

1 **Title:** Heat dissipation capacity influences reproductive performance in an aerial

2 insectivore

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14 **Author contribution statements**

15 ST, JN, and GB designed the research. ST performed all field sampling, analysed the data

16 and wrote the manuscript; ST, JN and GB edited the manuscript and approved the final

17 draft. The authors declare no conflict of interest.

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24 **Abstract**

25 Climatic warming will likely increase the frequency of extreme weather events, which
26 may reduce an individual's capacity for sustained activity due to thermal limits. We
27 tested whether the risk of overheating may limit parental provisioning of an aerial
28 insectivorous bird in population decline. For many seasonally breeding birds, parents are
29 thought to operate close to an energetic ceiling during the 2-3 week chick-rearing period.
30 The factors determining the ceiling remain unknown, although it may be set by an
31 individual's capacity to dissipate body heat (the heat dissipation limitation hypothesis).
32 To test this hypothesis, over two breeding seasons we experimentally trimmed the ventral
33 feathers of female tree swallows (*Tachycineta bicolor*) to provide a thermal window. We
34 then monitored maternal provisioning rates, nestling growth rates, and fledging success.
35 We found the effect of our experimental treatment was context-dependent and varied
36 with environmental conditions. Females with trimmed plumage fed their nestlings at
37 higher rates than controls when conditions were hot and non-windy, but the reverse was
38 true under cool and windy conditions. On average, nestlings of trimmed females were
39 heavier than controls, and had a higher probability of fledging. We suggest that removal
40 of a thermal constraint allowed females to increase provisioning rates, but additionally
41 provided nestlings with a thermal advantage via increased heat transfer during maternal
42 brooding. Our data provide partial support for the heat dissipation limitation hypothesis,
43 and suggest that depending on weather patterns, heat dissipation capacity can influence
44 reproductive success in aerial insectivores.

45 **Keywords**

46 Energy expenditure, thermal constraint, parental care, climate, activity

47 **Introduction**

48 With rising global temperatures, animals will experience warmer than average annual
49 temperatures, and increased frequency of heat waves and droughts (IPCC 2014). Under
50 such changing conditions, animals must maintain stable body temperatures (T_b) in the
51 face of heat stress (McKechnie and Wolf 2009). A rise in T_b above steady state levels
52 (i.e., hyperthermia) occurs when heat is generated and/or acquired from the environment
53 faster than it can be dissipated (Speakman and Król 2010). Non-fatal hyperthermia can
54 have several deleterious physiological consequences, including disrupted cellular
55 signalling (Boulant 1998); impaired synthesis and damage of proteins (Roti Roti 2008);
56 elevated levels of oxidative stress (Costantini et al. 2012); depressed innate and adaptive
57 immune function (Palermo-Neto et al. 2013); and impaired growth and development
58 (Baumgard and Rhoads 2013), among others.

59 Given the suite of physiological consequences that can develop from
60 hyperthermia, the capacity to dissipate body heat has recently been proposed as a key
61 factor shaping the behaviour, physiology, and ecology of endotherms (“Heat Dissipation
62 Limitation” (HDL) hypothesis (Speakman and Król 2010). Specifically, the HDL
63 hypothesis posits that in endothermic animals maximally sustained energy expenditure is
64 limited by an individual’s maximal capacity to dissipate body heat. Understanding the
65 limits to sustained energy expenditure, or sustained metabolic rate (SusMR), is important
66 because metabolic ceilings could impose constraints on life-history traits (Drent and Daan
67 2002; Peterson et al. 1990). For example, an energetic ceiling in chick-rearing birds could
68 theoretically influence clutch size because parent birds can only feed a certain number of

69 chicks based on their sustained level of energy expenditure (Peterson et al., 1990;
70 Monaghan and Nager, 1997).

71 There are several lines of indirect evidence, which support the HDL hypothesis.
72 For instance, activity levels decline with high ambient temperature (T_a) (Carroll et al.
73 2015; Theuerkauf et al. 2003; Zub et al. 2013); animals preferentially select habitats
74 within their home range to escape solar radiation at the expense of resource acquisition
75 (Lease et al. 2014; Street et al. 2015; van Beest et al. 2012); in birds, individuals with
76 bigger bills (larger “thermal windows”) are more active and spend more time singing on
77 hot days than do birds with smaller bills (Luther and Danner 2016).

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

86 Despite this direct evidence of an HDL for laboratory mammals, there have been
87 few experimental studies testing the HDL hypothesis in free-ranging animals (Valencak
88 et al., 2011;). Two recent studies on breeding tits, however, provided some experimental
89 evidence for the HDL hypothesis in free-ranging birds (Nilsson and Nord 2018; Nord and
90 Nilsson 2018). Nord and Nilsson (2018) removed the ventral plumage from breeding blue
91 tits, *Cyanistes caeruleus*, and found that feather-clipped parents had heavier nestlings

92 than controls, while maintaining lower body temperatures and without additional mass
93 loss. However, there were no differences in feeding rates between the treatments, and
94 only older parents had heavier nestlings. This result suggests that the limit to SusMR
95 might be influenced by life-history strategy, which could also explain why some species
96 (e.g., European Hare, *Lepus europaeus*, Pallus) do not exhibit an HDL (Valencak et al.
97 2011).

