

RESEARCH ARTICLE

Heat dissipation capacity influences reproductive performance in an aerial insectivore

Simon Tapper^{1,*}, Joseph J. Nocera² and Gary Burness³

ABSTRACT

Climatic warming is predicted to increase the frequency of extreme weather events, which may reduce an individual's capacity for sustained activity because of thermal limits. We tested whether the risk of overheating may limit parental provisioning of an aerial insectivorous bird in population decline. For many seasonally breeding birds, parents are thought to operate close to an energetic ceiling during the 2–3 week chick-rearing period. The factors determining the ceiling remain unknown, although it may be set by an individual's capacity to dissipate body heat (the heat dissipation limitation hypothesis). Over two breeding seasons we experimentally trimmed the ventral feathers of female tree swallows (*Tachycineta bicolor*) to provide a thermal window. We then monitored maternal and paternal provisioning rates, nestling growth rates and fledging success. We found the effect of our experimental treatment was context dependent. Females with an enhanced capacity to dissipate heat fed their nestlings at higher rates than controls when conditions were hot, but the reverse was true under cool conditions. Control females and their mates both reduced foraging under hot conditions. In contrast, male partners of trimmed females maintained a constant feeding rate across temperatures, suggesting attempts to match the feeding rate of their partners. On average, nestlings of trimmed females were heavier than controls, but did not have a higher probability of fledging. We suggest that removal of a thermal constraint allowed females to increase provisioning rates, but additionally provided nestlings with a thermal advantage via increased heat transfer during maternal brooding. Our data provide support for the heat dissipation limitation hypothesis and suggest that depending on temperature, heat dissipation capacity can influence reproductive success in aerial insectivores.

KEY WORDS: Energy expenditure, Thermal constraint, Parental care, Climate change, Activity

INTRODUCTION

Rising global temperatures will cause animals to experience warmer than average annual temperatures and increased frequency of heat waves and droughts (IPCC, 2018). Such changing conditions will challenge animals to maintain body temperature within acceptable limits in the face of heat stress (McKechnie and Wolf, 2019). A rise

in body temperature above steady-state levels (i.e. hyperthermia) occurs when heat is generated and/or acquired from the environment faster than it can be dissipated (Speakman and Król, 2010a). Non-fatal hyperthermia can have several deleterious physiological consequences, including disrupted cellular signalling (Boulant, 1998); impaired synthesis and damage of proteins (Roti Roti, 2008); elevated levels of oxidative stress (Costantini et al., 2012); depressed innate and adaptive immune function (Palermo-Neto et al., 2013); and impaired growth and development (Baumgard and Rhoads, 2013).

Given the suite of physiological consequences that can develop from hyperthermia, the capacity to dissipate body heat has recently been proposed as a key factor shaping the behaviour, physiology and ecology of endotherms [the 'heat dissipation limitation' (HDL) hypothesis; Speakman and Król, 2010a]. Specifically, the HDL hypothesis posits that in endothermic animals, maximally sustained energy expenditure is limited by an individual's maximal capacity to dissipate body heat. Understanding the limits to sustained energy expenditure, or sustained metabolic rate (SusMR), is important because metabolic ceilings could impose constraints on life-history traits (Drent and Daan, 2002; Peterson et al., 1990; Speakman and Król, 2010b). For example, an energetic ceiling in chick-rearing birds could theoretically influence clutch size because parent birds can only feed a certain number of chicks based on their sustained level of energy expenditure (Monaghan and Nager, 1997; Peterson et al., 1990; Visser et al., 2019).

There are several lines of indirect evidence that support the HDL hypothesis. For instance, activity levels decline with high ambient temperature (Carroll et al., 2015; Theuerkauf et al., 2003; Zub et al., 2013); animals preferentially select habitats within their home range to escape solar radiation at the expense of resource acquisition (Lease et al., 2014; Street et al., 2015; van Beest et al., 2012); individual birds with bigger bills (larger 'thermal windows') are more active and spend more time singing on hot days than do birds with smaller bills (Luther and Danner, 2016).


While there exists indirect evidence from studies across different taxa, direct tests of the HDL hypothesis have primarily been performed on lactating laboratory rodents. For example, when lactating animals are experimentally exposed to cooler temperatures, they can increase energy intake and milk production beyond levels seen at warmer ambient temperatures (Hammond et al., 1994; Johnson and Speakman, 2001; Ohrnberger et al., 2016). Furthermore, when the fur of lactating rodents is shaved, they consume more food, produce more milk and have heavier offspring compared with non-shaved controls (Gamo et al., 2016; Król et al., 2007), suggesting that the capacity to dissipate heat places limits on performance.

Despite direct evidence of HDL for laboratory mammals, there have been few experimental studies testing the HDL hypothesis in free-ranging animals (Valencak et al., 2011). Recent studies, however, provided some experimental evidence for the HDL

¹Environmental and Life Sciences Graduate Program, Trent University, 1600 West Bank Drive, Peterborough, ON, Canada, K9L 0G2. ²University of New Brunswick, Forestry and Environmental Management, Fredericton, NB, Canada, E3B 5A3.

³Department of Biology, Trent University, Trent University, 1600 West Bank Drive, Peterborough, ON, Canada, K9L 0G2.

*Author for correspondence (simontapper@trentu.ca)

 S.T., 0000-0003-3237-291X; J.J.N., 0000-0002-5913-8851; G.B., 0000-0002-1695-7179

hypothesis in free-ranging birds (Nilsson and Nord, 2018; Nord and Nilsson, 2019; Andreasson et al., 2020). Nord and Nilsson (2019) removed the ventral plumage from male and female breeding blue tits, *Cyanistes caeruleus*, and found that feather-clipped parents had heavier nestlings than controls, while maintaining lower body temperatures and without additional mass loss. However, there were no differences in feeding rates between the treatments, and only older parents had heavier nestlings. This result suggests that the limit to SusMR might be influenced by life-history strategy, which could also explain why in some species (e.g. European Hare, *Lepus europaeus*) a HDL has not been found (Valencak et al., 2011).

