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BODY TEMPERATURE AND REPRODUCTIVE EFFORT IN A LONG-LIVED
TROPICAL SONGBIRD

By

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Thesis

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Body Temperature and Reproductive Effort in a Long-Lived Tropical Songbird

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Heat production relative to dissipation rates have constrained reproductive effort and reduced fitness in short-lived, temperate birds. To determine whether heat constrains reproductive effort in long-lived taxa with low reproductive effort, we experimentally clipped plumage from tropical Gray-throated babblers (*Stachyris nigriceps*) to increase heat dissipation rates. Contrary to findings in short-lived species, we found no strong evidence of heat dissipation constraints on reproductive effort in our mid-elevation study. Clipped adults did not increase feeding rates compared to controls, but clipped females did spend more time incubating and brooding eggs and young. Increased time in the nest may reduce increased heat loss and energy expenditure following clipping of the belly plumage at our cool, mid-elevation study site. Furthermore, control parents in our study had lower body temperatures than songbirds that previously have been shown to be heat-limited. We suggest that heat production from the low reproductive effort of long-lived tropical songbirds may not generally be sufficient to create major thermal constraints. Ultimately, the degree to which heat limits reproductive effort may strongly depend on the environment and interspecific differences in evolved levels of reproductive effort and parental heat production during breeding.

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INTRODUCTION

The heat generated from maintenance and activity metabolism can raise body temperatures if heat production exceeds rates of heat dissipation (Guillemette et al. 2016, McKechnie 2022). The heat dissipation limit (HDL) hypothesis predicts that the maximal capacity to offload heat may limit energy expenditure and thus activity (Speakman and Król 2010 a, b). In breeding endotherms, high rates of heat production associated with reproductive activity and warmer environmental temperatures could produce conditions where activity may be limited by heat dissipation capacity, which could reduce fitness (Król et al. 2007, Nord and Nilsson 2019, Tapper et al. 2020a). Reproductive effort varies widely across species and the HDL hypothesis has been proposed as an explanation for why some species can work harder and raise more young than others (Speakman and Król 2010a, b). Experimentally alleviating heat dissipation constraints via clipping feathers or shaving fur has produced lower body temperatures and increased provisioning effort compared with control parents (Król et al. 2007, Sadowska et al. 2016, Nord and Nilsson 2019, Tapper et al. 2020a, b). However, the generality of heat dissipation limits on reproductive effort is unclear because current experimental evidence stems from laboratory settings where air temperatures are restricted, or from studies of short-lived temperate taxa with large brood sizes. The high reproductive effort of short-lived species (i.e. Tinkle 1969, Martin 2015) may increase the likelihood that they experience heat dissipation limits. In contrast, whether the lower reproductive effort of long-lived species creates sufficient heat to limit reproduction is unknown.

Tropical species provide an intriguing test case. The HDL *hypothesis* may act despite low reproductive effort for several reasons. Tropical organisms are thought to have narrower thermal tolerances than temperate taxa because they evolved in an environment with narrow variation in

environmental temperature (Janzen 1967, Ghalambor et al. 2006, but see Pollock et al. 2021). Consequently, interactions between warm environmental temperatures and reproductive activity in tropical endotherms may push heat production rates to levels that test limits of heat dissipation ability and thus impact performance. Additionally, humid conditions in the tropics could impede evaporative heat loss, forcing organisms to rely solely on passive heat dissipation (Powers 1992, Gerson et al. 2014). If the capacity for heat dissipation does constrain reproductive effort in tropical taxa, we might expect constraints (lower feeding effort, higher body temperature) to be most evident during afternoon hours when air temperatures are warmest.

The importance of air temperature on parental behaviors is suggested by two contrasting results. On the one hand, body temperature has been shown to increase with feeding rate, and feather clipping yielded higher feeding rates in one species when air temperatures were above ca. 22°C (Tapper et al. 2020b). On the other hand, feather clipping yielded lower feeding rates, possibly resulting from greater time spent brooding, when air temperatures were below ca. 17°C (Tapper et al. 2020b). Thus, air temperature may play an important interacting role in heat dissipation constraints on feeding and brooding behaviors.

Of course, long-lived tropical taxa may avoid heat dissipation constraints due to their low reproductive effort. Many tropical endotherms are long-lived (Martin 2015, Martin et al. 2017, Scholer et al. 2020) and prioritize survival because of the fitness benefits of future breeding (Williams 1966, Hirshfield and Tinkle 1975, Oteyza et al. 2021). Concordantly, long-lived species raise fewer young, resulting in low reproductive effort per breeding attempt (Ghalambor and Martin 2001, Martin 2015). Under a *low reproductive effort hypothesis*, long-lived tropical species may not experience excessively high body temperatures and heat dissipation constraints during reproduction. As a result, feeding rates may not be constrained by heat.

Understanding whether rates of heat production and dissipation constrains reproduction in long-lived tropical endotherms can provide new insight into the generality of heat limitations on parental effort across life histories. We explored the extent to which heat dissipation ability might be limiting reproductive effort in Gray-throated Babblers (*Stachyris nigriceps*). We chose Gray-throated Babblers because they are a relatively long-lived tropical species (75% annual adult survival; Martin et al. 2017) that inhabit cool mid-elevation forest. Further, this species may be likely to experience heat constraints because it typically cares for three young, one more than most tropical songbirds (see Martin 2015). Our mid-elevation study site provided an interesting test of the HDL hypothesis because average air temperatures were similar, but fluctuated less than in temperate areas where feather-clipping experiments have demonstrated heat constraints on reproductive effort (Nord and Nilsson 2019, Tapper et al. 2020a, b). We experimentally increased heat dissipation rates of parents using a feather clipping treatment to test whether heat dissipation constrained reproductive effort. We examined body temperature responses across treatments (clipped and unclipped) to air temperature, parent workload (number of offspring), and measured two metrics of reproductive effort: nest attentiveness and provisioning rates to test the two hypotheses. Under the *HDL hypothesis* we predicted that clipped parents would provision young at higher rates than controls, but that clipped and control birds would have similar attentiveness, as heat should not limit them from sitting on young. Further, we expected control birds to have similar body temperatures to songbirds found to be heat-limited in previous studies. Under the *low reproductive effort hypothesis*, we predicted that clipped and control adults would not differ in provisioning rates, but that clipped adults may increase attentiveness to save energy. Finally, we expected control parents to have lower body temperatures than for songbirds previously reported to be heat-limited.