98 One aspect largely ignored by previous studies examining the limits to SusMR is
99 the influence of other environmental factors on heat balance. For instance, wind carries
100 heat away from the body via convection, and increasing wind speeds decrease heat gain
101 from solar radiation (Wolf and Walsberg 1996). Further, rates of evaporative water loss
102 can be severely inhibited by high humidity, and thus variation in humidity could alter
103 activity levels (Gerson et al. 2014). Finally, in addition to the temperature, wind speed,
104 relative humidity, and precipitation have been shown to play an important role in
105 influencing foraging activity in aerial insectivores (Cox et al. 2019; Ouyang et al. 2015;
106 Rose 2009). Therefore, testing the HDL hypothesis in free-ranging animals should
107 attempt to control for these additional factors.

108 To determine whether heat dissipation constrains reproductive performance in
109 breeding birds, we experimentally manipulated the ability of female tree swallows
110 (*Tachycineta bicolor*) to dissipate body heat, by removing feather overlying the brood
111 patch. Tree swallows are an excellent model species in which to test the HDL hypothesis.
112 As aerial insectivores, they are active foragers, and can spend up to 16 hours per day
113 gathering insects to feed their nestlings. We predicted that, if in general (i.e., across
114 environmental conditions), the ability to dissipate body heat limits SusMR then (1)

115 trimmed birds would maintain higher feeding rates than control birds (2) trimmed birds
116 would have heavier offspring and (3) offspring of trimmed birds would have greater
117 fledging success than those of non-trimmed birds. Given that temperature does not occur
118 in isolation of other environmental factors, these predictions maybe context-dependent.

119

120 **Materials and methods**

121 **Study area and species**

122 All research was approved by the Trent University Animal Care Committee, in
123 accordance with the Canadian Council on Animal Care (AUP # 24747). We conducted
124 this study in May-July 2017 and 2018, on two nest-box breeding populations of tree
125 swallows located at the Trent University Nature Areas, Peterborough, Ontario, Canada
126 (44°21'N, 78°17'W) and at the Lakefield Sewage Lagoon, Lakefield, Ontario
127 (44°24'58.3"N 78°15'26.8"W). The Trent Nature Areas consists of relatively open grassy
128 fields, and there are about 70 boxes spaced ~10-20m apart. The Lakefield Sewage
129 Lagoon consist of two rectangular lagoons, with 50 boxes encircling the perimeter, and
130 spaced 10-20m apart. Females at both sites typically lay clutches of five to seven eggs,
131 with one egg laid each day. Once a clutch is completed, females incubate the nest for
132 approximately 14 days, and nestlings typically hatch synchronously. Nestlings typically
133 fledge 18-22 days post-hatch.

134

135 **General field methods**

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

138 completion. We used a marker pen to sequentially number eggs as they were laid; the
139 date the last egg was laid was considered to be day 0 of incubation. Hatch date (day 0) for
140 the brood was considered the first day when nestlings hatched.

141

142 **Experimental manipulation**

143 We captured females during early nestling provisioning (see capture protocol below), and
144 upon capture, randomly assigned females to either a trimmed or control condition, based
145 on a flip of the coin. In the trimmed condition, we removed the contour and downy
146 feathers covering the brood patch (details below) to expose the bare skin underneath
147 (Figure S1). We chose to remove feathers from this region because 1) it is highly
148 vascularized, increasing the chance of heat loss and 2) there would be minimal
149 interference with flight.

150 We performed trimming manipulations with two people: one person held the bird
151 ventral side up, while the other person, using surgical scissors, cut the feathers away.
152 Control females were handled identically, but instead of cutting the feathers, we
153 performed a “mock cut”, in which we cut the air above the brood patch. In 2018, we
154 additionally measured the size of the exposed area for all trimmed females ($n = 21$). We
155 quantified both the length and width of the exposed skin using a piece of string. The
156 median (\pm median absolute deviation, MAD) length of exposed skin was 3.1 ± 0.2 cm
157 (range: 2.6-3.7cm) and the median width of exposed skin (\pm MAD) was 1.9 ± 0.1 cm
158 (range: and 1.5-2.1cm). Assuming the trimmed area was an ellipse, the amount of
159 exposed skin would be 4.63cm^2 . The estimated percentage of total surface area trimmed
160 was $\sim 7\%$ (see supplementary material for details).

161 **Remote monitoring of activity**

162 As an index of activity, we quantified provisioning rate of females using passive
163 integrative transponder (PIT) tags. During late incubation (day 7 – day 10 post-clutch
164 completion), we captured females in their nest box and implanted them in the nape of the
165 neck with either 1) non-temperature sensitive (EM4100; #11001, GAO RFID, Ontario,
166 Canada) or 2) temperature-sensitive (Biotherm13; Biomark, Boise, Idaho, USA) PIT tags,
167 following Nicolaus et al. (2011). Data on body temperature from the Biotherm13 tags are
168 part of a parallel study. Following implantation, we recorded body mass, wing chord
169 (flattened), head-bill length, exposed culmen (*sensu* Borrás et al., 2014), and determined
170 age (second year or after second year) based on plumage coloration (Hussell 1983). Total
171 time in the hand was approximately 12 minutes. Details regarding the reader set-up are
172 described in the supplementary materials.

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

177 We had six females with data from both years. We attempted to give each bird the
178 opposite treatment that it received in 2017, but in an effort to keep the sample sizes
179 within the treatments approximately balanced, four individuals received the opposite
180 treatment and two received the same treatment.