Previous studies examining the limits to SusMR have largely focused on the influence of temperature on heat balance, while ignoring other environmental factors. Wind speed, relative humidity and precipitation, however, have been shown to play an important role in influencing foraging activity in birds, and in particular aerial insectivores (Cox et al., 2019; Ouyang et al., 2015; Rose, 2009). This is because wind carries heat away from the body via convection, and increasing wind speeds decrease heat gain from solar radiation (Wolf and Walsberg, 1996). Further, rates of evaporative water loss can be severely inhibited by high humidity, and thus variation in humidity could alter activity levels (Gerson et al., 2014). Therefore, testing the HDL hypothesis in free-ranging animals should attempt to control for these additional factors.

To determine whether heat dissipation constrains reproductive performance in breeding birds, we experimentally manipulated the ability of female tree swallows, *Tachycineta bicolor* (Vieillot 1808), to dissipate body heat, by removing feathers overlying the brood patch. Tree swallows are an excellent model species in which to test the HDL hypothesis. As aerial insectivores, they are active foragers, and can spend up to 16 h per day gathering insects to feed their nestlings. We predicted that if the ability to dissipate body heat limits SusMR, then (1) trimmed birds would maintain higher feeding rates than control birds, but only under warmer temperatures; (2) trimmed birds would have heavier offspring; and (3) offspring of trimmed birds would have greater fledging success than those of non-trimmed birds.

MATERIALS AND METHODS

Study area and species

All research was approved by the Trent University Animal Care Committee, in accordance with the Canadian Council on Animal Care (AUP no. 24747). We conducted this study in May–July 2017 and 2018, on two nest-box breeding populations of tree swallows located at the Trent University Nature Areas, Peterborough, ON, Canada (44°21'N, 78°17'W) and at the Lakefield Sewage Lagoon, Lakefield, ON, Canada (44°24'58.3"N, 78°15'26.8"W). The Trent Nature Areas consist of relatively open grassy fields, and there are about 70 boxes spaced ~10–20 m apart. The Lakefield Sewage Lagoon consist of two rectangular lagoons, surrounded by open grassy fields and farmland, and with 50 boxes encircling the perimeter that are spaced 10–20 m apart. The sites are situated ~10 km apart and should share similar weather patterns. Females at both sites typically lay clutches of 5–7 eggs, with one egg laid each day. Once a clutch is completed, females incubate the nest for approximately 14 days, and nestlings typically hatch synchronously. Nestlings typically fledge 18–22 days post-hatching (Winkler et al., 2011).

General field methods

Beginning in May each year, we checked nest boxes every other day until the presence of nest material was discovered, at which point

boxes were monitored every day until clutch completion. We used a marker pen to label eggs numerically in the sequence they were laid; the date the last egg was laid was considered to be day 0 of incubation and the date the first nestling hatched was considered to be day 0 of nestling provisioning.

Experimental manipulation

We captured females during early nestling provisioning (for capture protocol, see 'Remote monitoring of activity', below) and, upon capture, randomly assigned females to either a trimmed or control condition, based on a coin flip. In the trimmed condition, we removed the contour and downy feathers covering the brood patch (details below) to expose the bare skin underneath (Fig. S1). We chose to remove feathers from this region because (1) it is highly vascularized, increasing the chance of heat loss and (2) there would be minimal interference with flight. We also captured male swallows (see 'Remote monitoring of activity', below), but no males were trimmed.

We performed trimming manipulations with two people: one person held the bird ventral side up, while the other person, using surgical scissors, cut the feathers away. Control females were handled identically, but instead of cutting the feathers, we performed a 'mock cut', in which we cut the air above the brood patch. In 2018, we additionally measured the size of the exposed area for all trimmed females ($n=21$). We quantified both the length and width of the exposed skin using a piece of string. The median (\pm median absolute deviation, MAD) length of exposed skin was 3.1 ± 0.2 cm (range: 2.6–3.7 cm) and the median width of exposed skin (\pm MAD) was 1.9 ± 0.1 cm (range: 1.5–2.1 cm). Assuming the trimmed area was an ellipse, the amount of exposed skin would be 4.63 cm². The estimated percentage total surface area trimmed was ~7% (see Appendix for details). We are confident that this amount of trimming is sufficient to induce heat loss, as seen in similar treatments by Nord and Nilsson (2019) and implied in equations from Robertson et al. (2020) (see Appendix for details). Constriction of the vasculature in the exposed area around the brood patch would probably be insufficient to counter the energy loss induced by trimming.

Remote monitoring of activity

As an index of activity, we quantified provisioning rate of females using passive integrated transponder (PIT) tags. During late incubation (day 7–10 post-clutch completion), we captured females in their nest box and implanted PIT tags subcutaneously in the nape of the neck with either (1) non-temperature-sensitive (EM4100, no. 11001, GAO RFID, Pickering, ON, Canada) or (2) temperature-sensitive (Biotherm13, Biomark, Boise, ID, USA) PIT tags, following Nicolaus et al. (2011). Data on body temperature from the Biotherm13 tags are part of a parallel study. Following implantation, we recorded body mass, wing chord (flattened), head–bill length and exposed culmen (*sensu* Borras et al., 2000), and determined age (second year or after second year) based on plumage coloration (Hussell, 1983). Total time in the hand was, on average, approximately 12 min. Details regarding the PIT tag reader set-up are described in the Appendix.