METHODS

Study Area and Species

We studied a wild breeding population of Gray-throated Babblers from 1,450-1,870 meters above sea level in Kinabalu Park (6.0185 °N, 116.5416 °E), Sabah, Malaysia from February to June in 2019 and 2020. The montane field site is composed of humid tropical forest (Martin et al. 2015). The site is characterized by high average yearly precipitation (2788mm) and cool, relatively stable annual temperatures averaging 18°C (Kitayama 1992). Diurnal breeding season air temperature generally fluctuates between 15-22°C. We collected air temperature and rain data from a HOBO weather station placed in the understory at 1520m asl.

Gray-throated Babblers are a widely distributed species of Old-World passerine that range across much of Southeast Asia in submontane and montane forests (Collar and Robson 2020). Adults forage and nest in the understory and mid-story, which is generally shaded due to canopy cover. They typically lay three, but occasionally two egg clutches in enclosed dome nests (Kaiser et al. 2018). They are a group-living species that forages in social groups and occasionally act as facultative cooperative breeders with a small number of pairs receiving help from a third individual (Kaiser et al. 2018). However, we did not observe any cooperative breeding instances in the pairs used for this study. Both sexes contribute to incubation, brooding, and provisioning nestlings (Kaiser et al. 2018). Both sexes develop brood patches during breeding attempts, although male brood patches are somewhat less vascularized.

Body Temperature and Feather Clipping Methods

We netted both male and female parents at the nest in late incubation (days 13-16 of the 16 d incubation period) or early nestling (days 1-2) period. We injected temperature sensitive

Biomark (Boise, Idaho), Biotherm 13 passive integrated transponder (PIT) tags into the abdominal cavity of individuals from all nests (McCafferty et al. 2015). We also gave adults a unique combination of color bands to identify parents in video footage. Once PIT-tagged, we randomly assigned nests and associated adults to either a clipping or control (non-clipping) treatment. Following Nilsson and Nord (2019), we performed a 22% body surface area clip, removing plumage from the ventral feather tract with scissors exposing the belly (Figure 1A).

Nest Monitoring Methods

We monitored nests every 1-2 d until the nest was depredated or until the nestlings fledged. On the day following PIT-tagging, we stationed a camouflaged Biomark HPR+ PIT-tag reader antenna in the immediate vicinity of the nest (typically ≤ 8 cm; Figure 1B). We positioned antennas to read the adult's ID, body temperature, and time of day at ten second intervals whenever adults were present at the nest. We left antennas at the nest until the young fledged or the nest failed to reduce disturbance. The antenna was connected to the Biomark HPR+ PIT-tag reader, which we stationed 3-4m away from the nest and camouflaged using leaves and other natural debris. We deployed readers at least once in late incubation and at intervals throughout the nestling stage (early: nestlings aged 0-3 d, mid: 4-5 d) while nests remained active. Note that young fledge at 8-9 d and we did not wish to disturb at later ages and cause early fledging. We set up readers in the early morning, typically before 8:00am, and allowed them to record data for 24 hr. We also filmed nests on the days readers were present, using HD video cameras with 20X zoom set up ≥ 5 m from the nest (Martin 2015), to assess reader accuracy in detecting adult presence.

Statistical Methods

We analyzed all data using R* 4.0.3 (R Core Team 2020). We fit linear mixed effects models using the *lme4* package (Bates et al. 2015) to assess which variables influenced body temperature, nest attentiveness, and provisioning rates. We used manual stepwise selection to arrive at our final models, keeping only significant and marginally significant predictor variables, aside from the clipping treatment which was kept regardless of significance. In all models we included individual identity as a random effect to control for repeated measures.

Modeling body temperature responses to environmental temperature and parent workload. To assess how body temperature changed in response to environmental temperature and parental workload, we looked at body temperatures of birds arriving to the nest. We assumed that birds generate heat in activity when away from the nest and arrive at the nest with higher than normothermic body temperatures (Prinzinger et al. 1991, Speakman and Król 2010a, b; Nord and Nilsson 2019). We also modeled the maximum body temperature experienced per trip to the nest and found no differences from the arrival body temperature model. Therefore, only results from the arrival temperature model are presented. We defined a new trip to the nest, and thus an arrival body temperature, as an observation separated by ≥ 45 s from the previous visit by that individual.

We fit one model, including data from both incubation and nestling stages, with arrival body temperature as the dependent variable. The model included number of young (eggs or nestlings), total nest age (days since last egg laid), time of day, time of day², clipping treatment, sex, a clipping treatment * sex interaction, maximum daily air temperature, and presence of rain during sampling as fixed effects. Time of day was highly collinear with air temperature at our central climate measuring site, so we used time of day as a standard index of relative diurnal changes in air temperature and maximum daily air temperature to account for differences among

days. We predicted body temperature would have a parabolic relationship with time of day, with the hottest body temperatures occurring mid-day when air temperature was warmest. Thus, we included time of day². We used *ggpredict* (Lüdecke 2018) to compute effects of time of day on body temperature by clipping treatment and number of young.

Modeling provisioning in response to experimental clipping. We modeled provisioning rate as a parental effort metric across treatments. Provisioning rate is defined here as the number of food delivery trips made to the nest by one individual per unit time, and has previously been used to assess reproductive effort (Martin 2015). We used PIT tag data to assess visit rates per individual per day, supplementing with video data when PIT data did not capture the entire time frame. Provisioning was measured during the nestling stage, and sample sizes during the nestling stage were reduced due to COVID-19 impacts on the field season. Because we might expect the biggest effect from the clipping treatment during the hottest part of day, and because we had more samples during a smaller subset of daylight hours, we restricted provisioning analyses to 11:00-15:00.

We modeled daily provisioning per individual, expressed as the average number of trips to the nest during an hour, including nestling age, clipping treatment, sex, number of young, maximum daily air temperature, and a clipping*sex interaction as fixed effects. To increase control sample size, we included video data from non-PIT-tagged nests where both adults were color banded as pseudo-controls. Provisioning rates from true and pseudo controls did not differ ($t = -0.29$, $df = 6$, $P = 0.78$, $n = 10$), so these data were combined in the model.

