Weather matters: begging calls are temperature- and size-dependent signals of offspring state

Roslyn Dakin [a,*], **Jenny Q. Ouyang** [b,c], **Ádám Z. Lendvai** [c,**],
Mark F. Haussmann [d], **Ignacio T. Moore** [c] **and Frances Bonier** [e]

[a] Department of Zoology, University of British Columbia, 4200-6270
University Boulevard, Vancouver, BC, Canada V6T 1Z4
[b] Department of Biology, University of Nevada, Reno, NV, USA
[c] Department of Biological Sciences, Virginia Tech, Blacksburg, VA, USA
[d] Biology Department, Bucknell University, Lewisburg, PA, USA
[e] Department of Biology, Queen's University, Kingston, ON, Canada
[*]Corresponding author's e-mail address: roslyn.dakin@gmail.com
[**]Current affiliation: Department of Evolutionary Zoology and Human Biology,
University of Debrecen, Debrecen, Hungary

Abstract

Begging calls provide a way for parents to gauge offspring state. Although temperature is known to affect call production, previous studies have not examined the influence of ambient temperature at the nest. We recorded ambient temperature and begging calls of 3 day-old tree swallows (*Tachycineta bicolor*). Our results indicate that typical daily temperature flux can dramatically alter a brood's begging calls, depending on body size. Broods with small (low body mass) nestlings decreased the rate and length of their calls at colder temperatures, consistent with a biophysical constraint. In contrast, broods with large (high body mass) nestlings increased the rate of their calls at colder temperatures. Parents responded in a context-dependent manner, returning more rapidly after smaller nestlings gave longer begging calls. Our results suggest that the function of offspring begging calls is highly dynamic, with environmental conditions altering the relationship between begging calls and offspring state.

1. Introduction

Offspring begging calls are dynamic signals thought to mediate parental food provisioning in a wide variety of species (Kilner & Johnstone, 1997). These signals may be used by parents to favour particular offspring over others in the same brood (Royle et al., 2002). They may also influence parental allocation in the current brood over self-maintenance and future reproduction (Trivers, 1974; Wright & Leonard, 2002). Understanding the factors that underlie variation in begging calls can thus provide insight into signal function, the maintenance of signal honesty, and parental investment decisions that impact brood survival.

Most empirical studies of begging have focused on birds, with extensive evidence that begging intensifies following food deprivation (reviewed in Budden & Wright, 2001), consistent with the hypotheses that begging may function as a signal of hunger or a signal of offspring need (with need defined as the potential for offspring fitness gains; Godfray, 1991; Grodzinski & Lotem, 2007). However, the fact that begging intensifies following deprivation does not rule out other potential functions (Parker et al., 2002), such as the hypothesis that begging may also signal offspring condition or quality (Grafen, 1990; Mock et al., 2011; Rector et al., 2014). Indeed, a recent meta-analysis of 143 bird species showed that ecological context can explain the diversity of begging signal function across species (Caro et al., 2016). For species in high-quality environments, poor condition offspring often beg the most intensely (signalling need). In contrast, in low-quality environments, begging is more often positively associated with offspring condition (signalling quality; Caro et al., 2016). Begging is also influenced by social and physical aspects of the natal environment (Smith & Montgomerie, 1991; Leonard et al., 2000; Leonard & Horn, 2001c, 2005) and genetic factors (Dor & Lotem, 2009). Cross-fostering experiments indicate that the environment, including parental behaviour, has a much stronger influence on variation in begging behaviour than an individual's genetic origin (e.g., Dor & Lotem, 2009).

Temperature is an environmental factor that is known to influence the production of begging calls (Choi & Bakken, 1990; Leonard & Horn, 2001a) as well as other call types (e.g., mating calls; Gerhardt, 1978; Ryan, 1988). For instance, in a comparative study of nearly 500 vertebrate and insect species, Gillooly & Ophir (2010) showed that mating call production across

species is related to body temperature and body mass in a manner that is consistent with a biophysical constraint based on metabolic rate. Specifically, log-transformed call rate is positively associated with body temperature, and negatively associated with log-transformed body mass, as expected if metabolic rate determines the rate of neuronal and muscular activity required for call production (Gillooly & Ophir, 2010). These constraints of body mass and temperature are expected to apply to begging calls as well.

Several studies have experimentally tested the influence of temperature on the begging behaviour of isolated nestling birds under controlled laboratory conditions (Choi & Bakken, 1990; Evans, 1994; McCarty, 1996; Leonard & Horn, 2001a). For instance, Leonard & Horn (2001a) showed that nestlings that were deprived of food and provided with a heat source doubled their begging call length and tripled their call rate after 80 min of food deprivation, demonstrating how dramatically begging signals can change with food deprivation. However, when the nestlings in that study were deprived of food and allowed to cool, their response depended on body mass: larger individuals increased their begging rate initially, reaching a peak that was double their initial rate after about 20 min of combined food deprivation and cooling, and then decreased it. In contrast, smaller individuals that cool more rapidly (Dunn, 1979) maintained a more consistent begging rate when they were deprived of food and allowed to cool simultaneously (i.e., they did not show the same dramatic increase in begging rate seen in nestlings that were kept warm while they were deprived). It is unknown whether these effects of temperature also occur naturally at the nest.

