0.01$, $P = 0.98$; Fig. 3c), although growth rates of tarsi declined significantly as hatching dates became later in the breeding season ($F_{1,20} = 5.67$, $P = 0.03$).

Heating nests resulted in nestlings being significantly heavier than control nestlings at age 16 days ($F_{1,28} = 5.20$, $P = 0.03$); however, there was a significant treatment-by-area interaction ($F_{1,28} = 7.59$, $P = 0.01$) so we analyzed these data separately for each area. On the Hydro site, nestlings with heated boxes were significantly heavier than control nestlings ($F_{1,14} = 17.39$, $P < 0.001$), whereas we could detect no significant difference in mass at age 16 days on the Steward site

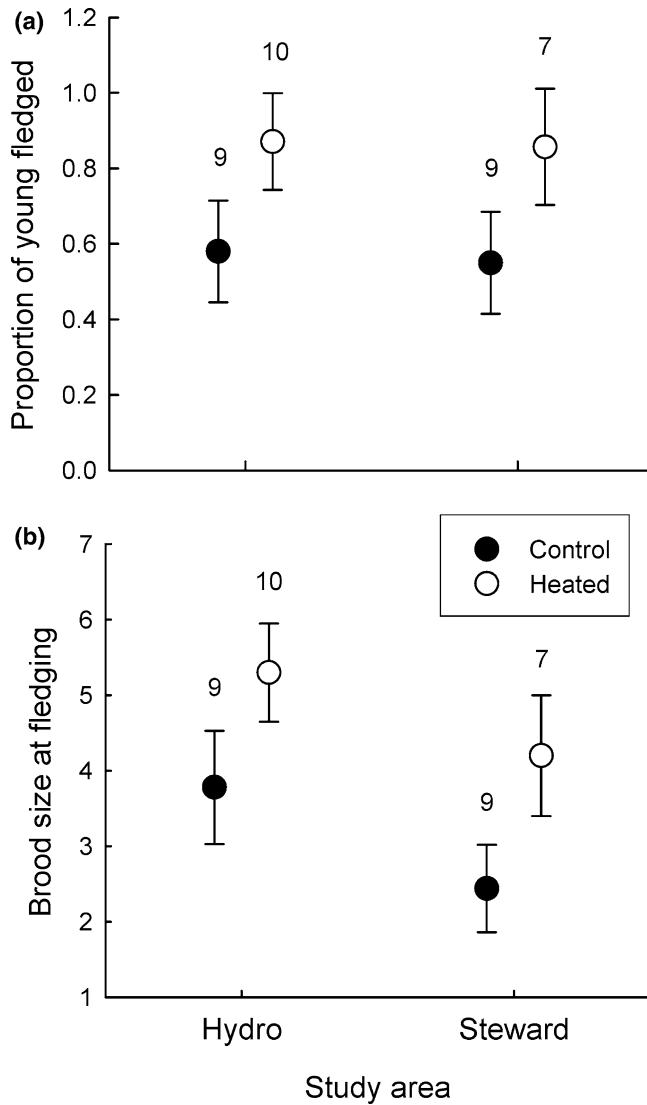


Fig. 2 **a** Proportion (\pm SE) of nestlings that fledged and **b** average brood size (\pm SE) at fledging in control or artificially heated nests. Means are presented separately for the two study areas (Hydro and Steward). Sample sizes above error bars refer to number of nests

($F_{1,14}=0.09$, $P=0.77$; Fig. 4a). Ninth primaries at age 16 days were longer in heated nests than control nests ($F_{1,30}=5.12$, $P=0.03$; Fig. 4b), but length of tarsus at 16 days of age was not influenced by our manipulation ($F_{1,26}=0.07$, $P=0.79$; Fig. 4c). Heating nest boxes did not affect CMI responses of nestlings compared with control nestlings ($F_{1,28}=0.11$, $P=0.74$; Fig. 4d).

The beneficial effects of heating nests that we detected were probably not a consequence of changes in parental behaviour, as we could find no significant difference between provisioning rates by parents in heated nests (13.0 ± 2.6 feeds/h) and those at control nests (14.4 ± 2.9 feeds/h; $F_{1,19}=0.14$, $P=0.72$). There was, however, a non-significant trend for provisioning rates to increase as brood sizes became larger ($F_{1,19}=3.91$, $P=0.06$).