On day 1–2 post-hatch, we captured females again and performed the experimental manipulation (control versus trimmed), recorded body mass and obtained a 50–75 μ l blood sample from the brachial vein as part of a parallel study. At day 10 of provisioning, we again measured body mass and collected a second blood sample.

Because tree swallows have biparental care, and we wanted to control for the effect of male provisioning activity on nestling

growth, we attempted to capture untagged males between days 4 and 6 of provisioning ($n=23/37$, 62% of untagged males), although we also caught individuals opportunistically outside of this period (days 1–11). Upon capture, we equipped each bird with a PIT tag and recorded the same morphometric data as for females during the late incubation capture.

We obtained data for six females and five males from both years of the study. We attempted in 2018 to give each female bird the opposite treatment that it received in 2017, but in an effort to keep sample sizes within the treatments roughly balanced, four individuals received the opposite treatment and two received the same treatment.

Nestling measurements

We measured nestlings between ~12:00 h and 18:00 h. To determine the effect of maternal treatment on nestling growth rate, we weighed nestlings on days 0 (hatching), 3, 6, 9 and 12 (i.e. peak body mass). We did not handle nestlings beyond day 12 to prevent premature fledging. In 2017, we weighed nestlings on a spring and digital scale and in 2018 on a digital scale only. This did not affect our conclusions, but see Appendix for details. As an index of nestling body size, we measured wing chord on day 12 using a wing-rule (with a stop). As part of another study, we collected a blood sample (~75 μ l) from each nestling on day 12. Fledging success was determined after checking all nest boxes on day 18 post-hatch, and on the following days until fledging completion. There were no instances of premature fledging as a consequence of checking the nest box.

Data compilation and organization

Feeding rate

Most adult females were caught when nestlings were 1–2 days of age (see details in ‘Remote monitoring of activity’, above), and we therefore only included feeding rate data between nestling ages 3–14 days; we also only used data collected between the hours of 05:00 h and 21:00 h because swallows at our study sites were relatively inactive outside of this window (S.T., unpublished data). Our feeding rate data range from 1 June 2017 to 29 June 2017 and from 31 May 2018 to 11 July 2018.

For data organization and statistical analyses, we used R (version 3.5.1, R Core Team; <http://www.R-project.org/>). To transform raw RFID reads into visits to the nest box, we used the function ‘visits’ from the package *feedr* (LaZerte et al., 2017). We considered repeated reads from the same individual as a singular event if successive reads were <60 s apart. Our RFID data do not allow us to distinguish brooding from feeding visits, and so we considered all trips to the nest box as feeding rate; although this assumption is erroneous, we anticipate the error to be roughly equal among all nests in the study. We defined feeding rate as the total number of visits per day divided by the total number of hours per day. We included each hour in the total number of hours spent provisioning if there was at least one read in the hour of interest. We chose this definition over a more typical provisioning rate (e.g. number of visits per 16 h, 05:00 h to 21:00 h) because of unequal numbers of observations across birds. Unequal observations were due to (1) birds with thermal tags having fewer overall hours of data (as a result of cycling of readers among boxes) and (2) because some birds had missing data as a result of equipment failure. This definition provides a more unbiased measure of feeding rate compared with one in which the total number of hours across all birds was assumed to be the same.

Environmental variables

We gathered data on daily mean ambient temperature ($^{\circ}$ C; hereafter referred to as T_a), wind speed (km h^{-1}), relative humidity (%) and total precipitation (mm) from Trent University’s weather station, which is located approximately 1.5 km from the Trent University Nature Areas and 9.5 km from the Sewage Lagoon, respectively (downloadable from Environment Canada; http://climate.weather.gc.ca/index_e.html).

Statistical analyses

For all analyses (i.e. feeding rate, nestling body mass, fledging success), we excluded nests that did not result in at least one fledgling. Unless otherwise stated, model parameters were estimated by restricted maximum likelihood; degrees of freedom and P -values were calculated using the Satterthwaite approximation in the *lmerTest* package (version 3.1.0; Kuznetsova et al., 2017); and confidence intervals (CI) were calculated with the Wald method in the *lme4* package (version 1.1-20; Bates et al., 2015). Means (\pm s.e.m.) reported are estimated marginal means, generated using the *emmeans* package (version 1.3.2; <https://CRAN.R-project.org/package=emmeans>). We considered $P \leq 0.05$ as statistically significant. We checked that our models met assumptions of normality and homogeneity of variance by visual inspection of the residuals.

Feeding rate

We tested for an effect of experimental treatment (trimmed or control) on maternal feeding rate (expressed as visits h^{-1}), and separately on paternal feeding rate, in two separate linear mixed effects models (*lme4*). We ran models for each sex because our feeding rate data for males captured a smaller range of T_a compared with that for females (males: 11–24 $^{\circ}$ C; females: 10.8–27.8 $^{\circ}$ C), and so we did not want to extrapolate our predictions for males outside of the T_a that they experienced. We chose not to include male feeding rate as a covariate in our model because males had fewer observations (i.e. total number of days of feeding visits) compared with females ($n=310$ male observations, $n=483$ female observations), which would have reduced our sample size for females. Our feeding rate analysis included a total of 55 females ($n=28$ control, $n=27$ trimmed) and 42 males ($n=24$ control, $n=19$ trimmed). We included treatment, brood size, lay date, chick age, year and the following environmental variables as main effects in our model: T_a , wind speed, relative humidity and total precipitation. To test whether the effects of maternal treatment were temperature dependent, we also included a treatment \times T_a interaction term. We checked for collinearity between our predictors by running a variance inflation factor test (‘vif’ function, *Car* package, version 3.0-3; Fox and Weisberg, 2019), and did not find evidence of variance inflation among our predictors (all VIF <3). In each year, we standardized lay date so that the first day on which a female laid an egg was given a value of 0. Males were given the same lay date as their partner. We did not control for breeding site in our model because in our study population, site is highly correlated with lay date: birds from the Sewage Lagoon laid their eggs approximately 2 weeks earlier than birds from the Trent Nature Areas (S.T., unpublished data). We also ran initial models with nestling age as a predictor, but this term was not significant ($P > 0.30$) and did not change our results; as a result, we left it out to reduce the number of terms in our final model. Our treatment sample sizes, however, were balanced between study sites (females: Sewage Lagoon: $n=18$ control, $n=16$ trimmed; Nature Areas: $n=10$ control, $n=11$ trimmed). In each model, we controlled for repeated observations from the

same individual across days and years by including bird (maternal or paternal) identity as a random effect.