Altricial birds that depend on parental provisioning are strongly influenced by ambient temperature. At hatch, altricial young are not yet capable of metabolic thermoregulation, but they develop this ability over 1–3 weeks at a rate that depends on individual body size (Dawson & Evans, 1957; Dunn, 1975; Marsh, 1980). Although brooding behaviour and nest construction give parent birds some control over heat loss of their offspring, the temperature measured inside a nest oscillates with local ambient temperature flux, changing by $>10°C$ per day even in cavity-nesting birds (Dawson et al., 2005; Ardia et al., 2006b). As a result, local ambient temperature variation can have a strong effect on offspring growth (e.g., McCarty & Winkler, 1999; Eeva et al., 2002; Dawson et al., 2005). Begging calls may provide an important signal of offspring state under these challenging weather conditions.

To investigate the relation between natural variation in ambient temperature and begging behaviour at the nest, we examined the begging behaviour of 3 day-old nestling tree swallows (*Tachycineta bicolor*) in a nestbox breeding population. At this age, the offspring are featherless and unable to regulate their own body temperatures metabolically (Marsh, 1980). We recorded whole-brood acoustic signals, as these signals influence parental provisioning behaviour (Bengtsson & Rydén, 1983; Leonard & Horn, 1998). Although we expected that temperature could also influence the dynamics of competition among offspring, these interactions were outside the scope of the present study. Our predictions, based on previous experimental studies of individual nestlings, were that: (1) deprived broods would beg more intensely (Leonard & Horn, 2001a), (2) under cold conditions, nestlings would lose the ability to perform begging (Choi & Bakken, 1990), and (3) broods with smaller nestlings would experience a more rapid decrease in their ability to perform begging calls with decreasing temperature, because of their increased rate of body heat loss (Dunn, 1979; Leonard & Horn, 2001a). We assessed begging intensity using the rate and length of offspring calls, based on previous studies of tree swallows that have shown that these two parameters increase with food deprivation (Leonard & Horn, 2001a; Leonard & Horn, 2005; Marques et al., 2011).

We also evaluated how begging signals and ambient temperatures were associated with parents' immediate responses in terms of the time taken to return to the nest. We expected that parents would return to the nest sooner after their broods gave more intense begging calls, as suggested by previous studies (e.g., Stamps et al., 1989; Leonard & Horn, 2001a, b). We also expected that parents would return to the nest sooner under warmer conditions, because warmer weather increases the activity of flying insect prey that tree swallows feed to their offspring (McCarty & Winkler, 1999; Winkler et al., 2013).

2. Material and methods

2.1. Field methods

We studied tree swallows nesting in boxes from May–June 2013 at the Queen's University Biological Station (QUBS) in Ontario, Canada (44°34′N, 76°19′W, approx. 135 m elevation). All nestboxes at this site have identical

dimensions (12.5 × 14.8 cm floor, interior height = 19.7 cm at the front rising to 24.6 cm at the rear) and are arranged in grids, facing the same cardinal direction. We determined the dates when egg laying and hatching began for all nests initiated in May 2013. At 27 nests, we recorded 60 min of audio on day 3 of the chick-rearing phase (hatch day = day 0), using an omnidirectional microphone (OLM-10 Lavalier Mic, Pearstone, NY, USA) mounted inside the nest box 14–24 cm above the nestlings (mean distance = 18.6 cm), with the microphone oriented parallel to the top of the nest (Fairhurst et al., 2013). We used Edirol R-09 and R-05 recorders (Roland, Los Angeles, CA, USA) placed on the ground below the nest box with input levels set to maximum to record mp3 files (48 kHz sample rate, 192 kb/s). All recordings were made between 7:30–14:00 local time, and ambient temperatures ranged from 12–29°C during recordings (Figure 1).

After setting up the microphone inside the nest box and counting the number of nestlings, an observer seated approximately 20 m away noted the times to the nearest minute whenever a parent entered or left the nest box. Parent tree swallows deliver food in 95–98% of these nest visits (McCarty, 2002), and visit frequency does not change systematically with time of day (Rose et al., 2009; Lendvai et al., 2015).

Observations began 5 min after setting up the audio recorders and continued for 60 min. Male and female parents were differentiated using plumage colour at 9 nests where the female was in her first year of breeding. Female tree swallows in their first year have predominantly brownish dorsal plumage that is easily distinguished from the uniformly blue–green dorsal plumage of
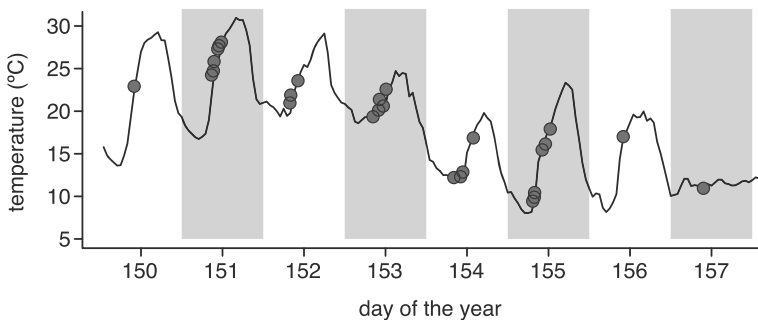

Figure 1. Ambient temperature flux during the breeding season at the Queen's University Biological Station in 2013. Alternating shaded and white bars denote calendar days. Circles mark the times of audio recordings at 27 nests, with points jittered for visibility.

males and older females (Hussell, 1983; Dakin et al., 2016). At the remaining nests, male and female parents were differentiated using either leg bands applied in previous years ($N = 2$ nests), or acrylic paint that was applied passively to only one parent during the incubation period ($N = 16$ nests). To apply paint marks, we mounted a small sponge with a dab of paint on the nest-box entrance during the egg incubation period until we observed the female entering the box and passively applying paint to her head (only females incubate; Ardia et al., 2006a).