Modeling nest attentiveness in response to experimental clipping. We also modeled nest attentiveness across treatments. Nest attentiveness is the total time spent on the nest by an individual over a specified time interval, and has previously been used as a measure of warming

effort (Martin et al. 2007, 2015; Riechert and Becker 2017). We used PIT tag data to determine nest attentiveness, occasionally relying on video data in instances where the PIT tag reader battery died before capturing the entire time frame. To calculate attentiveness, we determined arrival and departure times for each unique trip to the nest and used the sum of all durations to obtain the total time spent on the nest for a given individual for a given day. We were interested in the effect of clipping on parental behavior during daylight hours, so we selected 08:00-18:00 as our time window for the attentiveness model. We only included samples that spanned the entire timeframe in the analysis.

Daily attentiveness was measured during both incubation and nestling stages. We modeled daily attentiveness per individual, expressed as the average amount of time spent on the nest during an hour, including number of young, total age, total age², maximum daily air temperature, clipping treatment, sex, and a clipping*sex interaction as fixed effects. Total age² was included in the model because attentiveness has been shown to fluctuate non-linearly with age, where adults typically increase attentiveness during incubation and decrease after hatch (e.g., Mitchell et al. 2017, Martin et al. 2018). To increase sample sizes for control adults attending nestlings, we included video data from non-PIT-tagged nests where both adults were color banded as pseudo-controls. Attentiveness from true and pseudo controls did not differ based on linear model analyses that controlled for age and sex ($t = 0.87$, $df = 6$, $P = 0.42$, $n = 24$) so we combined these data in the model. We used *ggpredict* (Lüdtke 2018) to compute effects of total age on nest attentiveness by clipping treatment and sex.

RESULTS

Parent Body Temperature

We analyzed 1,144 arrival temperatures from 25 individuals at 15 nests. Body temperature had a strong parabolic relationship with time of day (Table 1). Body temperatures were highest in the middle of the day for both clipped and control adults when air temperatures were warmest and lowest in the mornings and late afternoons when air temperatures were cooler (Figure 2A, B, C). Body temperatures did not increase with visitation rates across the day because parents visited the nest at a significantly lower rate per hour during the warm mid-day than during the cooler mornings and late afternoons across both treatments ($t = -4.16$, $P < 0.001$, $n = 129$). Clipped females had lower body temperatures than control females during warm mid-day hours and into the late afternoon, but body temperatures were more similar across treatments during cool morning hours (treatment by time-of-day interaction: Table 1, Figure 2C). Body temperatures of clipped and control males did not differ (treatment by sex interaction: Table 1, Figure 2B, C). Body temperatures were higher for brood sizes of three than two young, regardless of clipping treatment (Table 1, Figure 2D). Body temperatures were also higher in individuals caring for older young (Table 1). The presence of rain during sampling and maximum daily air temperature did not contribute to explaining variation in body temperature ($t = -1.09$, $P = 0.28$; $t = -1.63$, $P = 0.10$, respectively).

Parental Responses to Experimental Trimming

Provisioning data consisted of 30 samples (16 individuals from 8 nests) and eight of these samples were pseudo-control data (6 individuals from 3 nests). Provisioning rate during the nestling period increased with nestling age (Table 2, Figure 3A), but clipped and control adults did not differ in the rate at which they provisioned young (Table 2). Provisioning was not influenced by sex, the number of young, maximum daily air temperature, or a clipping treatment-

sex interaction ($t = 0.16, P = 0.88$; $t = 1.21, P = 0.24$; $t = -1.02, P = 0.32$; $t = -0.76, P = 0.46$, respectively).

Attentiveness data consisted of 55 samples (21 individuals from 11 nests) and eight of these samples were pseudo-control data (6 individuals from 3 nests). Clipped females, but not males, spent more time in attentiveness on their nests than unclipped females across incubation and nestling stages (treatment by sex interaction: Table 3, Figure 3B). Daily attentiveness had a marginally significant parabolic relationship with age of young across both sexes and clipping treatments, increasing during incubation and decreasing after hatch (Table 3, Figure 3B). Daily nest attentiveness was not influenced by the number of eggs or young in the nest or maximum daily air temperature ($t = -0.36, P = 0.72$; $t = 0.49, P = 0.62$, respectively).

DISCUSSION

Heat dissipation can limit reproductive effort and reduce fitness (Speakman and Król 2010a, b, Nord and Nilsson 2019, Huang et al. 2020, Tapper et al. 2020a, b). However, such results have come from tests focused on short-lived temperate taxa that have high reproductive effort, which may make them particularly susceptible to heat constraints on parental effort (Valencak et al. 2010). Determining whether heat constraints exist in long-lived taxa with low reproductive effort helps to assess the generality of heat dissipation constraints on parental effort. Here we showed that long-lived Gray-throated Babblers may be unlikely to experience heat dissipation constraints during breeding due to their low evolved levels of reproductive effort and the cool environment where they live.

We conducted our test with a tropical species that commonly has three young, which is 50% (1 young) greater than the typical brood size of two observed for most tropical passerine

species (Martin 2015). This larger brood size thereby provided a somewhat conservative test of the potential for heat constraints in long-lived tropical birds. We found that body temperature increased in the warm afternoons and with reproductive effort; parents caring for more and older young exhibited higher body temperatures (Table 1, Figure 4). Body temperature may increase with brood size because foraging intensity and energy expenditure are greater in parents caring for larger broods (Deerenberg et al. 1995, Sanz and Tinbergen 1999), causing them to generate more heat and arrive to the nest with higher body temperatures. Nonetheless, average body temperatures of control individuals ($41.6 \pm 0.24^{\circ}\text{C}$ [least squares mean \pm SE]; $n = 533$) were lower than those reported for shorter-lived temperate songbirds caring for larger numbers of offspring (42.0 - 43.1°C , Figure 4; Nilsson and Nord 2018, Nord and Nilsson 2019, Andreasson et al. 2020, Tapper et al. 2020b) and compared to other active passerines (Prinzinger et al. 1991, Thompson et al. 2018, but see Nilsson et al. 2016). The maintenance of comparatively low body temperatures may indicate that long-lived parents with low levels of reproductive effort do not work hard enough to produce the excess heat, which might result in higher body temperatures (i.e. 43 - 46°C ; McKechnie and Wolf 2019) and might constrain reproduction.