181

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184 **Nestling measurements**

185 Nestlings were measured between ~1200 – 1800h. To determine the effect of maternal
186 treatment on nestling growth rate, we weighed nestlings at days 0 (hatch), 3, 6, 9 and 12
187 (i.e., peak body mass). We did not handle nestlings beyond day 12 to prevent premature
188 fledging. In 2017, we weighed nestlings on a spring and digital scale and in 2018 on a
189 digital scale only. This did not affect our conclusions, but see supplementary material for
190 details. As an index of nestling body size, we measured wing chord on day 12 using a
191 wing-rule (with a stop). As part of another study, we collected a blood sample (~75 μ L)
192 from each nestling at day 12. Fledging success was determined after checking all nest
193 boxes on day 18 post-hatch, and in the following days as necessary. There were no
194 instances of premature fledging from checking the nest box.

195

196 **Data compilation and organization**

197 *Feeding rate*

198 Most adult females were caught when nestlings were 1-2 days of age (see *female*
199 *captures* above), and we therefore only included feeding rate data between nestling ages
200 3 to 14d, and between the hours of 0500 and 2100. We only included data collected
201 within 0500 and 2100h because swallows are relatively inactive during this window
202 (S.Tapper, unpublished data). Our feeding rate data range from 01-Jun-2017 to 29-Jun-
203 2017 and from 31-May-2018 to 11-Jul-2018.

204 For data organization and statistical analyses, we used R (version 3.5.1, R Core
205 Team). To transform raw RFID reads into visits to the nest box, we used the function
206 “visits” from the package *feedr* (LaZerte et al. 2017). We considered repeated reads from

207 the same individual as a singular event if successive reads were < 60s apart. We defined
208 daily feeding rate as the total number of visits per day / the total number of hours in
209 which the bird was logged on the reader (i.e., an integer). We included each hour toward
210 the total number of hours spent provisioning if there was at least one read in the hour of
211 interest. We chose this definition over a typical standardized provisioning rate (e.g.,
212 number of visits/16hrs (0500-2100h) because of unequal number of observations across
213 birds. Unequal observations were due to 1) birds with thermal tags having fewer overall
214 hours of data (due to cycling of readers among boxes) and 2) because some birds had
215 missing data as a result of equipment failure. This definition provides a relatively
216 unbiased measure of feeding rate compared with one in which the total number of hours
217 across all birds was assumed to be the same (i.e., standardized).

218

219 *Environmental variables*

220 We gathered data on daily mean ambient temperature (°C), wind speed (km·hr⁻¹), relative
221 humidity (%), and total precipitation (mm), from Trent University's weather station,
222 which is located approximately 1.5km from the Trent University Nature Areas and 9.5km
223 from the Sewage Lagoon and (downloadable from Environment Canada,
224 http://climate.weather.gc.ca/index_e.html). We calculated averages over 24h, because
225 overnight and early morning weather could have carry-over effects on feeding behaviour
226 the next day. To avoid multiple univariate statistical tests we collapsed our four weather
227 variables using principle component analysis (PCA). We centered and scaled the data
228 prior to calculation of the correlation matrix. The first two PCs explained a combined
229 total of 69.1% (PC1 = 41.54%, PC2 = 27.58%) of the variation in weather. PC1 was

230 loaded primarily by relative humidity and total precipitation (Table 1), while PC2 was
231 predominately loaded by wind speed and temperature (Table 1). We included both PC1
232 and PC2 scores in our statistical models because we were interested in how the different
233 weather variables related to treatment independently of each other (i.e., humidity and
234 precipitation vs. wind speed and temperature),

235

236 **Statistical analyses**

237 For all analyses (i.e., feeding rate, nestling body mass, fledging success), we only
238 included nests that fledged at least one nestling. Unless otherwise stated, model
239 parameters were estimated by restricted maximum likelihood, degrees of freedom and *p*-
240 values were calculated using the Satterthwaite approximation in the lmerTest package
241 (version 3.1-0, Kuznetsova et al., 2017), and confidence intervals were calculated with
242 the Wald method in the lme4 package (version 1.1-20, Bates et al., 2015). Means reported
243 are estimated marginal means, generated using the emmeans package (version 1.3.2,
244 Lenth, 2019). We considered *P*-values ≤ 0.05 as statistically significant. We checked that
245 our models met assumptions of normality and homogeneity of variance by visual
246 inspection of the residuals.

247

248 **Feeding rate**

249 We tested for an effect of experimental treatment (trimmed or control) on maternal
250 feeding rate (expressed as visits·hr⁻¹) using linear mixed effects models (lme4). In 2017,
251 there were a total of 18 females included in the analysis (Control₂₀₁₇ = 10, Trimmed₂₀₁₇ =
252 8), while in 2018 there were a total of 37 females (Control₂₀₁₈ = 18, Trimmed₂₀₁₈ = 19).

253 We included brood size, treatment, PC1 score, PC2 score, year, lay date, and chick age as
254 main effects in our model, and interactions terms for: (1) treatment x PC1, and (2)
255 treatment x PC2. In each year, we standardized lay date so that the first day in which a
256 female laid an egg was given the value of 0. We controlled for repeated observations
257 from the same individual across days by including bird identity as a random effect.

258 After running the initial model and assessing diagnostic plots, we detected one
259 observation with a standardized residual that was > 3 standard deviations above 0 (all
260 others < 2.8), which we considered an outlier. Exclusion of this point did not change our
261 results, but improved model fit, and so was excluded from the analysis.