2.2. Offspring begging intensity

We used Raven 1.5 (Bioacoustics Research Program, 2014) to generate spectrograms (Hann window, 512 samples, 93.8 Hz grid spacing, 256 hop size) of the period following each observed parental visit, with the exact time of the visit in the recording defined using the sound the parent made upon making contact with the nestbox (Figure 2a, b; sounds are provided in the Supplementary material in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x). To quantify the begging signals received by parent tree swallows, we examined a 45 s time window following this arrival time, which is approximately the mean duration of parental feeding visits (43.3 s, Leonard et al., 1997; see also Figure 2c, d). If the next parental visit occurred before 45 s had elapsed ($N = 23$ visits), the previous visit was still used, but was truncated at the other parent's arrival time.

As measures of begging intensity, we quantified two features of brood begging calls that are known to increase following food deprivation: (1) average begging call length and (2) per capita begging rate, or the number of calls emitted per nestling per unit time (Leonard & Horn, 2001a, 2005; Marques et al., 2011). Using spectrograms, we measured the length of each begging call in seconds and took the average for the brood over each parental visit. As a measure of per capita begging rate, we counted the number of begging calls emitted by the brood during the visit period (up to 45 s, but shorter if the other parent arrived before 45 s had elapsed), and then divided that number by the duration of time and the number of nestlings. The begging calls were short enough that they did not overlap. We did not assess call amplitude or frequency, because these two parameters do not change reliably with food deprivation in tree swallows at the age when we studied them (Leonard & Horn, 2006), and because our recordings were not calibrated to measure absolute amplitude.
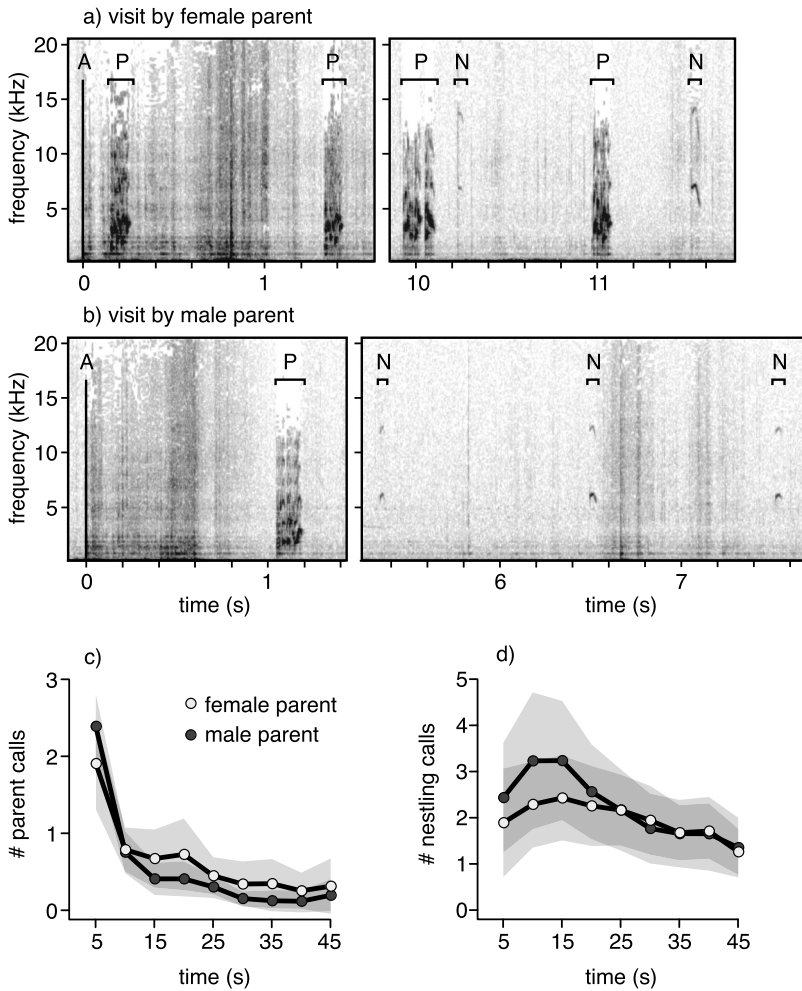
Figure 2. Sound spectrograms of parent-offspring interactions (a, b). A = sound of the parent arriving at the nest box; P = parental '*chirp*' call; N = nestling begging '*tseep*' call. The corresponding audio files are available as Supplementary material in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/ 1568539x. The incidence of parent and offspring calls is highest immediately after parental arrival and decreases thereafter (c, d). Each plot shows the grand mean number of calls for 5 s intervals, with shaded 95% confidence intervals. Note that the data in panels c and d include nests and visits that were not included in further statistical analyses.