Our experiment showed that clipped females had cooler body temperatures than control females, in agreement with observations from previous feather clipping experiments (Figure 2B, C; Nord and Nilsson 2019, Tapper et al. 2020b). Thus, our experiment provided the key manipulation needed to test whether heat was limiting reproduction. Provisioning rate is thought to be a key influence on parental energy expenditure that also is the primary source of metabolic heat generation (Part et al. 1992, Tinbergen and Dietz 1994, Nudds and Bryant 2000, Guillemette et al. 2016), but we found that provisioning efforts did not increase in response to clipping in either sex. This result contrasts with tests in temperate zone taxa (Sadowska et al. 2016, Tapper

et al. 2020a, but see Nord and Nilsson 2019, Andreasson et al. 2020). Importantly, however, provisioning rates in our tropical species were much lower than those recorded in temperate feather-clipping experiments (Figure 3A; Nord and Nilsson 2019, Andreasson et al. 2020, Tapper et al. 2020a). The lack of increased provisioning despite greater heat dissipation from clipping fits with the observed low body temperatures to suggest that excess heat production was not a major constraint on parental effort in our long-lived tropical species.

Our test, however, was at mid-elevation where air temperatures are cooler than at lowland tropical sites. As such, our results may not be representative of lowland tropical species. Warmer conditions in the lowland tropics diminish the gradient between body and ambient temperature, resulting in reduced rates of passive heat dissipation (Porter and Gates 1969). Furthermore, lowland tropical species may live closer to their upper thermal tolerance limits (Deutsch et al. 2008, Tewksbury et al. 2008). The interaction between physiological constraints and environmental temperature and humidity could make heat dissipation more limiting to reproductive effort in the warmer tropical lowlands (Weathers 1977, 1997; Powers 1992, Speakman and Król 2010a). Indeed, experimental clipping of birds in the temperate region impacted reproductive effort in a temperature dependent manner: clipped parents showed higher effort than controls when ambient temperatures were warm, but lower effort when conditions were cooler (Tapper et al. 2020b). Similarly, the cooler environmental temperatures at our site experienced by birds and the lack of an increase in effort by clipped birds suggests a lack of thermal constraints on reproduction. Future studies should test whether heat dissipation constrains reproductive effort in long-lived species of the lowland tropics that experience warmer environmental temperatures than those documented here.

Cool environmental temperatures at our mid-elevation site may also help to explain results for nest attentiveness. The clipping treatment did not impact male nest attentiveness, whereas clipped females significantly increased attentiveness compared with control females (Table 3, Figure 3B). This result fits with the fact that clipped females had lower body temperatures than control females, while male body temperature did not differ between treatments (Table 1, Figure 2B, D). Female Gray-throated Babblers have larger and more heavily vascularized brood patches than males, that would have amplified increases in thermal conductance following the clipping of belly feathers and produced increased rates of heat loss compared to males (Herreid and Kessel 1967, Porter and Gates 1969, Wolf and Walsberg 2000). As a consequence, females may have increased brooding of offspring using the enclosed nest and young to reduce their thermal conductance and self-maintenance costs (Walsberg and King 1978, Buttemer et al. 1987, Martin et al. 2017a, Sukhchuluun et al. 2018, Lowney et al. 2020) especially given the consistently cool ambient temperatures at our field site (avg 18°C; Kitayama 1992). This interpretation may also explain the results of Tapper et al. (2020a) who found that feeding rates of clipped parents were reduced at air temperatures typical of our site, and they suggested the reduced feeding may reflect more time spent brooding.

While we find little evidence of heat constraints on reproductive effort in this population of tropical mid-elevation songbirds at present, increased global temperatures could make heat dissipation more problematic in the future. Birds may have evolved various morphological or physiological strategies to effectively regulate temperature under current climate conditions (e.g., Weathers and van Riper 1982, Wolf and Walsberg 2000). However, increasing environmental temperatures will negatively impact heat dissipation by reducing the gradient between air and body temperature, reducing passive rates of heat loss (Porter and Gates 1969) and possibly

activity (van de Ven et al. 2019). Such changes may be especially problematic for tropical organisms that evolved narrow thermal tolerances in response to relatively stable environmental temperatures (Deutsch et al. 2008, Tewksbury et al. 2008). Further tests are needed to determine how interactions between climate, warming temperatures, and evolved reproductive effort strategies will impact the propensity to experience heat dissipation constraints on effort now and in the future.

In conclusion, Gray-throated Babbler parents in our study maintained comparatively low body temperatures while caring for offspring, providing some evidence that they are not heat limited. The results of our feather clipping experiment further suggested that the reproductive effort of this long-lived tropical songbird inhabiting a cool mid-elevation forest is not constrained by heat production. We propose long-lived species that have evolved less-active strategies may not work hard enough to produce excessive heat or experience physiological heat dissipation constraints on reproductive effort. Yet, this idea needs tests in warmer lowland environments. The HDL hypothesis suggests differences in body size and insulation impact heat dissipation capacity and explain reproductive effort across species (Speakman and Król 2010a, b). While this may or may not be true broadly, species vary greatly in their reproductive effort for a given body size (Martin 1995, 2015; Peach et al. 2001). Ultimately, the degree to which heat limits reproductive effort may strongly depend on the environment and interspecific differences in evolved levels of reproductive effort and parental heat production during breeding.