After running the initial models and assessing diagnostic plots, we detected three observations (two in the female model, one in the male model) with standardized residuals that fell at least two standardized deviations from all other residuals. These observations were from the same nest and occurred within the same 2 days. Exclusion of these points (3 out of 793) improved the fit of both the female and male models, and so they were excluded from the analysis.

Nestling morphology and fledging success

We tested for differences in nestling growth rate between treatments using a three-parameter logistic growth curve, which has been shown to model tree swallow growth accurately (McCarty, 2001; Zach and Mayoh, 1982). At each age (i.e. 0, 3, 6, 9, 12 days post-hatch), we calculated the average nestling mass, per brood, and used this as our dependent variable, because we did not track individual nestlings in 2017. There was a total of 28 and 30 nests for control and trimmed birds, respectively.

We constructed the growth curve model using the 'nlme' function from the nlme package (version 3.1-137; Pinheiro et al., 2014). To describe the patterns of nestling growth, we calculated three parameters from the growth curve: the asymptotic mass (A ; i.e. peak mass in grams, ~day 12 post-hatch), the inflection point (I ; i.e. point of steepest growth) of the growth curve (in days), and the growth rate constant (K ; i.e. steepness of the growth curve). We estimated our parameter starting values using the 'SSlogis' function from the stats package (base R).

We included 'maternal identity' as a random intercept on the asymptotic parameter to control for statistical non-independence in the growth rate among nestlings that were from the same females. A random intercept for 'maternal identity' was initially applied to all growth rate parameters (A , K , I); however, application of a random intercept to the asymptotic parameter alone explained the greater variance in our data (see Appendix, Table A1, for more details). We also included brood size as a covariate to control for the possibility that larger broods have smaller chicks. We calculated confidence intervals and predictions using bootstrapping with replacement based on 1000 replications.

We tested for differences in day 12 nestling wing length between treatments using a linear mixed-effects model (lme4). Our model included main effects of treatment, lay date (standardized), year, brood size (at day 12), and maternal identity as a random effect to control for both statistical non-independence of returning mothers ($n=6$) between years and nestlings within the same brood.

To determine whether treatment affected an individual nestling's fledging success, which we defined as either 1 (fledged) or 0 (did not fledge), we used a generalized linear mixed model (glmer function in lme4) with a binomial error distribution and a logit link. We used the same model structure as we did for nestling wing length, except that we used brood size at day 0 (hatch) to control for the number of nestlings in each nest on fledging success. After plotting the predictions from the model, we noticed differences in variance between treatments, and subsequently ran an F -test (using the var.test function in stats package, base R) on the predicted probabilities from the model. Results from the F -test confirmed violation of homogeneity of variance ($F_{162,145}=5.290$, 95% CI [3.84, 7.26], $P<0.0001$) and we re-ran our model weighting for treatment (using the 'weights' argument) to control for the heteroscedasticity in the residuals.

RESULTS

Maternal feeding rate

On average, maternal feeding rate (mean±s.e.m.) for control and trimmed females was 11.7 ± 0.55 and 11.5 ± 0.53 visits h^{-1} , respectively. Feeding rate was negatively related to the three environmental control variables: wind speed, relative humidity and total precipitation (Table 1), indicating that birds foraged less on windy, rainy and more humid days. Feeding rate differed significantly between treatments as a function of T_a (i.e. treatment× T_a , $P=0.001$; Fig. 1A, Table 1). At the highest T_a (~27°C), trimmed birds made ~26% more trips per hour (12.02 visits h^{-1} trimmed versus 9.51 visits h^{-1} control, 40.16 extra visits given a 16 h day) than controls. At the lowest T_a (~11°C), however, trimmed birds made 23% fewer trips per hour (8.66 visits h^{-1} trimmed versus 10.69 visits h^{-1} control, 33 visits, given a 16 h day) than control birds. Feeding rate increased with brood size ($P=0.002$; Table 1); females raising larger broods (7 nestlings) made ~3 more visits to the nest per hour than mothers raising small broods (3 nestlings). Provisioning rate was not related to lay date ($P=0.191$; Table 1).

Paternal feeding rate

On average, paternal feeding rate (mean±s.e.m.) for mates of control and trimmed females was 10.5 ± 0.66 and 11.6 ± 0.79 visits h^{-1} , respectively. Male feeding rate was significantly and negatively related to total precipitation, but not to relative humidity and wind speed (Table 2). Paternal feeding rate differed significantly with maternal treatment as a function of T_a (i.e. treatment× T_a , $P=0.032$; Fig. 1B, Table 2). Partners of trimmed females maintained a consistent feeding rate across T_a , and had higher feeding rates than their female partners at low T_a , while partners of control females decreased their feeding rate with increasing T_a . At the highest T_a (~24.5°C), partners of trimmed females made ~35% more trips per hour (10.49 visits h^{-1} trimmed versus 7.75 visits h^{-1} control, 44 extra visits given a 16 h day). As for their female partners, feeding rate increased with brood size, although for males, this relationship was not statistically significant ($P=0.087$; Table 2).