When parent tree swallows arrive at the nest they typically give calls that stimulate their nestlings to beg (Figure 2a, b; Leonard et al., 1997). We thus omitted visits where parents did not call, including two nests where parental calls were never detected, as we did not want to analyse events where we could not be certain that a parent-offspring interaction occurred (Leonard et al., 1997). We also omitted one nest where no nestling calls were detected and where the female brooded continuously for 27 min. Two other nests had average brood begging call rates of 0 (i.e., no nestling calls were detected), but parental visit behaviour was typical and parents gave calls that stimulate begging as observed at the other nests. Thus, we included these two nests with a call rate of zero in our analyses of begging rate; however, we also note that our conclusions remain the same even if they are excluded.

At the 24 nests analysed, we observed 310 parental visits, 289 (93%) of which could be detected in the audio recordings. The remaining 7% of visits could not be detected in the audio recordings. However, there was no evidence that these missing visits biased our results (see additional data in Appendix A). Parents called during 234 of the visits we detected in the audio recordings, with brood begging rates quantified over a grand mean of 43.5 s per visit (range of nest means 31–45 s) and 4.8 visits per parent (range of parent means 1–10; $N = 45$ parents at 24 nests; note that at some nests one parent is missing either because that parent did not visit during our observation period, or because no visits met the above criteria).

2.3. Ambient temperature

Local hourly air temperatures were recorded using two HOBO™ data loggers placed at the Queen's University Biological Station, taking an average of the two data loggers (Figure 1). We estimated ambient temperatures at the time of each nest visit using linear interpolation of these averages in R 3.0.2 (R Core Team, 2014) using the zoo package (v 1.7-11; Zeileis et al., 2015). At our study site, all of the nestboxes were located in open, unshaded grass fields, facing the same direction, which would have minimized temperature variation among nests resulting from external factors. We cannot exclude other sources of variation in nest temperature, such as the amount and construction of nesting material. Nevertheless, the temperature inside of a nestbox is strongly correlated with local ambient temperature flux in tree swallows (Dawson et al., 2005; Ardia et al., 2006b). Thus, all else being equal, ambient temperature provides an indication of internal nestbox temperature flux in this species.

To account for the potential influence of parental brooding behaviour on the nestlings, we defined periods when a parent stayed on the nest for more than 1.5 min as brooding periods. Both male and female parents were observed to perform brooding behaviour (maximum duration on the nest: 13 min for males; 18 min for females, among the nests analysed), although female tree swallows are the primary brooders (Leonard et al., 1997).

2.4. Offspring body mass

We measured body mass ($\pm$ 0.01 g) of each nestling the day after the audio recordings, during a time when the parents were captured for a separate experiment (Ouyang et al., 2015). We used the average body mass for each brood in our analysis (mean $= 6.8$ g, range 5.0–8.8 g, $N = 24$ nests). We checked whether average body mass was associated with parental feeding and brooding behaviours (see Section 3.1).

2.5. Ethical note

All procedures followed the guidelines of the Canadian Council on Animal Care (CCAC) and the Association for the Study of Animal Behaviour, and were approved by the Queen's University Animal Care Committee. Offspring were weighed at the nest with the whole brood removed temporarily and held on cotton for the duration of time required to weigh each nestling. We do not examine brood fate here, because of a separate corticosterone hormone manipulation applied after the observations in this study (Ouyang et al., 2015).

2.6. Data analysis

To address our first question about the factors influencing begging call production, we used generalized linear mixed models (GLMMs) in R 3.0.2 (R Core Team, 2014) to examine brood begging call rate and call length as dependent variables, modelling these variables for each parental nest visit. For per capita begging call rate, Gaussian and Poisson model assumptions were not met. We therefore used a negative binomial model with a log link, implemented in the glmmADMB package (v 0.8.0; Skaug et al., 2015), to model per capita begging call rate. For begging call length, we used a Gaussian mixed model with the identity link implemented in the nlme package (v 3.1-120; Pinheiro et al., 2015). Models of begging call features also included a random effect of brood to account for multiple observations of the same nest.

We included the following fixed effects as predictors of brood begging intensity: sex of the visiting parent, date, brood size, time elapsed since the last parental arrival (as a measure of the extent of food deprivation), the total brooding time, ambient temperature, average offspring body mass, and the two-way interaction between ambient temperature and average offspring body mass. We included parental sex and brood size to allow for the possibility that parental and sibling behaviour might influence begging. For instance, the presence of begging nestmates can induce nestling begging (Smith & Montgomerie, 1991; Leonard et al., 2000; Leonard & Horn, 2001c). Additionally, male and female parents may differ in behaviours that stimulate begging (Leonard et al., 1997).

To address our second question about the factors influencing parental behaviour, we analysed the length of time parents spent away from the nest before returning as the dependent variable. Again this was modelled at the level of individual nest visits. We analysed this measure of return latency by log-transforming it and fitting a Gaussian mixed model in nlme (Pinheiro et al., 2015). We included the following fixed effects as predictors of return latency: sex of the visiting parent, date, brood size, per capita begging call rate, average begging call length, ambient temperature, and average offspring mass. This model also included random effects of parent identity nested within brood. To allow for the possibility that male and female parents may differ in how they respond to begging, and that they might respond in a temperature- or offspring size-dependent manner, we also checked eight two-way interaction terms. We entered the interaction terms in the following order: parent sex × brood size, parent sex × per capita begging rate, parent sex × begging call length, parent sex × ambient temperature, ambient temperature × per capita begging rate, ambient temperature × begging call length, mean offspring mass × per capita begging rate, and mean offspring mass × begging call length.