LITERATURE CITED

- Andreasson, F., A. Hegemann, A. Nord, and J.-Å. Nilsson (2020). Experimental facilitation of heat loss affects work rate and innate immune function in a breeding passerine bird. *Journal of Experimental Biology* 223:1–9.
- Anon (2020). R: A language and environment for statistical computing. [Online.] Available at <https://www.r-project.org/>.
- Azad, K. M. A., M. Kikusato, A. M. Hoque, and M. Toyomizu (2010). Effect of chronic heat stress on performance and oxidative damage in different strains of chickens. *Journal of Poultry Science* 47:333–337.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Buttemer, W. A., L. B. Astheimer, W. W. Weathers, and A. M. Hayworth (1987). Energy savings attending winter-nest use by Verdins (*Auriparus flaviceps*). *The Auk* 104:531–535.
- Collar, N., and C. Robson (2020). Gray-throated Babbler (*Stachyris nigriceps*). *Cornell Lab of Ornithology, Ithaca, NY, USA*. [Online.] Available at <https://birdsoftheworld.org/bow/species/gytbab1/cur/introduction>.
- Deerenberg, C., I. Pen, C. Dijkstra, B.-J. Arkies, G. H. Visser, and S. Daan (1995). Parental energy expenditure in relation to manipulated brood size in the European Kestrel *Falco tinnunculus*. *Zoology* 99:39–48.
- Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and

- P. R. Martin (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* 105:6668–6672.
- Gerson, A. R., E. K. Smith, B. Smit, A. E. McKechnie, and B. O. Wolf (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology* 87:782–795.
- Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang (2006). Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integrative and Comparative Biology* 46:5–17.
- Ghalambor, C. K., and T. E. Martin (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494–497.
- Guillemette, M., A. J. Woakes, J. Larochelle, E. T. Polymeropoulos, J.-M. Granbois, P. J. Butler, D. Pelletier, P. B. Frappell, and S. J. Portugal (2016). Does hyperthermia constrain flight duration in a short-distance migrant? *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:1–8.
- Herreid, C. F., and B. Kessel (1967). Thermal conductance in birds and mammals. *Comparative Biochemistry And Physiology* 21:405–414.
- Hirshfield, M. F., and D. W. Tinkle (1975). Natural selection and the evolution of reproductive effort. *Proceedings of the National Academy of Sciences of the United States of America* 72:2227–2231.
- Huang, Y. X., H. H. Li, L. Wang, H. X. Min, J. Q. Xu, S. L. Wu, J. Cao, and Z. J. Zhao (2020).

The ability to dissipate heat is likely to be a more important limitation on lactation in striped hamsters with greater reproductive efforts under warmer conditions. *Physiological and biochemical zoology* : PBZ 93:282–295.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. *The American Naturalist* 101:233–249.

Kaiser, S. A., T. E. Martin, J. C. Oteyza, C. Armstad, and R. C. Fleischer (2018). Direct fitness benefits and kinship of social foraging groups in an Old World tropical babbler. *Behavioral Ecology* 29:468–478.

Kitayama, K. (1992). An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102:149–171.

Król, E., M. Murphy, and J. R. Speakman (2007). Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. *The Journal of Experimental Biology* 210:4233–4243.

Lowney, A. M., D. Bolopo, B. A. Krochuk, and R. L. Thomson (2020). The large communal nests of Sociable Weavers provide year-round insulated refuge for weavers and Pygmy Falcons. *Frontiers in Ecology and Evolution* 8:1–13.

Lüdecke, D. (2018). ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software* 3:772.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.

Martin, T. E. (2015). Age-related mortality explains life history strategies of tropical and

temperate songbirds. *Science* 349:966–970.

Martin, T. E., S. K. Auer, R. D. Bassar, A. M. Niklison, and P. Lloyd (2007). Geographic variation in avian incubation periods and parental influences on embryonic temperature. *Evolution* 61:2558–2569.

Martin, T. E., A. J. Boyce, K. Fierro-Calderón, A. E. Mitchell, C. E. Armstad, J. C. Mouton, and E. E. Bin Soudi (2017a). Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes. *Functional Ecology* 31:1231–1240.

Martin, T. E., J. C. Oteyza, A. J. Boyce, P. Lloyd, and R. Ton (2015). Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. *American Naturalist* 186:223–236.

Martin, T. E., M. M. Riordan, R. Repin, J. C. Mouton, and W. M. Blake (2017b). Apparent annual survival estimates of tropical songbirds better reflect life history variation when based on intensive field methods. *Global Ecology and Biogeography* 26:1386–1397.

Martin, T. E., R. Ton, and J. C. Oteyza (2018). Adaptive influence of extrinsic and intrinsic factors on variation of incubation periods among tropical and temperate passerines. *The Auk: Ornithological Advances* 135:101–113.

McAnulty, S. R., L. McAnulty, D. D. Pascoe, S. S. Gropper, R. E. Keith, J. D. Morrow, and L. B. Gladden (2005). Hyperthermia increases exercise-induced oxidative stress. *International Journal of Sports Medicine* 26:188–192.

McCafferty, D. J., S. Gallon, and A. Nord (2015). Challenges of measuring body temperatures of free-ranging birds and mammals. *Animal Biotelemetry* 3:1–10.

- McKechnie, A. E. (2022). Regulation of body temperature: patterns and processes. In Sturkie's Avian Physiology (C. G. Scanes and S. Dridi, Editors). 7th edition. Charlotte Cocks, London, pp. 1211–1244.
- McKechnie, A. E., and B. O. Wolf (2019). The physiology of heat tolerance in small endotherms. *Physiology* 34:302–313.
- Mitchell, A. E., F. Tuh, and T. E. Martin (2017). Breeding biology of an endemic Bornean turdid, the Fruithunter (*Chlamydochaera jefferyi*), and life history comparisons with *Turdus* species of the world. *The Wilson Journal of Ornithology* 129:36–45.
- Nilsson, J.-Å., M. N. Molokwu, and O. Olsson (2016). Body temperature regulation in hot environments. *PLoS ONE* 11:1–9.
- Nilsson, J. Å., and A. Nord (2018). Testing the heat dissipation limit theory in a breeding passerine. *Proceedings of the Royal Society B: Biological Sciences* 285:1–7.
- Nord, A., and J. Å. Nilsson (2019). Heat dissipation rate constrains reproductive investment in a wild bird. *Functional Ecology* 33:250–259.
- Nudds, R. L., and D. M. Bryant (2000). The energy cost of short flights in birds. *The Journal of Experimental Biology* 203:1561–1572.
- Oteyza, J. C., J. C. Mouton, and T. E. Martin (2021). Adult survival probability and body size affect parental risk-taking across latitudes. *Ecology Letters* 24:20–26.
- Part, T., L. Gustafsson, and J. Moreno (1992). “Terminal investment” and a sexual conflict in the Collared Flycatcher (*Ficedula albicollis*). *The American Naturalist* 140:868–882.
- Peach, W. J., D. B. Hanmer, and T. B. Oatley (2001). Do Southern African songbirds live longer