Nestling morphology and fledging success

Nestlings from trimmed mothers were heavier (mean±s.e.m.) by 1.74 ± 0.58 g at their asymptote (~day 12 post-hatch) compared with nestlings from control mothers at their asymptote (i.e. treatment, $P=0.002$; Fig. 2, Table 3). We did not detect any significant differences in the inflection point (~day 5 post-hatch) between groups ($P=0.190$; Table 3), nor in the growth rate constant (i.e. steepness of curves) between groups ($P=0.312$; Table 3). Brood size was negatively related to asymptotic mass ($P=0.018$; Table 3) and

Table 1. Factors contributing to variation in the feeding rate of female tree swallows

Predictor	Estimate	95% CI	P -value
Intercept	17.27	12.45, 22.08	<0.001
Mean wind speed	-0.30	-0.39, -0.20	<0.001
Mean relative humidity	-0.08	-0.11, -0.05	<0.001
Total precipitation	-0.05	-0.10, 0.00	0.033
Mean T_a	-0.07	-0.19, 0.05	0.239
Brood size	0.85	0.15, 1.55	0.017
Year	0.001	-0.98, 0.98	0.998
Lay date	-0.08	-0.20, 0.04	0.189
Treatment	-4.93	-8.02, -1.83	0.002
Treatment× T_a	0.27	0.10, 0.43	0.001

T_a , ambient temperature. Fixed effect coefficient estimates with 95% confidence intervals (CI) and P -values (bold indicates statistical significance).

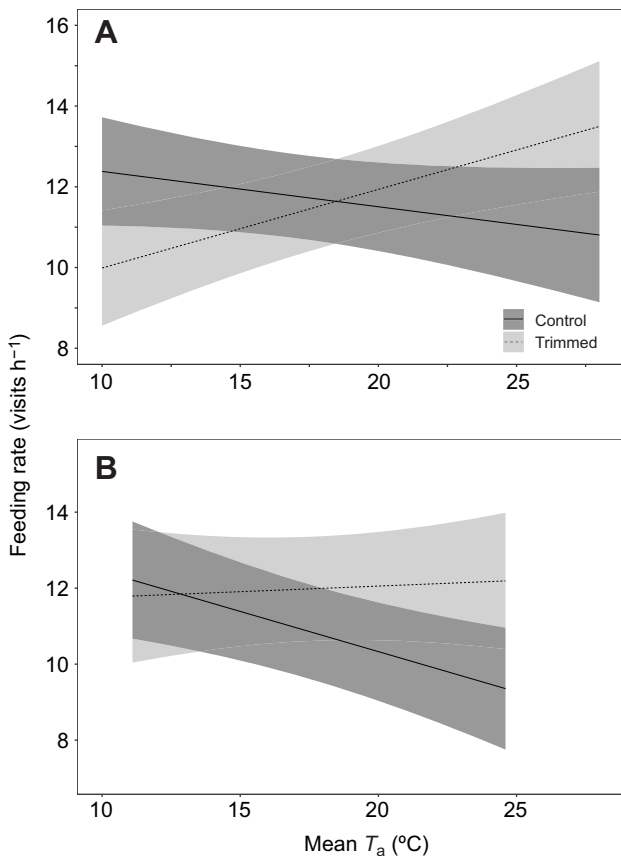


Fig. 1. Effect of maternal treatment on provisioning rate across mean daily ambient temperature in tree swallows. (A) Control and trimmed females differed in their feeding rate as a function of ambient temperature (T_a ; $P=0.001$), as determined by a linear mixed effect model. (B) Male partners of control and trimmed females also differed in their feeding rate with respect to T_a ($P=0.032$), as determined by a linear mixed effect model. Bands around lines represent the 95% confidence interval (CI). Note that the temperature range we observed for females and males differs. Sample sizes by sex and treatment: $n=28$ control, $n=27$ trimmed females; $n=18$ control, $n=24$ trimmed males.

the inflection point ($P=0.010$; Table 3), meaning that larger broods had lighter nestlings at their peak mass compared with smaller broods, despite reaching their point of steepest growth earlier. Wing length at day 12 did not statistically differ between treatments ($\beta=0.17$, 95% CI $[-0.03, 0.38]$, $P=0.093$), although nestlings in

Table 2. Factors contributing to variation in the feeding rate of male tree swallows

Predictor	Estimate	95% CI	<i>P</i> -value
Intercept	10.66	3.58, 17.73	0.003
Mean wind speed	-0.01	-0.13, 0.11	0.898
Mean relative humidity	-0.01	-0.05, 0.02	0.407
Total precipitation	-0.07	-0.13, -0.00	0.036
Mean T_a	-0.20	-0.35, -0.06	0.005
Brood size	0.88	-0.13, 1.88	0.087
Year	1.22	-0.74, 3.18	0.223
Lay date	-0.07	-0.27, 0.12	0.452
Treatment	-3.03	-7.23, 1.17	0.158
Treatment $\times T_a$	0.23	0.02, 0.45	0.032

Treatment refers to the treatment of the female partner; males were not manipulated. T_a , ambient temperature. Fixed effect coefficient estimates with 95% confidence intervals (CI) and *P*-values (bold indicates statistical significance).