In all models, interaction terms were entered one at a time, and were retained only if the *p*-value was less than 0.1 (Engqvist, 2005). We used Wald *Z*-tests and *t*-tests to evaluate the significance of fixed effects for negative binomial and Gaussian models, respectively. All models met assumptions for residual distributions and had variance inflation factors <8 after mean-centering the predictors. To check whether our model results were robust to influential datapoints, we examined Cook's distance for the Gaussian models

using the package influence.ME (v 0.9-6; Nieuwenhuis et al., 2015), and confirmed that all Cook's D values were <1. For the negative binomial model, Cook's D diagnostics were not available, so we performed two additional checks. First, we confirmed that the results of this model did not change when we refit the model excluding all observations with residual values >1.5 ($N = 17$ observations excluded). Second, we refit the model excluding all observations from a single nest. We repeated this 24 times, once for each nest. In each case, the results remained the same, indicating that no single nest was overly influential in driving the results.

Main effects were considered significant if $p < 0.05$, but were not tested in the presence of an interaction involving two continuous variables; in these instances, we interpret the strength and direction of the interaction and provide additional comparisons for specific ranges of the predictor variables. For temperatures, our additional comparisons examined the ranges of <15°C, 15–25°C, and >25°C, respectively, because 15 and 25°C were approximately the 25th and 75th percentiles in our dataset; these values were also close to the average daytime low and high temperatures of 14 and 23°C. For body mass, our additional comparisons tested for differences between broods with below-average (<6.8 g) and above-average (>6.8 g) nestling body mass.

Table 1 provides descriptive statistics and details of sample sizes for these analyses. Note that in order to consider deprivation as a predictor of begging intensity, our analyses of begging call features include only visits where the previous parental visit was observed. Additionally, the number of visits analysed for begging call length was less than the number analysed for begging call rate, because call length could not be calculated for visits with no calls.

3. Results

3.1. Offspring mass and parental care

Average offspring body mass was positively correlated with the total number of visits to the nest by the male ($R^2 = 0.16$, $p = 0.05$, $N = 24$ nests), but not the female parent ($R^2 = 0.06$, $p = 0.26$, $N = 24$; see also Dakin et al., 2016). Average offspring body mass on day 4 was not significantly correlated with the total duration that the offspring were brooded during observations ($R^2 = 0.03$, $p = 0.43$, $N = 24$ nests) or with the average time latency between parental visits ($R^2 = 0.06$, $p = 0.23$, $N = 24$ nests).

Table 1.
Descriptive statistics for offspring begging calls and parental feeding behaviours.

	Sample size	Grand mean	Range of means
Brood			
Begging call rate per capita	216 visits[1]	4.9 calls/min per nestling	0–23.5
Begging call length	143 visits[2]	53 ms	32–82
Time elapsed since last parental arrival	216 visits[1]	5.0 min	1.7–13.6
Total brooded time per hour	24 broods[4]	22.4 min	0–47.0
Offspring mass	24 broods	6.8 g	5.0–8.8
Parental			
Nest visits per hour	14 females[4]	female 7.7 visits/h	3–13
	19 males[4]	male 7.2 visits/h	3–13
Time in nestbox per visit	22 females	female 3.6 min	0–15.0
	23 males	male 0.5 min	0–6.5
	24 broods		
Time out of nest before returning	14 females	female 6.7 min	2.0–17.0
	19 males	male 7.3 min	2.5–17.0
	20 broods		

Grand means were calculated by taking the mean for each sampling unit (brood or parent, depending on who performed the behaviour), and then averaging across those sampling units.

[1] Includes only instances when the time of the previous visit was known.
[2] Includes instances when the time of the previous visit was known, and offspring begged.
[3] Includes only instances when offspring begged and the parent's next visit could be identified.
[4] Mean and range of hourly values reported.

Table 2.
Mixed-effects model of per capita begging call rate (No. of calls/min per nestling).

Fixed effect	Estimate	95% CI	z	p
Sex of parent (male vs. female)	−0.33	−0.63, −0.04	−2.20	0.03
Date (day of year)	−0.38	−1.11, 0.36	−1.00	0.32
Brood size (No. of offspring)	0.45	−0.35, 1.25	1.10	0.27
Time since last parent arrival (min)	0.06	0.02, 0.09	3.39	<0.001
Total brooding time (min)	0.03	−0.05, 0.10	0.72	0.47
Offspring mass (g)	4.19	1.24, 7.14	–	–
Ambient temperature (°C)	1.29	0.43, 2.16	–	–
Offspring mass × ambient temperature	−0.21	−0.34, −0.07	−3.02	0.003

Begging call rate was modelled with a negative binomial error distribution and a log link. The model includes a random effect of brood ($N = 216$ parental visits to 24 broods). All fixed effects except for parent sex are continuous variables. Note that main effects are not tested in the presence of a significant interaction involving that variable.

3.2. Offspring begging intensity

Three-day old broods called at an average rate of about 5 calls/min per nestling during parental visits, with an average call length of 53 ms (Table 1). There was a significant interaction between offspring mass and temperature for per capita begging call rate (Table 2) and average begging call length (Table 3). As temperatures increased, broods with the smallest nestlings

Table 3.
Mixed-effects model of brood begging call length (ms).