262

263 **Nestling morphology and fledging success**

264 We tested for differences in nestling growth rates between treatments using a three-
265 parameter logistic growth curve, which has been shown to model tree swallow growth
266 accurately (McCarty 2001; Zach and Mayoh 1982). Our sample size in 2017 and 2018
267 was 19 ($\text{Control}_{2017} = 12$, $\text{Trimmed}_{2017} = 9$) and 37 ($\text{Control}_{2018} = 18$, $\text{Trimmed}_{2018} = 19$)
268 nests respectively. At each time point on the growth curve (i.e., 0, 3, 6, 9, 12d post-
269 hatch), we calculated the average nestling mass, per brood, and used this as our
270 dependent variable, because we did not track individual nestlings in 2017.

271 We constructed the growth curve model using the “nlme” function from the nlme
272 package (version 3.1-137, Pinheiro et al., 2014). To describe the patterns of nestling
273 growth, we calculated three parameters from the growth curve: the asymptotic mass (A)
274 (i.e., peak mass, ~ day 12 post-hatch) (in grams), the inflection point (i.e., point of
275 steepest growth) (I) of the growth curve (in days), and the growth rate constant (i.e.,

276 steepness of growth curve) (K). We estimated our parameter starting values using the
277 “SSlogis” function from Stats package (base R).

278 We included ‘maternal identity’ as a random intercept on the asymptotic
279 parameter to control for statistical non-independence in the growth rate among nestlings
280 that were dammed from the same females. A random intercept for ‘maternal identity’ was
281 initially applied to all growth rate parameters (A , K , I), however, application of a random
282 intercept to the asymptotic parameter alone explained the greater variance in our data (see
283 supplementary material, Table S1, for more details). Confidence intervals and predictions
284 were calculated using bootstrapping with replacement based on 1000 replications.

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

290 To determine whether treatment affected an individual nestling’s fledging
291 success, which we defined as either 1 (fledged) or 0 (did not fledge), we used a
292 generalized linear mixed model (glmer function in lme4) with a binomial error
293 distribution and a logit link. We used the same model structure as we did for nestling
294 morphology. After plotting the predictions from the model, we noticed differences in
295 variance between treatments, and subsequently ran an F-test (using the var.test function
296 in stats package, base R) on the predicted probabilities from the model. Results from the
297 F-test confirmed violation of homogeneity of variance ($F_{163,145} = 6.78$, 95% CI [4.93,

298 9.31], $P < 0.0001$) and we re-ran our model with the inclusion of a variance structure
299 (using with the “weights” argument) to control for heteroskedasticity between treatments.

300

301 **Results**

302 **Feeding rate**

303 On average, maternal feeding rate (visits·hr⁻¹) (\pm SE) did not differ between treatments (P
304 = 0.165; control birds: 11.8 ± 0.55 , trimmed birds: 11.4 ± 0.53). Feeding rate was
305 negatively related to PC1 score ($P < 0.0001$, Fig. 1, Table 2), indicating that birds foraged
306 less on wetter and more humid days. We did not detect an interaction between treatment
307 and PC1 score ($P = 0.122$, Table 2), but there was a trend of higher feeding rates in
308 control birds on wetter and more humid days relative to trimmed birds (Fig. 1). Feeding
309 rate differed significantly between treatments as a function of PC2 score (i.e., treatment x
310 PC2 score, $P = 0.020$, Fig. 2, Table 2). At the highest PC2 score (i.e., 1, indicating high
311 temperature, low wind speed), trimmed birds made 5.5% more trips per hour (~8 extra
312 visits, given a 16hr day) than controls. However, at the lowest PC2 score (i.e., 0, meaning
313 low temperature, high wind speed), trimmed birds made 23% less trips per hour (~32
314 visits, given a 16hr day) than control birds. Feeding rate increased with brood size ($P =$
315 0.045, Table 2); females raising larger broods (7 nestlings) made ~3 more visits to the
316 nest per hour than mothers raising small broods (3 nestlings). Provisioning rate was also
317 negatively related to lay date ($P = 0.055$, Table 2), meaning that earlier nesting birds had
318 higher feeding rates than later nesting birds.

319

320

321 **Nestling morphology and fledging success**

322 The best model for describing nestling mass included a random intercept on asymptotic
323 mass (supplementary material, Table S1). Nestlings from trimmed mothers were heavier
324 (\pm SE) by 1.71 ± 0.48 g at their asymptote (\sim day 12 post-hatch) compared with nestlings
325 from control mothers at their asymptote (i.e., Treatment, $P = 0.001$, Fig. 3, Table 3). We
326 did not detect any significant differences in the inflection point (\sim day 5 post-hatch)
327 between groups ($P = 0.061$, Table 3), nor in the growth rate constant (i.e., steepness of
328 curves) between groups ($P = 0.548$). Wing length did not statistically differ between
329 treatments ($\beta = 0.18$, 95% CI [-0.03, 0.38], $P = 0.090$), although nestlings in 2017 had
330 longer wings than nestlings in 2018 (i.e., Year, $\beta = -0.38$, 95% CI [-0.57, -0.20], $P <$
331 0.001). Lay date was negatively related to wing length ($\beta = -0.03$, 95% CI [-0.05, -0.01],
332 $P = 0.006$).

333 The probability of fledging (\pm SE) was significantly higher for nestlings in
334 trimmed ($98.4 \pm 0.03\%$) compared to control broods ($94.1 \pm 0.01\%$) (Odds Ratio = 3.93,
335 95% CI [1.03, 14.96], $P = 0.045$, Fig. 4), and did not differ significantly between years
336 (Odds Ratio = 2.62, 95% CI [0.77, 8.89], $P = 0.122$). Similar to nestling morphology, lay
337 date was negatively related to fledging success (Odds Ratio = 0.87, 95% CI [0.76, 1.00],
338 $P = 0.054$).