- than their European counterparts? *Oikos* 93:235–249.
- Pollock, H. S., J. D. Brawn, and Z. A. Cheviron (2021). Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. *Functional Ecology* 35:93–104.
- Porter, W. P., and D. M. Gates (1969). Thermodynamic equilibria of animals with environment. *Ecological Monographs* 39:227–244.
- Powers, D. R. (1992). Effect of temperature and humidity on evaporative water loss in Anna's Hummingbird (*Calypte anna*). *Journal of Comparative Physiology B* 162:74–84.
- Prinzinger, R., A. Prebmar, and E. Schleucher (1991). Body temperature in birds. *Comparative Biochemistry and Physiology* 99:499–506.
- Riechert, J., and P. H. Becker (2017). What makes a good parent? Sex-specific relationships between nest attendance, hormone levels, and breeding success in a long-lived seabird. *The Auk: Ornithological Advances* 134:644–658.
- Sadowska, E. T., E. Król, K. M. Chrzascik, A. M. Rudolf, J. R. Speakman, and P. Koteja (2016). Limits to sustained energy intake. XXIII. Does heat dissipation capacity limit the energy budget of lactating bank voles? *Journal of Experimental Biology* 219:805–815.
- Sanz, J. J., and J. M. Tinbergen (1999). Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the Great Tit *Parus major*. *Behavioral Ecology* 10:598–606.
- Scholer, M. N., M. Strimas-Mackey, and J. E. Jankowski (2020). A meta-analysis of global avian survival across species and latitude. *Ecology Letters* 23:1537–1549.

Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology* 208:1717–1730.

Speakman, J. R., and E. Król (2010a). The heat dissipation limit theory and evolution of life histories in endotherms- time to dispose of the disposable soma theory? *Integrative and Comparative Biology* 50:793–807.

Speakman, J. R., and E. Król (2010b). Maximal heat dissipation capacity and hyperthermia risk: Neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* 79:726–746.

Sukhchuluun, G., X.-Y. Zhang, Q.-S. Chi, and D.-H. Wang (2018). Huddling conserves energy, decreases core body temperature, but increases activity in Brandt 's voles (*Lasiopodomys brandtii*). *Frontiers in Physiology* 9:1–10.

Tapper, S., J. J. Nocera, and G. Burness (2020a). Heat dissipation capacity influences reproductive performance in an aerial insectivore. *Journal of Experimental Biology* 223:1–9.

Tapper, S., J. J. Nocera, and G. Burness (2020b). Experimental evidence that hyperthermia limits offspring provisioning in a temperate-breeding bird. *Royal Society Open Science* 7:1–12.

Tewksbury, J. J., R. B. Huey, and C. A. Deutsch (2008). Putting the heat on tropical animals. *Science* 320:1296–1297.

Thompson, M. L., S. J. Cunningham, and A. E. McKechnie (2018). Interspecific variation in avian thermoregulatory patterns and heat dissipation behaviours in a subtropical desert. *Physiology and Behavior* 188:311–323.

- Tinbergen, J. M., and M. W. Dietz (1994). Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Function* 5:563–572.
- Tinkle, D. W. (1969). The concept of reproductive effort and its relation to the evolution of life histories of lizards. *The American Naturalist* 103:501–516.
- Valencak, T. G., K. Hackländer, and T. Ruf (2010). Peak energy turnover in lactating European hares: A test of the heat dissipation limitation hypothesis. *The Journal of Experimental Biology* 213:2832–2839.
- van de Ven, T. M. F. N., A. E. McKechnie, and S. J. Cunningham (2019). The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia* 191:205–215.
- Walsberg, G. E., and J. R. King (1978). The energetic consequences of incubation for two passerine species. *The Auk* 95:644–655.
- Weathers, W. W. (1977). Temperature regulation in the Dusky Munia, *Lonchura fuscans* (Cassin) (Estrildidae). *Australian Journal of Zoology* 25:193–199.
- Weathers, W. W. (1997). Energetics and thermoregulation by small passerines of the humid, lowland tropics. *The Auk* 114:341–353.
- Weathers, W. W., and C. I. van Riper (1982). Temperature regulation in two endangered Hawaiian Honeycreepers: The Palila (*Psittirostra bailleui*) and the Laysan Finch (*Psittirostra cantans*). *The Auk* 99:667–674.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's

principle. *The American Naturalist* 100:687–690.

Wolf, B. O., and G. E. Walsberg (2000). The role of the plumage in heat transfer processes of birds. *American Zoologist* 40:575–584.

TABLES

Table 1. Linear mixed-effects model of factors explaining variation in arrival body temperature (°C) of parents caring for eggs and nestlings. Arrival body temperatures are defined as the first body temperature recorded following a period greater than 45 seconds off the nest in adults caring for eggs or nestlings. Individual ID was included as a random effect to account for repeated measures of individuals.

Variable	β	SE	df	t-value	P
Marginal $R^2 = 0.404$, Conditional $R^2 = 0.851$					
Young (3)	0.77	0.11	1124.0	7.32	< 0.001
Time of day	0.01	6.82e-04	1119.0	20.54	< 0.001
Time of day ²	-9.52e-06	4.68e-07	1119.0	-20.35	< 0.001
Total Age	0.18	0.01	1013.0	13.27	< 0.001
Sex	9.53e-03	0.51	23.2	0.02	0.985
Clipping treatment (Y)	-0.53	0.34	453.2	-1.58	0.115
Clipping (Y) * Time of day	-9.28e-04	1.81e-04	1112.0	-5.13	< 0.001
Clipping (Y) * Sex (M)	1.07	0.36	504.4	2.95	0.003

Only significant ($p < 0.05$) and marginally significant predictor variables were included in final models aside from clipping treatment, which was kept regardless of significance. Maximum daily air temperature and the presence of rain during sampling were tested as predictor variables but excluded due to non-significance.

Table 2. Linear mixed-effects model of factors explaining variation in daily provisioning rate per hour of parents caring for nestlings. Individual ID was included as a random effect to account for repeated measures of individuals.