Fixed effect	Estimate	95% CI	t	p
Sex of parent (male vs. female)	−0.78	−3.90, 2.35	−0.49	0.63
Date (day of year)	−1.81	−6.61, 2.98	−0.74	0.47
Brood size (No. of offspring)	0.10	−4.72, 4.92	0.04	0.97
Time since last parent arrival (min)	−0.10	−0.48, 0.28	−0.52	0.61
Total brooding time (min)	0.33	−0.14, 0.79	1.37	0.19
Offspring mass (g)	20.27	1.09, 39.44	–	–
Ambient temperature (°C)	7.85	2.30, 13.40	–	–
Offspring mass × ambient temperature	−1.11	−2.00, −0.22	−2.45	0.02

Call length was modelled with a Gaussian error distribution and identity link, and a random effect of brood ($N = 143$ parental visits to 22 broods). All fixed effects except for parent sex are continuous variables. Note that main effects are not tested in the presence of a significant interaction involving that variable.
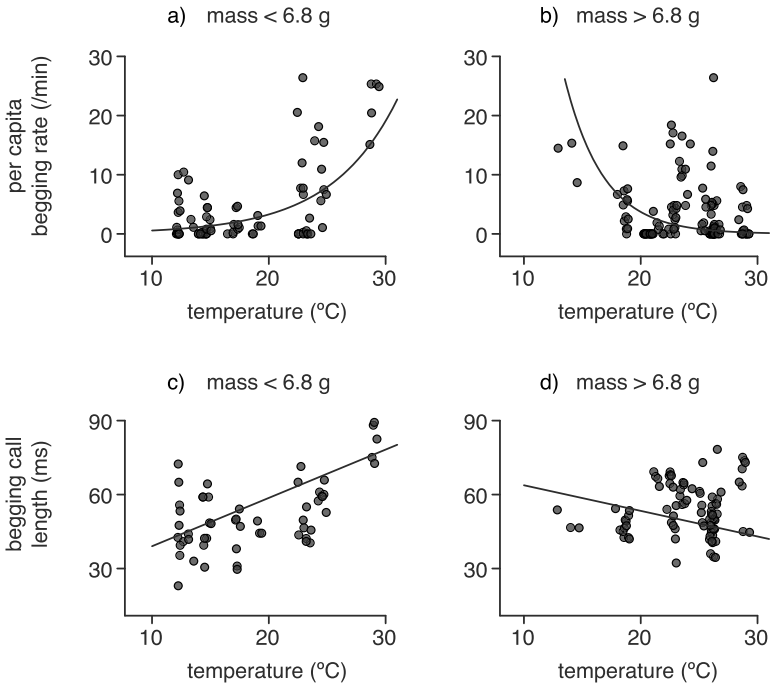
Figure 3. As ambient temperature increases, begging call rate (a) and begging call length (c) increase for broods with smaller nestlings. In contrast, begging call rate (b) and length (d) decrease with ambient temperature for broods with larger nestlings. Lines show regression predictions from the analyses in Tables 2 and 3, with covariates set to their mean values, and body mass set to 5.4 g in (a, c) and 8.0 g in (b, d). Note that offspring mass is treated as a continuous variable in analyses, with separate categories shown here as a means of illustrating the interaction between two continuous variables (mass and temperature). Points are shaded semi-transparently to indicate the density of overlapping data.

called at a higher rate and gave longer begging calls (Figure 3a, c), whereas broods with the largest nestlings called less often and gave shorter calls (Figure 3b, d). Per capita begging call rate increased with the time elapsed since the last parental arrival (Table 2), consistent with previous studies (e.g., Leonard & Horn, 2001a). Per capita begging call rate also tended to be slightly lower during visits by the male parent, as compared with maternal visits (Table 2). Neither call length nor call rate were significantly related to number of young in the brood or the total brooding time (Table 2, Table 3).

To illustrate how ambient temperature alters the relationship between nestling mass and begging intensity, Figure 4 shows predicted values from the fitted models in Tables 2 and 3. All else being equal, as the ambient tem-

Table 4.
Mixed-effects model of the latency for parents to return to the nest.

Fixed effect	Estimate	95% CI	t	p
Sex of parent (male vs. female)	0.05	−0.25, 0.35	0.34	0.74
Date (day of year)	−0.06	−0.21, 0.08	−0.85	0.41
Brood size (No. of offspring)	−0.22	−0.51, 0.06	−1.53	0.15
Ambient temperature (°C)	−0.02	−0.09, 0.04	−0.75	0.45
Begging call rate (calls/min per offspring)	0.02	−0.01, 0.04	1.42	0.16
Begging call length (ms)	−0.11	−0.19, −0.03	–	–
Offspring mass (g)	−0.82	−1.50, −0.15	–	–
Begging call length × offspring mass	0.01	0.00, 0.03	2.24	0.03

The amount of time parents spent out of the nest (min) was log-transformed and modelled with a Gaussian error distribution and identity link, with random effects of parent identity nested within brood ($N = 96$ parental visits by 33 parents to 20 broods). All fixed effects except for parent sex are continuous variables. Note that main effects are not tested in the presence of a significant interaction involving that variable.

perature warms from 13.5 to 23.5°C, the smallest nestlings (per capita brood body mass = 5.4 g, in the 10th percentile) are predicted to increase their begging call rate from 1 to 5 calls/min, and they are predicted to increase their begging call length from 46 to 64 ms. In contrast, the largest nestlings (per capita brood body mass = 8.0 g, the 90th percentile) are predicted to decrease their call rate from 34 calls/min to 1 call/min over this same temperature range, and decrease their call length from 59 to 49 ms.