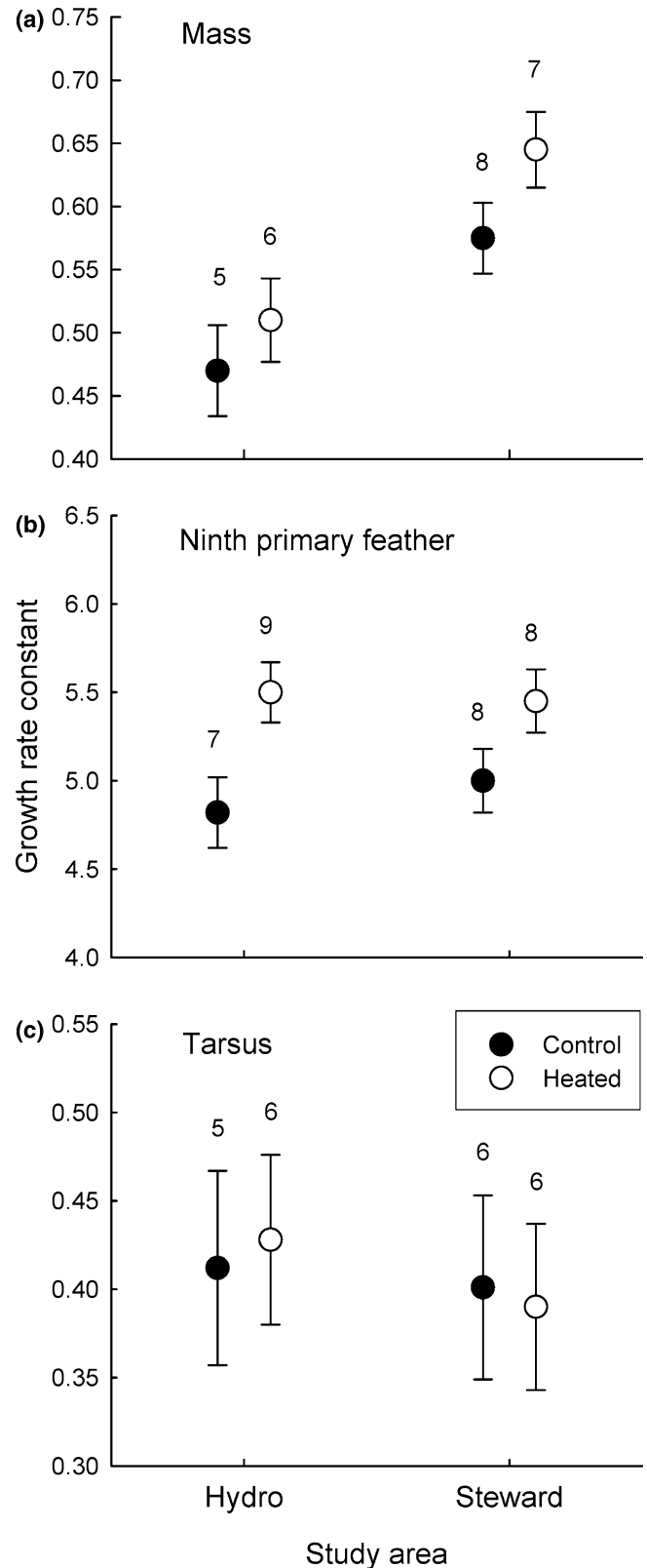
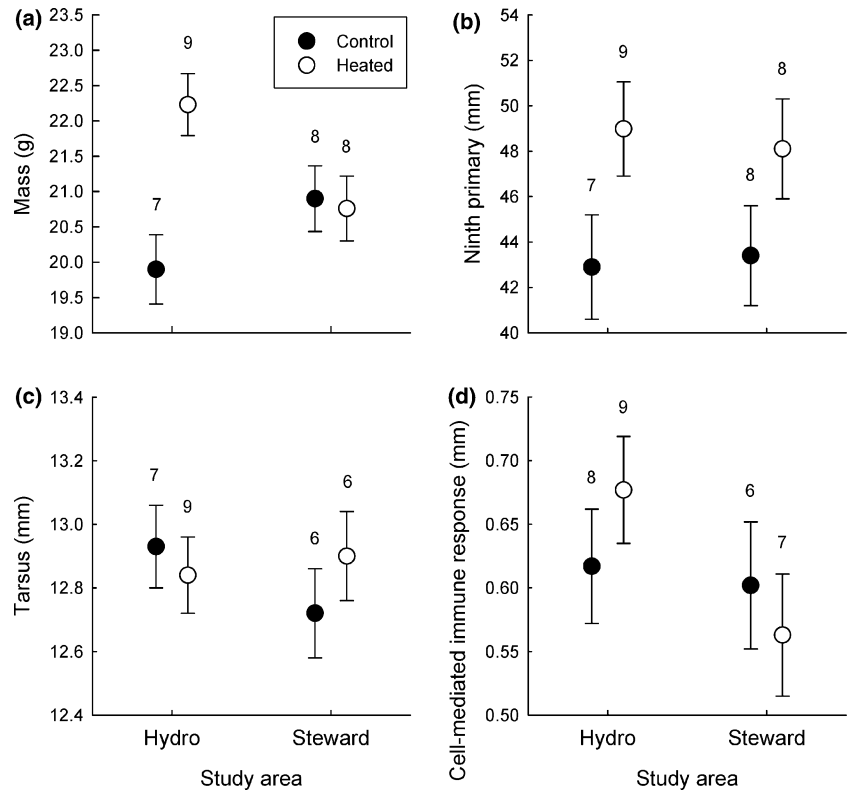