339

340 **Discussion**

341 We found that the ability to dissipate body heat affected the reproductive performance of
342 female tree swallows in a context-dependent manner, providing partial support for the
343 HDL hypothesis. We had predicted that trimmed birds would maintain higher feeding

344 rates than control birds due to the increased capacity to dissipate body heat. Instead, an
345 individual's feeding rate depended on the interactive effects of multiple environmental
346 factors. When it was hot and wind speeds were low (high PC2 score), trimmed birds
347 tended to provision their offspring more than control birds, but this pattern was reversed
348 when it was cool and windy (low PC2 score) (Fig. 2).

349 The relatively higher activity rates of trimmed birds at high PC2 scores (hot and
350 calm) compared with control birds is consistent with studies from the mammalian
351 literature, in which experimental fur removal in mice allows for higher sustained energy
352 expenditure during lactation, as measured via increases in food intake and milk
353 production (Gamo et al. 2016; Król et al. 2007). It is also consistent with the idea that
354 different mechanisms (e.g., heat dissipation vs. peripheral limitation) can constrain
355 SusMR in different circumstances (Wen et al. 2017). For instance, lactating laboratory
356 mice appear to face a heat dissipation limitation at warm (30 °C), but not room (i.e., 21
357 °C), temperatures (Wen et al. 2017). Given that the relative effect of PC2 on feeding rate
358 was much weaker at the high end of the scale (i.e., when warm and calm trimmed birds
359 made 5% more trips than controls) versus the low end of the scale (i.e., when cool and
360 windy trimmed birds made 23% fewer trips than controls), our study provides only partial
361 support to the HDL hypothesis.

362 Wind speed can reduce foraging rates in tree swallows, and daily average wind
363 speed can have a greater effect on feeding rate than average temperature, presumably
364 because high winds make aerial insects more difficult to find and/or by increasing the
365 flight costs during foraging (Rose 2009). If flight costs were increased in windy
366 conditions, thereby increasing energy expenditure and T_b (Wolf et al. 2000), trimmed

367 birds would have an advantage because of increased heat dissipation capacity. However,
368 this would only be advantageous if temperatures were also warm, as this would minimize
369 heat gain from solar radiation (Wolf and Walsberg 1996). In the context of our study,
370 temperature and wind were negatively related in PC2, so the birds were not experiencing
371 warm and windy conditions, but rather were experiencing cool and windy conditions.
372 Thus, it is likely that trimmed birds would have difficulty maintaining heat balance in
373 cool air temperatures and high wind speeds, because heat loss to the environment would
374 occur more quickly than any heat generated via metabolism (Zerba et al. 1999).

375 There was a significant decline in feeding rate with increasing PC1 score (relative
376 humidity and precipitation). While we did not detect a statistically significant interactive
377 effect of treatment and PC1 ($P = 0.12$) on feeding rate, trimmed birds appeared to feed
378 their nestlings less frequently at high PC1 scores (high precipitation, high relative
379 humidity) than at low PC1 scores (low precipitation, low relative humidity) (Fig. 1).
380 Precipitation has been found to negatively influence feeding rate in passerines (Öberg et
381 al. 2014; Winkler et al. 2013), and it is generally assumed that the decline in foraging rate
382 is caused by a reduction in insect activity (Cox et al. 2019; Irons et al. 2017; Winkler et
383 al. 2013). If however precipitation did decrease tree swallow foraging rate due to lowered
384 insect activity, this should have affected both treatments equally, but this tended not to be
385 the case as Fig. 2 shows. Rain has a “cooling effect” on the subjective temperature an
386 animal experiences, which would make thermoregulation more difficult for an animal
387 with less insulation (i.e., a trimmed bird). Furthermore, precipitation is typically
388 associated with cloud cover, which would limit thermal radiation reaching the birds.
389 Therefore, precipitation may have influenced foraging rate because of the challenges of

390 thermoregulating under cool and wet conditions, rather than because of reduced insect
391 activity.

392 Relative humidity can also influence activity level in birds (Gerson et al. 2014).

393 When T_a exceeds T_b , heat cannot be lost via dry heat transfer, and evaporative heat
394 transfer is the only means to dissipate metabolic heat. While T_a never exceeded T_b in our
395 study (max $T_a=34^\circ\text{C}$, mean $T_b\sim 41^\circ\text{C}$, S. Tapper, unpublished data), relative humidity
396 still plays an important role in thermoregulation because it decreases the potential for
397 evaporative heat loss (Gerson et al. 2014). In our study, as precipitation and relative
398 humidity increased together in PC1, temperature simultaneously decreased in PC1. Birds
399 in our study were therefore likely experiencing cool and wet conditions, rather than warm
400 and wet conditions. If increased precipitation had a cooling effect on air temperature, then
401 this would explain why trimmed birds had lower foraging rates than control birds at
402 higher PC1 scores.