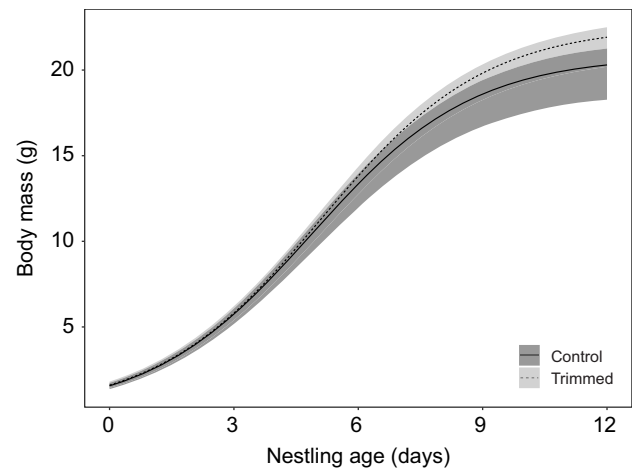


Fig. 2. Estimated growth trajectories of nestlings from control broods and those in which females had been trimmed. Growth rates were modelled using a three-parameter logistic regression. Bands around lines represent the 95% CI obtained from bootstrapping ($n=1000$ iterations). Nestlings of trimmed mothers had a greater asymptotic mass than nestlings of control mothers ($P=0.002$). There were 309 nestlings from 58 nests ($n=30$ control, $n=28$ trimmed).

2017 had longer wings than nestlings in 2018 (i.e. year, $\beta=-0.38$, 95% CI $[-0.57, -0.20]$, $P<0.001$). Wing length was negatively related to lay date ($\beta=-0.03$, 95% CI $[-0.05, -0.01]$, $P=0.009$), and was not significantly related to brood size ($\beta=0.04$, 95% CI $[-0.09, 0.18]$, $P=0.541$).

The mean (\pm s.e.m.) probability of fledging was higher for nestlings in trimmed ($97.9\pm 0.01\%$) compared with control broods ($94.3\pm 0.03\%$), but this difference was not statistically significant (odds ratio=2.90, 95% CI $[0.82, 10.25]$, $P=0.098$; Fig. 3), and did not differ significantly between years (odds ratio=2.83, 95% CI $[0.84, 9.59]$, $P=0.094$). The probability of fledging, however, was more variable for control compared with trimmed birds, as stated above in Materials and Methods ($F_{162,145}=5.290$, 95% CI $[3.84, 7.26]$, $P<0.0001$). Lay date was negatively related to fledging success (odds ratio=0.86, 95% CI $[0.75, 0.98]$, $P=0.023$), and brood size at hatching was also negatively related to fledging success (odds ratio=0.37, 95% CI $[0.17, 0.79]$, $P=0.010$).

DISCUSSION

We found that the ability to dissipate body heat affected the reproductive performance of female tree swallows in a context-dependent manner, providing partial support for the HDL hypothesis. An individual's feeding rate depended on the interactive effects of T_a and treatment: when it was hot, trimmed

Table 3. Parameter estimates for nestling growth trajectories

Parameter	Predictors	Estimates	95% CI	<i>P</i> -value
Asymptote (A)	Intercept	24.32	21.57, 28.00	<0.0001
	Treatment	1.74	0.75, 3.05	0.002
	Brood size	-0.67	-1.37, -0.17	0.018
Inflection point (I)	Intercept	6.14	5.25, 7.15	<0.0001
	Treatment	0.17	-0.09, 0.46	0.190
	Brood size	-0.24	-0.42, -0.08	0.010
Growth rate constant (K)	Intercept	1.94	1.45, 2.46	<0.0001
	Treatment	0.08	-0.08, 0.26	0.312
	Brood size	-0.01	-0.11, 0.08	0.824

Fixed effect coefficients with bootstrapped 95% confidence intervals (CI) and *P*-values (bold indicates statistical significance).

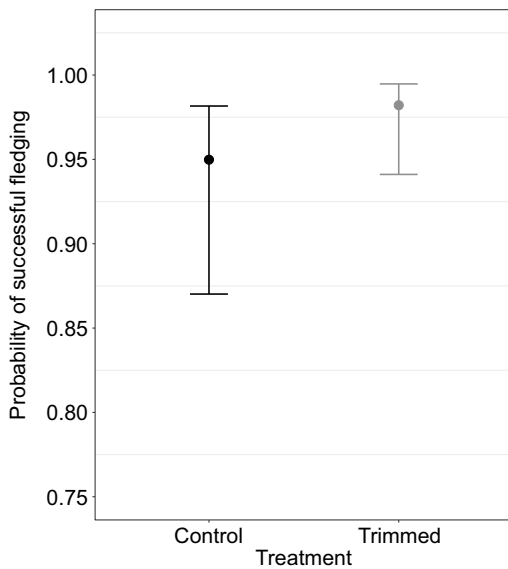


Fig. 3. Predicted probability of nestling fledging success as a function of treatment. Data are means \pm 95% CI, converted from odds ratios to probabilities. Maternal treatment (i.e. trimming) did not influence probability of fledging (generalized linear mixed model, $P=0.069$), but instead influenced the variance in individual fledging success (F -test, $P<0.0001$). There were 309 nestlings from 58 nests ($n=30$ control, $n=28$ trimmed).

females provisioned their offspring more than control birds, but this pattern was reversed when it was cool (Fig. 1A).

The relatively higher activity rates of trimmed females at high T_a compared with control birds is consistent with studies from the literature on mammals, in which experimental fur removal in mice allows for higher sustained energy expenditure during lactation, as measured via increases in food intake and milk production (Gamo et al., 2016; Król et al., 2007). It is also consistent with the idea that different mechanisms (e.g. heat dissipation versus peripheral limitation) can constrain SusMR in different circumstances (Wen et al., 2017). For instance, when laboratory mice are at cool temperatures (21°C), milk production during lactation is limited by the capacity of the mammary glands (i.e. the limitation is found in the peripheral tissues). In contrast, under warm conditions (30°C), maximal milk production appears to be limited by the capacity of an individual to dissipate heat (Wen et al., 2017).