Fig. 3 Average growth rate constants of **a** mass, **b** ninth primary feathers and **c** tarsus for nestling tree swallows in control nests or those that were artificially heated. Means (\pm SE) are presented separately for the two study areas (Hydro and Steward). Sample sizes above error bars refer to number of nests. See Methods for further details of calculation of growth rate constants

Fig. 4 Average **a** mass, **b** length of ninth primary, **c** length of tarsus of nestling tree swallows at 16 days of age, and **d** CMI response at 12 days of age in control or artificially heated nests. Means (\pm SE) are presented separately for the two study areas (Hydro and Steward) and sample sizes above errors bars indicate number of nests



Discussion

Growth of altricial species of birds is thought to be constrained by the ability of chicks to assimilate or process food, or by the rate at which tissues proliferate (Ricklefs 1969; Ricklefs et al. 1994). Indeed, much of the literature on avian growth has focussed on food abundance and quality, probably because these represent the material and energy necessary to add tissue to the body (Quinney et al. 1986; Schew and Ricklefs 1998; Lepczyk and Karasov 2000; Dawson and Bidwell 2005). In contrast, the effect of thermal conditions of the nest on growth has received relatively little study, and much of the work examining effects of temperature on offspring growth has come from studies on precocial birds feeding in cold climates. Such studies have shown that chicks exposed to cold temperatures tend to spend less time foraging, and more time being brooded (Krijgsveld et al. 2003). Because their thermoregulatory costs are higher, chicks in cold environments consume more food and so the trade-off between growth and thermoregulation is shifted in favour of thermoregulation, and growth rates are compromised (Krijgsveld et al. 2003).

McCarty (2001) showed that despite substantial variation in growth rates of tree swallows across North America, there was no association with either latitude or longitude, which led him to conclude that large-scale climatic variation likely does not play a role in determining geographic variation in growth rates of swallows.

While much of the large-scale spatial and temporal variation in the growth of swallows may be due to differences in food supply (McCarty 2001; see also Gebhardt-Henrich and Richner 1998), our experimental study suggests that climatic conditions within a breeding season that alter thermal regimes of nest sites can have significant influences on offspring. When we elevated temperature at nest boxes, nestlings had enhanced rates of growth, longer ninth primaries, and on one of the two study areas, were significantly heavier just prior to fledging (Figs. 3, 4). Previously reported growth rate constants for mass of tree swallows have ranged from 0.391 to 0.56 (all rates computed using logistic growth equations; Dunn 1975; Marsh 1980; Zach and Mayoh 1982; Quinney et al. 1986; McCarty 2001). Control birds in the present study had an average growth rate constant of 0.52, while nestlings with heated nest boxes had an average growth rate constant of 0.58 (Fig. 3). The latter growth rate is among the highest, to our knowledge, recorded for tree swallows.