Variable	β	SE	df	t-value	P
Marginal $R^2 = 0.277$, Conditional $R^2 = 0.278$					
Age	0.25	0.08	25.2	3.32	0.003
Clipping treatment (Y)	0.25	0.22	21.1	1.15	0.26

Only significant ($p < 0.05$) predictor variables were included in final models aside from clipping treatment, which was kept regardless of significance. Maximum daily air temperature, sex, number of young, and a clipping treatment-sex interaction were tested but excluded due to non-significance.

Table 3. Linear mixed-effects model of factors explaining variation in daily nest attentiveness, measured as the average proportion of time per hour parents spent on the nest incubating or brooding. Individual ID was included as a random effect to account for repeated measures of individuals.

Variable	β	SE	df	t-value	P
Marginal $R^2 = 0.463$, Conditional $R^2 = 0.520$					
Total Age	323.97	176.62	40.9	1.83	0.07
Total Age ²	-10.15	5.50	40.9	-1.85	0.07
Clipping treatment (Y)	574.30	165.82	18.2	3.46	0.003
Sex (M)	-107.63	164.71	20.5	-0.65	0.52
Clipping (Y): Sex (M)	-709.58	221.71	17.9	-3.20	0.005

Only significant and marginally significant ($p < 0.075$) predictor variables were included in final models aside from clipping treatment, which was kept regardless of significance. Maximum daily air temperature and number of young in the nest were tested as predictor variables but excluded due to non-significance.

FIGURES

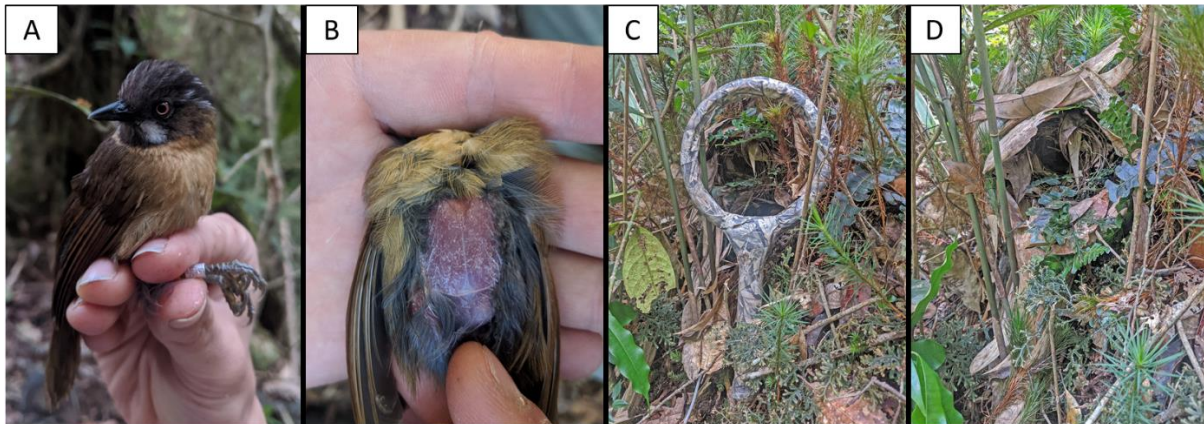


Figure 1. (A) Gray-throated Babbler (*Stachyris nigriceps*) in the hand and (B) receiving a 22% body surface area clipping treatment applied to the ventral feather tract. (C) PIT-tag antenna stationed at a Gray-throated Babbler nest entrance before and (D) after camouflaging.