To further explore the interaction between offspring body mass and temperature, we tested the difference in begging performance for below average (<6.8 g) and above average (>6.8 g) nestling size classes at different temperature ranges. When ambient temperature was below 15°C, the smaller nestlings called at significantly lower rates than the larger nestlings (small 1.8 calls/min per nestling vs. large 12.8 calls/min per nestling; $p = 0.03$; $N = 40$ visits to 5 nests), although there was no significant difference in call length at cold temperatures when comparing size classes (small 50 ms vs. large 49 ms; $p = 0.95$; $N = 25$ visits to 5 nests). At moderate temperatures between 15 and 25°C, there was no significant difference between the two size classes in either call rate (small 5.6 calls/min per nestling vs. large 3.9 calls/min per nestling; $p = 0.64$; $N = 100$ visits to 13 nests) or call length (small 50 ms vs. large 54 ms; $p = 0.51$; $N = 67$ visits to 12 nests). At the warmest temperatures above 25°C, the smaller nestlings called at significantly higher rates (small 22.2 calls/min per nestling vs. large 2.5 calls/min
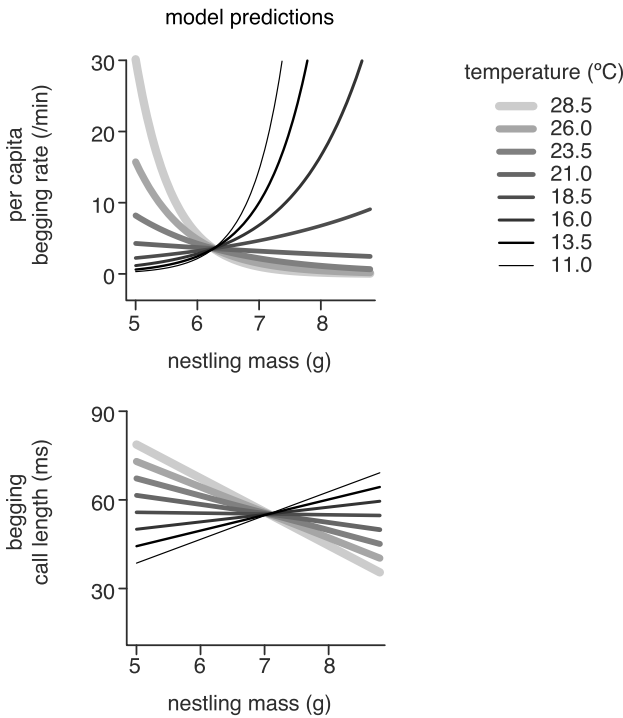
model predictions

Figure 4. Predictions for the fitted models in Tables 2 and 3. At warm temperatures, the smallest nestlings are predicted to beg the most intensely (i.e., consistent with "signal of need"). At cold temperatures, the largest nestlings are predicted to beg the most intensely (consistent with "signal of quality"). All other covariates were set to their mean values to determine the predicted values.

per nestling; $p = 0.001$; $N = 76$ visits to 7 nests) and produced significantly longer calls (small 82 ms vs. large 53 ms; $p = 0.03$; $N = 51$ visits to 6 nests) than the larger nestlings.

3.3. Parental provisioning behaviour

There was a significant interaction between average offspring mass and begging call length (Table 4). Parents that experienced longer begging calls returned to the nest sooner for their subsequent visit if they had smaller nestlings (Figure 5a). However, the return latency of parents with larger nestlings was not associated with begging call length (Figure 5b). We did not detect a significant association between parent return latency and per capita begging call rate (Figure 5c), nor did we detect a significant association between parent return latency and ambient temperature (Figure 5d). None of
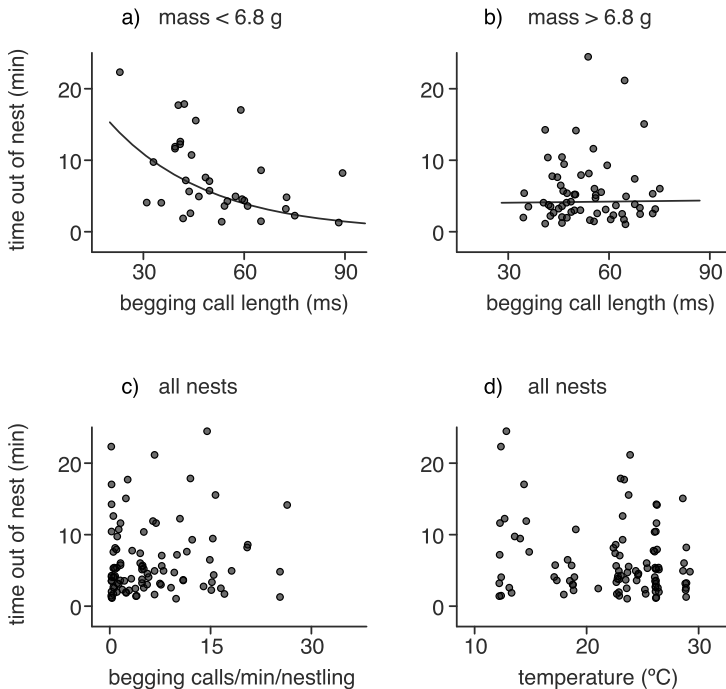
Figure 5. Parent tree swallows (a) returned to the nest sooner after experiencing longer begging calls by small nestlings, but (b) the time taken by parents to return to the nest was not associated with begging call length for parents with large nestlings. The time taken by parents to return to the nest was also not associated with per capita begging call rate (c) or ambient temperature (d). Lines in panels a and b show regression predictions from the analysis in Table 4, with covariates set to their mean values, except for body mass which was set to 5.4 g in (a) and 8.0 g in (b). Note that offspring mass is treated as a continuous variable in analyses, with separate categories shown in (a, b) as a means of illustrating the interaction between the two continuous variables (mass and call length). Points are shaded semi-transparently to indicate the density of overlapping data.