403 We predicted that due to increased activity rates, trimmed females would have
404 heavier nestlings than controls. In line with this prediction, trimmed females had
405 nestlings that reached higher asymptotic masses (\sim day 12 post-hatch, Fig. 4) compared
406 with control females. However, the mechanism by which this prediction supports the
407 HDL hypothesis is unlikely to be due to feeding rate alone, because trimmed birds had a
408 relatively minor advantage in feeding rate at high PC1 (hot and non-windy) scores
409 relative to their disadvantage at low PC1 scores (cool and windy). The heavier offspring
410 of trimmed females may in part be due to trimmed females transferring more heat to their
411 offspring during brooding compared with control mothers. Tree swallow nestlings do not
412 develop feathers until around 6 to 7 days post-hatch (Marsh 1980), and mothers typically

413 continue brooding until swallows reach 5 days of age (McCarty 1996). Although we did
414 not estimate heat transfer of the brood patch/trimmed area between treatments, in a study
415 similar to ours, Nord and Nilsson (2018) trimmed ~22% of the total surface area of male
416 and female blue tits resulting in an approximate 47% increase in estimated heat transfer
417 for trimmed compared to control birds. However, Nord and Nilsson (2018) trimmed a
418 greater proportion of the plumage than we did (22% in their study, 7% in ours), as we did
419 not remove feathers covering the pectoral muscles. Nevertheless, it is plausible that a 7%
420 difference in estimated heat transfer between treatments could lead to an advantage in
421 terms of increased growth and survivorship (Dawson et al. 2005; Klaassen et al. 1994;
422 Pérez et al. 2008). For instance, if nestlings were experiencing cool temperatures and
423 responded by increasing metabolic rate (Nord and Nilsson 2011), then nestlings from
424 trimmed broods receiving direct heat transfer from the enlarged bare skin surface could
425 have had more energy to put into growth rather than maintaining homeothermy.

426 Nestlings from trimmed broods may also have been heavier than controls because
427 of adults providing nestlings with different quantities, or quality of food (Sofaer et al.
428 2018; Twining et al. 2016), or because male swallows adjusted their provisioning strategy
429 in accordance with female behaviour, thus leading to differences in the total feeding
430 frequency per nest (Akçay et al. 2016; Lendvai et al. 2018).

431 We predicted that in addition to producing heavier and structurally larger
432 nestlings at day 12, nestling fledging success would be greater in trimmed compared to
433 control broods. In line with this prediction, fledging success was higher for nestlings from
434 trimmed broods ($P = 0.045$) and was also less variable compared to control broods (Fig.
435 4). This suggests lower overall mortality for nestlings in trimmed compared to control

436 broods. In birds, fledging success is typically correlated with post-fledging survival and
437 recruitment (McCarty 1996; Weatherhead and Dufour 2000). While we do not have the
438 data to examine post-fledging survival, it is possible that increased fledging success and
439 less variance around fledging success for trimmed birds could also mean less variability
440 in post-fledging survival, which would suggest a possible fitness benefit for trimmed
441 birds.

442 In conclusion, our data demonstrate that heat dissipation capacity is an important
443 factor influencing female tree swallow behaviour and breeding success. We provide
444 evidence that even a small adjustment to the ventral plumage can cause birds to modulate
445 their activity levels, as measured indirectly via provisioning rate. Therefore, this supports
446 the HDL hypothesis's predictions that heat dissipation can alter SusMR in free-living
447 animals.

448 As global temperatures and frequencies of heat waves increase (IPCC 2014), the
449 physiological parameter of heat balance will be of higher concern for all birds,
450 particularly aerial insectivores such as tree swallows. The birds in our study did not
451 experience temperatures beyond their T_b , but we provide evidence that under such
452 extreme conditions, being unable to effectively dissipate body heat could decrease
453 reproductive success. Our study also highlights the likely reason why birds mostly keep
454 their plumage during the breeding season: because cool, rainy, and windy weather can
455 negatively affect foraging rate and potentially thermoregulation. In addition to warming
456 temperatures, climate change may also reduce the food supply of tree swallows (Irons et
457 al. 2017; Winkler et al. 2013). Tree swallows may then have to contend with both the
458 effects of reduced food supply and overheating while feeding their young.

459

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470

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- 637

Tables

Table 1 Rotated matrix values of principal component analysis scores for 2017 and 2018 environmental data. To improve interpretation of results, we multiplied PC1 by -1 so that relative humidity and precipitation were positively related to PC1 score. The first two PCs explained a combined 69.1 % variance in the weather data (PC1 = 41.54 %, PC2 = 27.58 %).

Variable	PC1	PC2
Temperature	-0.36	0.56
Wind speed	0.17	-0.74
Relative humidity	0.67	0.21
Precipitation	0.62	0.30

Table 2 Factors contributing to variation in maternal feeding rate. Fixed effect coefficient estimates with 95% confidence intervals (CI), and *P*-values.

Predictor	Estimate	95% CI	<i>P</i>-value
Intercept	10.13	5.87 – 14.39	<0.001
Treatment	-1.30	-3.13 – 0.53	0.165
PC1	-5.48	-7.12 – -3.84	<0.001
PC2	0.75	-0.98 – 2.49	0.394
Year	0.01	-0.97 – 0.99	0.977
Lay date	-0.12	-0.24 – 0.00	0.055
Brood size	0.74	0.03 – 1.45	0.045
Nestling age	0.01	-0.06 – 0.07	0.856
Treatment x PC1	-1.86	-4.22 – 0.50	0.123
Treatment x PC2	2.84	0.46 – 5.22	0.020

Table 3 Parameter estimates for nestling growth trajectories. Fixed effect coefficients with 95% confidence intervals (CI), and *P*-values.