At low T_a , trimmed females may have faced higher thermoregulatory costs compared with control females. Although we did not quantify heat transfer of the brood patch/trimmed area between treatments, we removed approximately 7% of the plumage from trimmed birds, which presumably led to increased heat transfer to the environment. In a similar study, Nord and Nilsson (2019) trimmed ~22% of the total surface area of male and female blue tits, resulting in an approximate 47% increase in estimated heat transfer. Assuming a similar ratio, tree swallow females with trimmed brood patch feathers would have had a ~15% increase in heat transfer. At low T_a , this would increase metabolic costs (Szafrńska et al., 2014), which may have led to trimmed birds devoting more time to feeding themselves than their young, or more time brooding in their nest boxes.

Paternal feeding rate differed as a function of maternal treatment and T_a (Fig. 1B). Male partners of control females decreased their feeding rate as T_a increased, as would be expected if males were at risk of overheating. Male partners of trimmed females, however, maintained a consistent feeding rate across T_a . One reason for this may be that tree swallow males may attempt to match their level of

parental effort to those of their partners (Lendvai et al., 2018), although we did not formally test this. But if the activity of tree swallows is constrained by the risk of overheating, then males of trimmed females should not be able to maintain a constant provisioning rate at higher T_a . Indeed, at high T_a , male partners of trimmed females tended to feed their nestlings less frequently than did their mates (at 24.6°C, 11.84 \pm 0.89 visits h⁻¹ for males, 12.80 \pm 0.66 visits h⁻¹ for females, means \pm s.e.m.). This suggests male partners of trimmed females may be unwilling or unable to increase their feeding rate to fully match that of their mate, which is consistent with the HDL hypothesis. A formal test of this would require including males and females in the same model, with a three-way interaction between sex, treatment and temperature, and associated *post hoc* analysis. This analysis was beyond the scope of the current study, which did not seek to understand within-treatment (and between-sex) differences in feeding rate. In contrast, at low T_a , male partners of trimmed females fed their offspring more frequently than their mates (at 11.1°C, 11.42 \pm 0.97 visits h⁻¹ for males, 10.20 \pm 0.68 visits h⁻¹ for females, means \pm s.e.m.). This may be because trimmed females spend more time brooding than control females, which could occur if trimmed females sought to minimize heat loss at low T_a by sitting on their brood. In contrast to our results, Nord and Nilsson (2019) found no effect of feather trimming on either female or male provisioning rate in blue tits. The authors suggested that feather-trimmed individuals may have increased their foraging effort by means other than nest visit rate, such as by increasing the quantity of prey brought back to chicks. This could also be the case in our study if enhanced heat dissipation allowed individuals to offset the thermal load that would arise from carrying larger masses of food (*sensu du Plessis et al., 2012*).

We predicted that as a result of increased maternal activity rates, nestlings of trimmed females would be heavier than nestlings of controls. In line with this prediction, trimmed females had nestlings that reached a higher asymptotic mass (~day 12 post-hatch; Fig. 2). However, this increase in mass is unlikely to be due to maternal feeding rate alone, because trimmed birds had mates with relatively higher feeding rates across T_a than mates of controls. Additionally, we cannot discount the possibility that trimmed females transferred more heat to their offspring during brooding than did control mothers. Tree swallow nestlings do not develop feathers until around 6–7 days post-hatch (Marsh, 1980), and mothers typically continue brooding until swallows reach 5 days of age (McCarty, 1996). It is plausible that the 7% difference in plumage coverage, and consequently difference in heat transfer, between treatments contributed to increased growth and survivorship (Dawson et al., 2005; Klaassen et al., 1994; Pérez et al., 2008). For instance, if nestlings were experiencing cool temperatures and responded by increasing metabolic rate (Nord and Nilsson, 2011), then nestlings from trimmed broods receiving direct heat transfer from the enlarged bare skin surface would have had more energy to put into growth rather than maintaining homeothermy. Nestlings from trimmed broods may also have been heavier than controls because of adults providing nestlings with different quantities or quality of food (Sofaer et al., 2018; Twining et al., 2016).

We predicted that in addition to producing heavier nestlings at day 12, nestling fledging success would be greater in trimmed compared with control broods. In line with this prediction, there was a trend toward higher fledging success in trimmed compared with control broods ($P=0.098$) and fledging success was also less variable compared with that of control broods (Fig. 3). This suggests lower overall mortality for nestlings in trimmed compared with

control broods. In birds, fledging success is typically correlated with post-fledging survival and recruitment (McCarty, 1996; Naef-Daenzer and Gruebler, 2016). While we do not have the data to examine post-fledging survival, it is possible that less variance around fledging success for trimmed birds could also mean less variability in post-fledging survival, which would suggest a possible fitness benefit for trimmed birds.

In conclusion, our data demonstrate that heat dissipation capacity is an important factor influencing female tree swallow behaviour and breeding success. Even a small adjustment to the ventral plumage caused individual birds to modulate their activity levels, as measured indirectly via provisioning rate. Our study also highlights a likely reason why birds mostly keep their plumage during the breeding season: because cool weather can increase thermoregulatory demands and negatively affect foraging rate. In addition to warming temperatures, climate change may also reduce the food supply of breeding aerial insectivores (Irons et al., 2017; Winkler et al., 2013). A reduced food supply may necessitate additional foraging effort, exacerbating the risk of overheating. This may put additional physiological stress on breeding birds, which could lead to reduced nest success (van de Ven et al., 2019) and exacerbate population declines.