There were several differences between our two study sites, both pre-manipulation and post-manipulation. Birds at the Hydro site had larger clutch and brood sizes, and offspring were heavier and had longer tarsi at 4 days of age (just prior to beginning our experiment) than at the Steward site. In addition, we could detect significant effects of heating nests on mass at 16 days of age only at the Hydro site (Fig. 4). There are two possible mechanisms that may explain these differences be-

tween sites. First, it has been demonstrated that several species of hole-nesting passerines adjust clutch size, and hence brood size, to cavity size (see Rendell and Robertson 1993; Stewart and Robertson 1999), which may account for the differences we detected in clutch and brood sizes between sites. Second, McCarty (2001) showed that growth rates of tree swallows differed between two of his study sites, and these were only 2 km apart and appeared to have similar food abundance. He attributed the site-specific growth rates to differences in density of nests; parents at high density sites may have to forage farther from the nests to avoid intra-specific competition (see also Bryant 1978). This may also explain the site-specific results for mass at 16 days of age, as well as the pre-manipulation differences, in our study. Nests at the Hydro site were much more dispersed than at the Steward site, and so there may have been relatively little interference among foraging adults at the Hydro site. As our study was not designed specifically to address differences among sites, more research is required to understand the causes of these patterns.

Although previous non-manipulative research has shown the importance of temperature in influencing growth of offspring, results have not always been consistent. For example, McCarty and Winkler (1999) demonstrated that ambient temperature had direct effects on growth of tree swallows, particularly when offspring were young. Their study also showed that growth was affected indirectly by ambient temperature through its effects on abundance of aerial insects. Similarly, Eeva et al. (2002) found that although ambient temperature influenced mass growth in both temperate and sub-arctic breeding populations of pied flycatchers (*Ficedula hypoleuca*), there were no systematic differences between the two areas despite large differences in ambient temperature. They concluded that birds breeding in colder climates were adapted to the low temperatures that occurred there, whereas birds breeding in more southerly areas lacked such adaptations because they rarely encountered extremes in temperatures. Murphy (1985) also showed that ambient temperature was an important factor in determining growth of eastern kingbirds (*Tyrannus tyrannus*); however, while he showed that warmer temperatures resulted in enhanced growth of primaries, warm weather caused significant reductions in mass gain. Kingbirds are open cup nesters, with nests typically exposed to direct sunlight and high temperatures. As a consequence, nestlings are often subjected to heat stress (Murphy 1985). While our manipulation resulted in temperatures of nests being significantly warmer than control nests, the range of temperature variation was within that previously documented at nests of tree swallows (Chaplin et al. 2002), so our birds were probably not subjected to temperatures high enough to result in hyperthermia. Our experimental results clearly show that increasing temperatures of nest sites enhanced offspring growth and size in a temperate environment.

The actual mechanism by which nestling tree swallows with heated nests had enhanced growth and size is

not entirely clear. Both Gebhardt-Henrich and Richner (1998) and McCarty (2001), suggested that much of the variation in growth rates within species is due to variation in parental quality or food supplies. Indeed, food supply is a very important determinant of growth, as demonstrated by Quinney et al. (1986) who found significant differences in growth of tree swallows between two areas that differed only with respect to food supply (see also McCarty and Winkler 1999). Clearly, food supply cannot directly account for the differences observed in our study, because alterations of prey availability that often result from natural variation in ambient temperature (e.g., Turner 1984; Keller and van Noordwijk 1994) have not confounded our results. Nonetheless, we believe that the beneficial effects of higher nest temperatures that we have demonstrated are indirectly manifested via food. For example, the addition of extra heat may have altered the behaviour of parents. If nestlings were sufficiently warm as a result of our manipulation, then this would have allowed the female parent to devote more time to foraging and less time to brooding offspring (Visser 1998). While this may be an important consideration when nestlings are young, female tree swallows rarely brood offspring older than 5 days of age (McCarty 1996; R.D. Dawson, unpublished data). Alternatively, the benefits accrued through our manipulation may also be a consequence of changes in behaviour of offspring. If nestlings were able to reduce energy allocation to thermoregulation as a result of our manipulation, then they may have been able to devote more energy to increasing rates and intensity of begging. Although begging is known to result in significant increases in metabolic rate, this activity constitutes only a very small fraction of the daily energy budget (McCarty 1996; Bachman and Chappell 1998; Leonard et al. 2003). Coupled with the finding that it is less costly to beg as temperatures become warmer (McCarty 1996), our manipulation may have allowed chicks to invest far more energy into begging than control chicks, with the consequence that parents may have increased their rates of provisioning. This too seems unlikely as an explanation because chicks spend more time begging when they are colder (McCarty 1996), and we could not detect significant differences in provisioning by parent swallows to heated and control nests.