Parameter	Predictors	Estimates	95% CI	<i>P</i>-value
Asymptote (<i>A</i>)	Intercept	21.1	20.15 – 21.67	<0.001
	Treatment	1.68	0.37 – 2.72	0.001
Inflection point (<i>I</i>)	Intercept	4.75	4.65 – 5.08	<0.001
	Treatment	0.21	-0.08 – 0.51	0.064
Growth rate constant (<i>K</i>)	Intercept	1.91	1.76 – 2.01	<0.001
	Treatment	0.05	-0.12 – 0.23	0.548

Figures

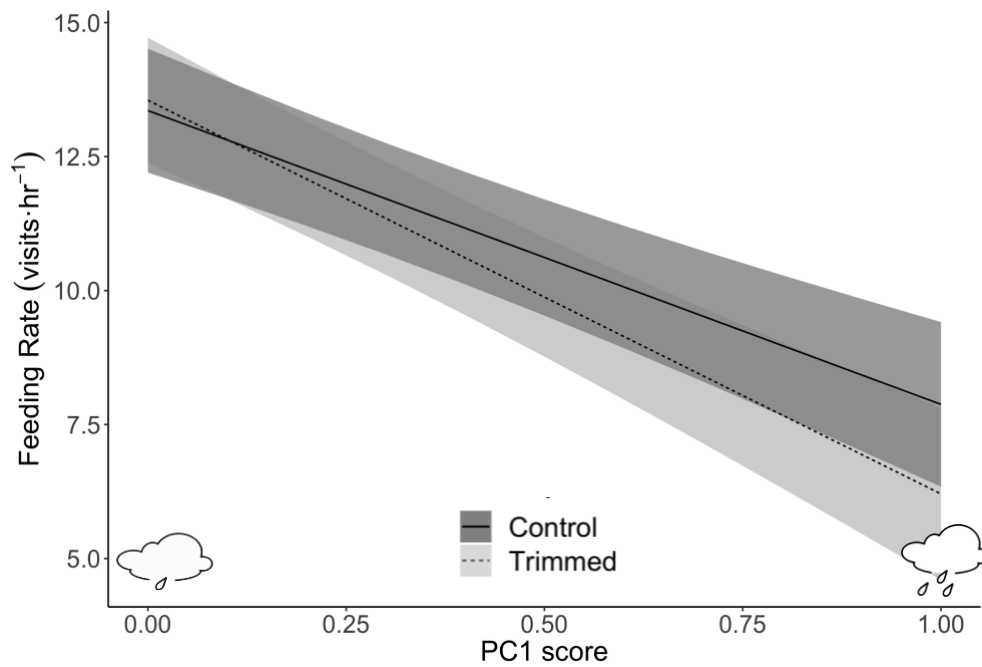


Fig. 1 Prediction plot of female provisioning rate (\pm 95% CI) in relation to PC1 score. All other predictors in the model are held at their constant value. Low PC1 scores represent low rainfall and low humidity conditions, while high PC1 scores represent high rainfall and high humidity conditions. As relative humidity and rainfall increased, females with an increased capacity to dissipate heat (i.e., trimmed) decreased feeding rates more sharply than control birds. Sample sizes ($N_{\text{control}}=28$, $N_{\text{trimmed}}=27$).

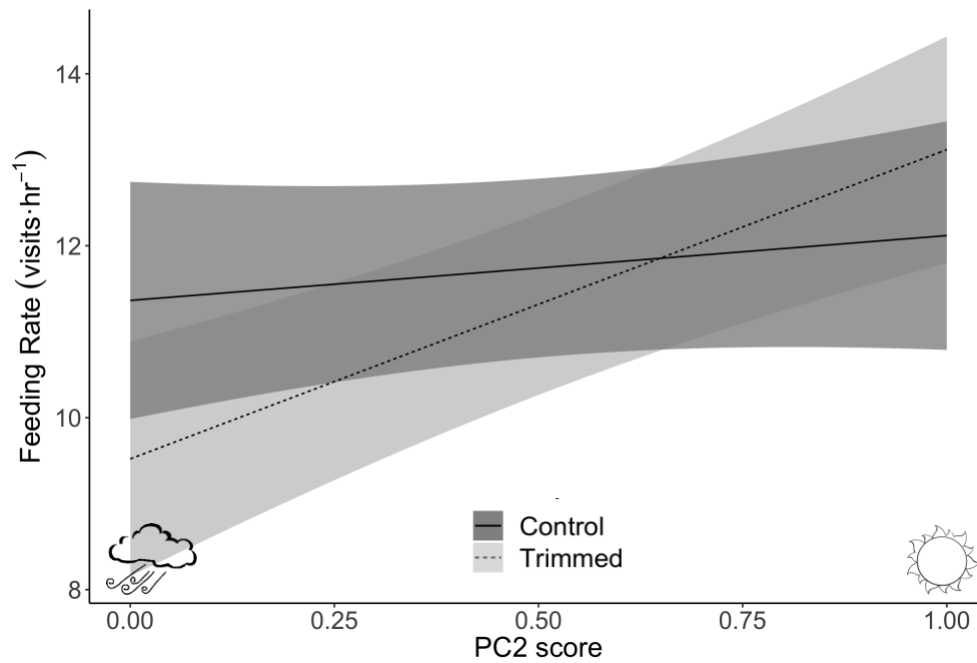


Fig. 2 Prediction plot of female feeding rate (\pm 95% CI) in relation to PC2 score. All other predictors in the model are held at their constant value. Low PC2 scores represent cool and windy conditions, while high PC2 scores represent hot and calm conditions. As temperature increased and wind speed decreased, females with an increased capacity to dissipate heat (i.e., trimmed) increased feeding rates, while control birds remained relatively constant across PC2 scores. Sample sizes ($N_{\text{control}}=28$, $N_{\text{trimmed}}=27$).