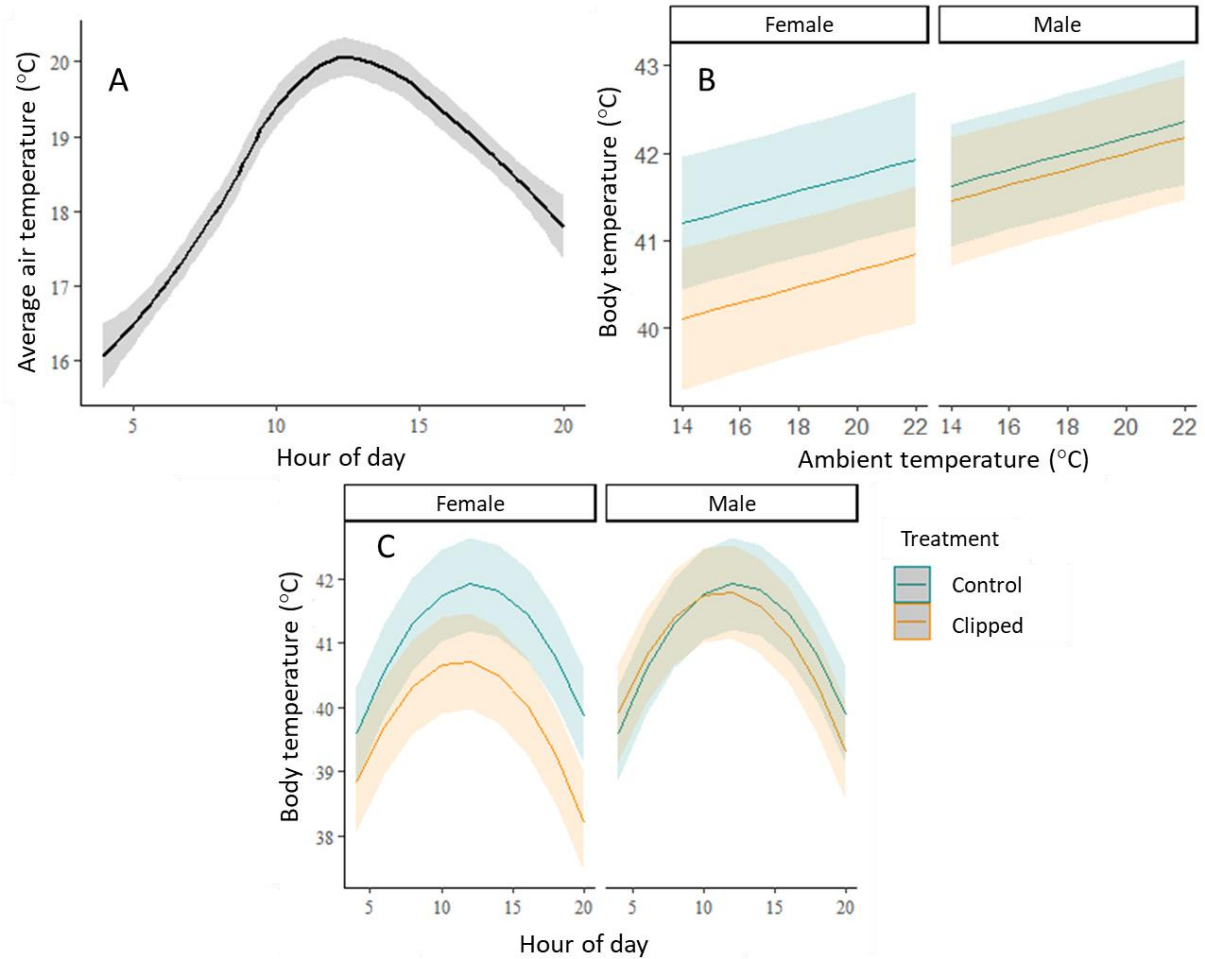


Figure 2. (A) Air temperatures (°C) averaged by hour for the duration of the 2020 breeding season (Feb.–Jun.). Data were collected from a weather station at 1520m elevation. (B) Mean estimated marginal effects and 95% confidence intervals showing the relationship between body and ambient temperature by clipping treatment and sex. (C) Mean estimated marginal effects and 95% confidence intervals showing the relationship between body temperature and time of day by clipping treatment and sex. Treatment legend refers to panels 2B and 2C.

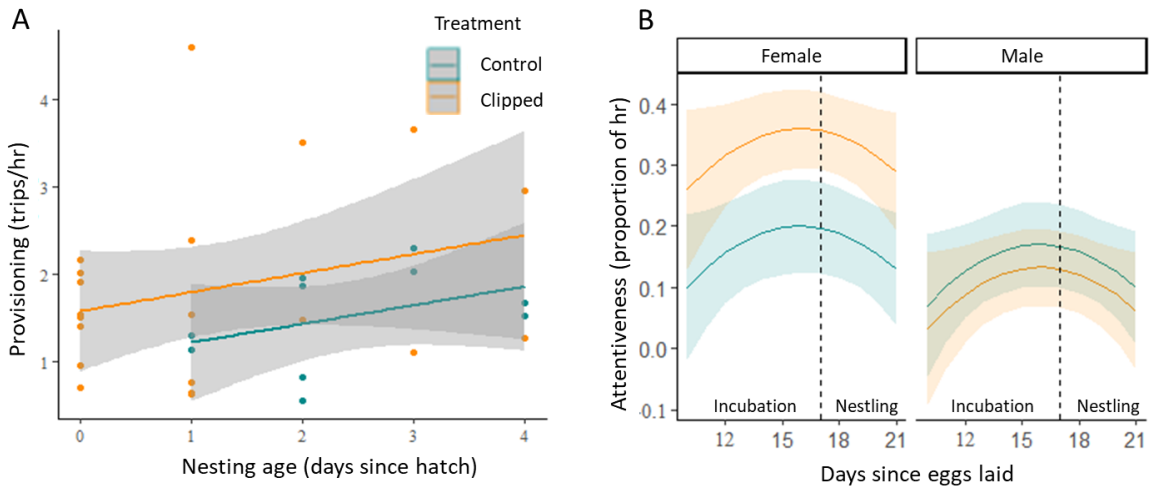


Figure 3. **(A)** The relationship between nestling age (days since hatch) and provisioning (average rate of trips/hr) by clipping treatment. Shaded areas denote 95% confidence intervals. **(B)** Mean estimated marginal effects and 95% confidence intervals showing the relationship between total age (measured in days since last egg laid) and nest attentiveness (measured as the average proportion of time per hour on the nest) by sex and clipping treatment. Vertical dashed lines denote mean hatch day. Adults were not target netted until mid to late incubation, so data are presented from mid incubation onwards. Treatment legend refers to both panels.

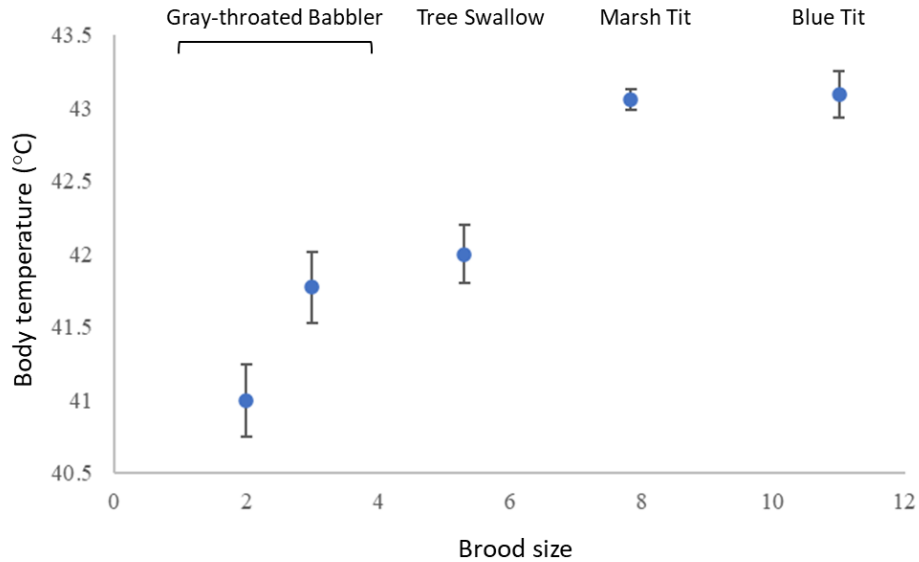


Figure 4. Average body temperatures (\pm standard error) vs. average brood size for breeding, free-living songbirds reported in the literature. Gray-throated Babbler body temperatures were calculated by brood size using a least squared means approach. Body temperatures and average brood sizes from other species were retrieved from Tapper et al. 2020b (tree swallow body temperature), Tapper et al. 2020a Dryad repository (tree swallow average brood size), Nord and Nilsson 2018 (marsh tit temperature and brood size), and Nilsson and Nord 2019 (blue tit temperature and brood size).