As global temperature and frequency of heat waves increase (IPCC, 2018), the physiological parameter of heat balance will be of higher concern for many birds, including aerial insectivores, such as tree swallows. Although the birds in our study did not experience temperatures beyond their body temperature (S.T., unpublished data), we provide evidence that even under non-extreme conditions, an inability to dissipate heat adequately could have fitness consequences. The capacity of tree swallows and other aerial insectivores to increase thermal tolerance via non-reversible phenotypic plasticity or local thermal adaptation remains unknown. Such adjustments, however, may provide individuals with the capacity to maintain high activity levels in the face of extreme climatic events (McKechnie and Wolf, 2019).

APPENDIX

Estimated percentage of trimmed surface area

To approximate the proportional amount of surface area of the ventral plumage of female swallows that we exposed, we divided the estimated surface area of the trimmed region (4.63 cm²; Fig. A1) by the total body surface area of the external plumage (66.7 cm²; 4.63/66.7=6.9%). We used the total surface area of the external plumage of a similarly sized species, the dark-eyed junco (*Junco hyemalis*; mass 19.4 g, total surface area of exposed plumage 66.7 cm²; Walsberg and King, 1978) as our estimate for tree swallows (*sensu* Nord and Nilsson, 2019). Tree swallow mass during the breeding season ranges from 17 to 22 g (Winkler et al., 2011).

Table A1. Model selection results for determining the optimal random effect structure in the nestling growth rates model

Random effect structure	ΔAIC	AIC	log(L)	Number of parameters
Asymptote (A)	0.00	911.64	-448.18	11
Inflection point (I)	78.14	989.78	-483.89	11
Growth rate constant (K)	116.53	1028.17	-503.08	11

We assigned a random intercept on the asymptote, inflection point or growth rate constant. The variance explained by the random intercept was greatest in the model where the random effect was on the asymptote. log(L), log likelihood.



Fig. A1. An example of a female tree swallow from the trimming treatment. The median amount of ventral region exposed was 3.1 × 1.9 cm (length × width).

Remote monitoring of activity (reader set-up)

To record parental activity, we used two different radio frequency identification (RFID) readers that received data from the two types of PIT tags (non-temperature sensitive and temperature sensitive). Non-temperature-sensitive tags were read by Generation 2 RFID readers (Cellular Tracking Technology, Rio Grande, NJ, USA) (Bonter and Bridge, 2011), while temperature-sensitive tags were read by Biomark HPR Plus readers. Generation 2 readers ($n=50$) were placed under each nest box, and were connected to an antenna (125 kHz, no. AN0101, QKits, Kingston, ON, Canada) mounted around the entrance hole of the nest box. In this way, individuals were 'logged' as they entered and exited the box. We set the 'delay interval', i.e. the length of time that determines how often the same tag can be logged consecutively, to 5 s, to avoid generating a large number of reads when a bird sat at the antenna for an extended period of time. Readers were programmed to turn on and off at 04:00 h and 22:00 h, respectively. We set up antennas at least 24 h prior to capturing females for the first time. Biomark HPR plus readers ($n=3$) were connected to loop antennas (17.5 cm), which were positioned so that they encircled the nest box entrance. We cycled the Biomark readers among nests daily so that each nest received a reader for approximately 24 h, three times throughout the breeding period (early, middle and late-stage provisioning). Early, middle and late-stage provisioning were defined as days 2–5, 6–9 and 10–14 post-hatch, respectively.

Nestling mass measurements

In 2017, we weighed nestlings on a digital scale on day 0 (Acculab, ± 0.001 g) and on a Pesola spring scale (± 0.025 g) from day 3 to day 12 post-hatch. In 2018, we weighed nestlings on a digital portable scale (Smart Weigh Digital Pro Pocket, ± 0.01 g) from day 0 to day 12. It would be highly unlikely if the use of different scales affected our results, because we balanced sample sizes between treatments, within years (2017: $n=12$ control, $n=9$ trimmed; 2018: $n=18$ control, $n=19$ trimmed) and so this would only influence the estimated effect of ‘year’ on nestling growth rate. Nevertheless, we weighed a random subset of adult birds with both the Pesola and the Smart Weigh scale and found that the mean mass was significantly different between scale types (mean of differences = -0.094 , $t = -2.84$, 95% CI $[-0.16, -0.02]$, $P = 0.012$). Despite this statistical difference, a difference of ~ 0.1 g is one small source of variation that could be captured within ‘year’ and seems likely to have minimal biological meaning relative to the other sources of variation (e.g. weather, date of measurements).

Nestling growth rate (model selection)

We included ‘maternal identity’ as a random effect on each parameter (i.e. A , K , I ; Table A1) individually and subsequently used an AIC approach to select the optimal random effect structure. We initially ran models with random effects on multiple parameters (e.g. A and K), but these models did not converge and so we assumed that they were over-parameterized and did not consider them further.

Acknowledgements

We thank A. Schubert and J. Baici for help with data collection, D. Marshall for help with antenna construction, E. Bridge for assistance with data loggers, A. Gerson for loaning RFID equipment, J. Robertson for advice on statistics and S. Morin for helpful edits. We also thank two anonymous reviewers whose comments helped improve the manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.T., J.N., G.B.; Methodology: S.T., J.N., G.B.; Formal analysis: S.T.; Resources: J.N., G.B.; Data curation: S.T.; Writing - original draft: S.T.; Writing - review & editing: S.T., J.N., G.B.; Supervision: J.N., G.B.; Funding acquisition: S.T., J.N., G.B.

Funding

This research was supported by funds from the Natural Sciences and Engineering Research Council of Canada (NSERC) (RGPIN-04158-2014) and an internal research grant provided by Trent University. S.T. was supported in part by an Ontario Graduate Scholarship.

Data availability

All data are available from the Dryad digital repository (Tapper et al., 2020): dryad.tqjq2bvz

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