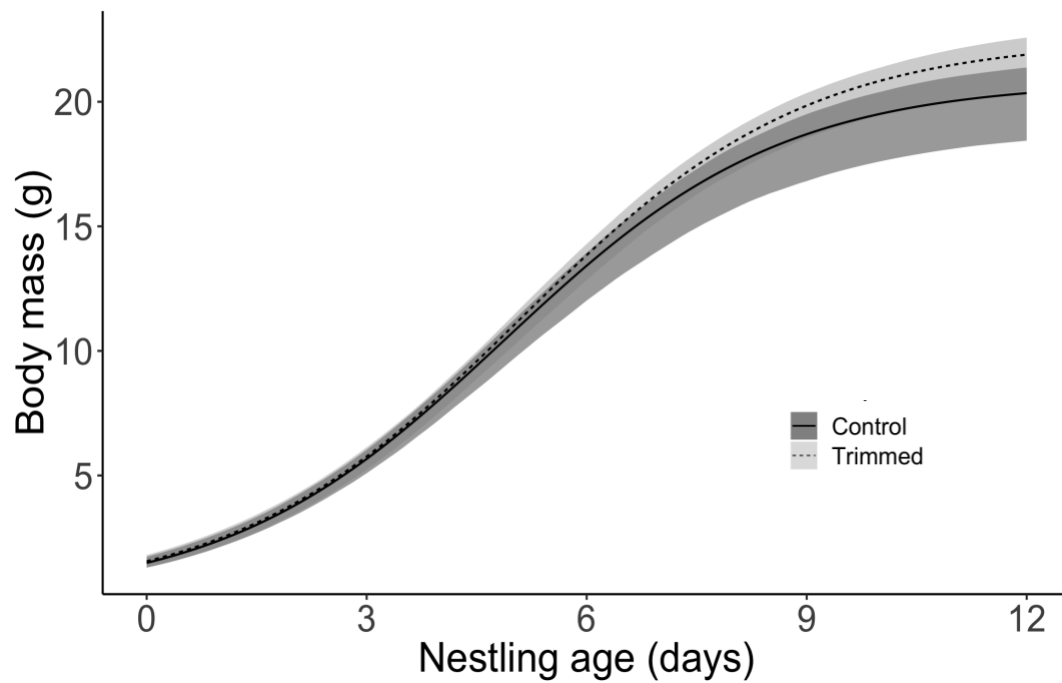


Fig. 3 Estimated growth trajectories comparing the growth of nestlings from control broods and from those in which females had increased heat dissipation capacity (i.e., trimmed). Bands around lines represent the 95% confidence intervals obtained from bootstrapping. There were 309 nestlings from 58 nests ($N_{\text{Control}}=30$, $N_{\text{Trimmed}}=28$).

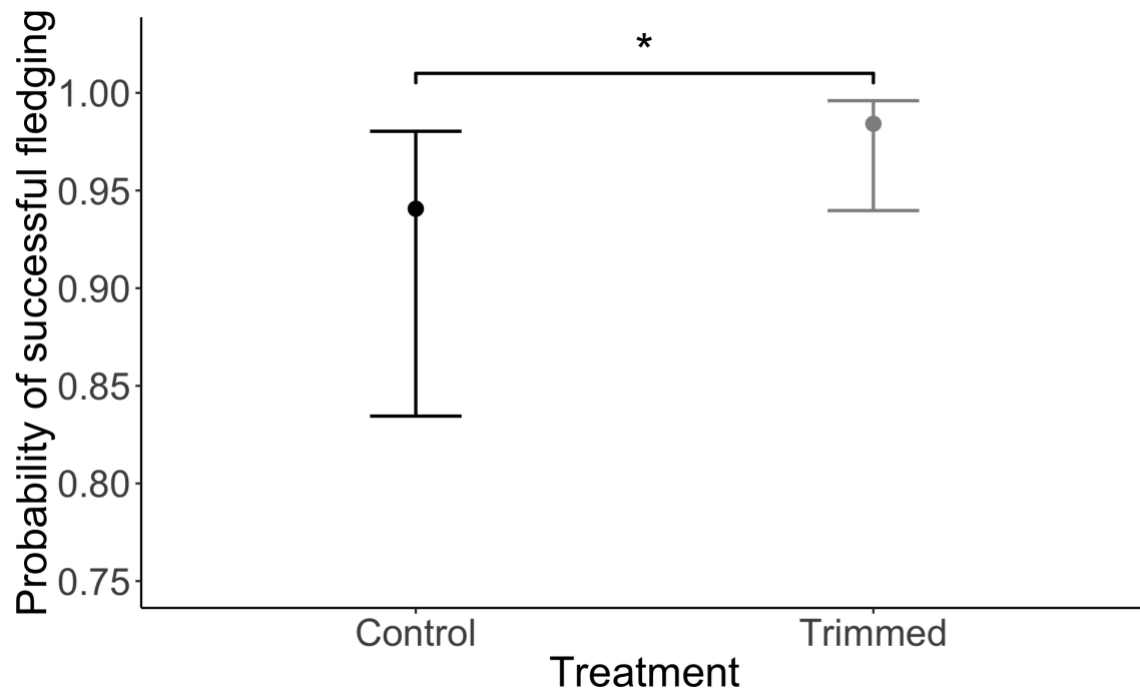


Fig. 4 Predicted probability of nestling fledging success as a function of treatment (\pm 95% confidence intervals), converted from odds ratios to probabilities. * $P < 0.05$. There was a higher probability that nestlings from trimmed broods would fledge over nestlings from control broods. There were 309 nestlings from 58 nests ($N_{\text{Control}}=30$, $N_{\text{Trimmed}}=28$)