Dunn (1979) reported that in broods of five offspring, nestling tree swallows could effectively maintain homeothermy when they were 5 days old. When ambient temperatures are low, metabolic heat production must be increased to compensate for heat loss to the environment (Visser 1998); therefore, nestlings need to expend energy generating sufficient heat for approximately 2 weeks before they leave the nest. Tree swallows are also well-known for lining their nests with feathers (Robertson et al. 1992), which may play a role in stabilizing the microclimate of the nest. Winkler (1993) compared offspring in nests where all feathers were experimentally removed to nests with intact feather linings, and showed that nestlings were significantly heavier

in nests where feathers were present. He suggested that these results were due to feathers providing supplemental insulation to the brood which would decrease the rate of heat loss in nests. This process may explain our results; heat loss to the environment is proportional to thermal conductance and the difference in temperature between the body and the environment (Visser 1998). Heating nests may have allowed nestlings to devote more energy to growth because less heat was dissipated to the environment of their nests.

In contrast to our results for mass and ninth primary, we could detect no effect of heating nests on size of tarsi at 16 days of age or on growth rate of tarsi (Figs. 3, 4). Similarly, Lepczyk and Karasov (2000) could find no effect of short-term food deprivation on growth of either culmen or tarsus in house sparrows (*Passer domesticus*). Growth of both culmen and tarsus represent increases in size of skeletal structures, and it may be that in birds like tree swallows and house sparrows, growth of these components is limited by other factors. For example, recent research on one of our study areas (Hydro site) has demonstrated that tarsus length of tree swallows at 16 days of age is significantly increased by providing supplemental calcium (Dawson and Bidwell 2005). For such skeletal structures, the availability of minerals such as calcium may play a much larger role in determining size than energy limitations or trade-offs between thermoregulation and growth. Tarsus length is also known to have a heritable component in tree swallows (Wiggins 1989).

Fitness consequences and implications

In addition to benefits for offspring through enhanced growth and size, experimental increases in nest temperature also enhanced survival of young while in the nest. Broods with heated nests were less likely to suffer brood reduction, and as a consequence heated nests fledged significantly more offspring than did control nests (Fig. 2). It does not appear that the enhanced survival of young in heated nests was a result of their having more robust immune systems, as we could detect no differences in CMI response between heated and control nests (Fig. 4). Most mortality of nestling tree swallows at our study area occurred during periods of inclement weather (R. D. Dawson, unpublished data). During these times, offspring may become hypothermic as parents are unable to provide adequate food, so it seems probable that elevated temperatures allowed chicks to survive these periods of cool weather.

It is unclear whether the higher mass or longer ninth primaries of chicks at day 16 in the heated group will translate into larger adult size. Body size is thought to have a large heritable component in birds (e.g., Ryan 2001), and several studies have demonstrated that when food is restricted for a period of time during brood rearing, even though such chicks have reduced growth rates, they still attain similar adult size as control birds

(e.g., Negro et al. 1994; Lepczyk and Karasov 2000). Faster development will nonetheless have benefits for offspring because it will reduce the period of exposure to nest predators (Lack 1968; Keller and van Noordwijk 1994), and as demonstrated at our Steward study site, this is a consideration that is important even for cavity nesters utilizing artificial boxes. Similarly, studies of passerine birds have shown that condition of nestlings at fledging is positively related to their probability of recruitment (Gebhardt-Henrich and Richner 1998). In addition, McCarty (2001) has shown that tree swallows with high rates of growth of mass, wing and tarsus had a higher probability of being recaptured in subsequent breeding seasons, a result that has been documented previously in other species (e.g., Tinbergen and Boerlijst 1990; see also Gebhardt-Henrich and Richner 1998). Collectively, these findings suggest that increasing temperatures of nest sites can have direct fitness consequences for tree swallows. Our study provides additional insight into factors that may limit reproductive success of birds breeding in temperate environments.

Finally, there is currently a great deal of interest in documenting effects of global climate change on ecological systems (Ottersen et al. 2001), and our results may also provide insight into some of these possible consequences for avian populations. Much recent work has focussed on changes in laying date in response to warming climates (references in Hussell 2003), but the effects of increased temperatures on other aspects of avian life-histories are generally unknown. Both Visser et al. (2003) and Winkler et al. (2002) concluded that understanding the responses of birds to changing climates will be dependent on integrating all aspects of avian life histories. Much insight can be gained from manipulative experiments such as ours that alter microclimates, and assess the associated consequences for birds, both beneficial and detrimental. We encourage other researchers to undertake these manipulative experiments to more fully understand the responses of birds to climate change.

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