the other predictors we examined were significantly associated with the time it took parents to return to the nest (Table 4).

4. Discussion

Ambient temperature varied over a wide range at our study site from approximately 10°C to 30°C (Figure 1). This provided an opportunity to examine the effect of ambient temperature variation on begging call dynamics at the nest. We found that as the ambient temperature increased, the smallest nestlings

begged more often and gave longer calls (Figure 3a, c), whereas the largest nestlings decreased their begging intensity (Figure 3b, d). Our results are thus consistent with the prediction that broods with smaller nestlings experience a more rapid decrease in performance with decreasing temperature. These temperature-dependent shifts represent a substantial change in the signals received by parents, and in the relationship between begging intensity and offspring mass (Figures 3 and 4).

Why did the smallest nestlings decrease their begging intensity as ambient temperatures cooled? Body temperatures of individual nestlings with lower body mass drop more rapidly than body temperatures of larger individuals (Dunn, 1970; Marsh, 1980; Leonard & Horn, 2001a). Thus, smaller individuals cool faster when it is cold. Sub-optimal body temperature may reduce an individual's ability to beg in spite of its hunger and/or need, either because its muscles drop below the threshold temperature necessary for tetanic contraction (Choi & Bakken, 1990; Gillooly & Ophir, 2010), or because sufficient energy is no longer available to perform calling behaviour (Leech & Leonard, 1996; McCarty, 1996; Martín-Gálvez et al., 2011) as a result of reduced parental feeding and/or offspring digestive efficiency. These constraints are relaxed in warm weather, increasing the upper limit on call rate and length (Gillooly & Ophir, 2010). The rate of cooling may be further influenced by the number and average body size of other nestmates.

Why did the heaviest nestlings reduce their begging rate, such that they begged less than very small nestlings under the warmest conditions? One possibility is that under the warmest conditions, heavier offspring may have reduced their begging rate because they were receiving sufficient food from their parents to satisfy their hunger or needs (McCarty & Winkler, 1999; Winkler et al., 2013). Parent tree swallows deliver a bolus that contains multiple insect prey items on each parental provisioning visit (Mengelkoch et al., 2004; Brasso & Cristol, 2008); thus, the quantity and quality of prey delivered may have varied with temperature, even though we did not detect an association between ambient temperature and the time it took parents to return to the nest for their next visit (Figure 5d; see also Rose, 2009). Insect prey activity is increased in warmer temperatures, facilitating foraging by parent tree swallows (McCarty & Winkler, 1999; Winkler et al., 2013). It is also possible that under colder conditions, the largest offspring need more food to meet their needs, and/or they may digest and metabolize the food they receive more efficiently as temperatures warm (Grodzinski et

al., 2009). Finally, an alternative hypothesis is that the largest nestlings may have altered their begging behaviour at warm temperatures for other reasons, for instance if they were performing behaviours to shed heat. Red-winged blackbird nestlings have been shown to slightly decrease their begging performance at body temperatures above 42°C (Choi & Bakken, 1990).

Our results suggest that parents of small nestlings had an immediate response to the call length of their offspring, because they tended to return to the nest more rapidly after hearing longer begging calls (Table 4, Figure 5a). However, return latency was not associated with call length for parents of the largest nestlings (Figure 5b). This suggests that parents respond to nestling calls in a size-dependent manner. When small nestlings produced short begging calls, parents took much longer to return to feed them than the average brood with large nestlings (Figure 5a, b). Although we did not detect a relationship between per capita begging call rate and parents' return latency, a previous experiment has shown that parent tree swallows are more likely to allocate food delivery to individual nestlings paired with playback of higher begging rates, holding other acoustic features constant (Leonard & Horn, 2001b). This raises the possibility that different aspects of offspring calls may influence parental behaviour in different ways (Rector et al., 2014). For instance, different signal components may influence allocation towards particular individuals vs. effort invested in the current brood as a whole. Further studies that experimentally manipulate different signal components are needed to test this hypothesis.

Comparing our study to previous studies of tree swallow begging calls, the average per capita begging call rate in this study was consistent with the rate at which individual 4–5-day-old tree swallow nestlings called in the laboratory after being fed and then deprived of food for 10–20 min (Leonard & Horn, 2006). The average begging call length in this study (53 ms) was considerably longer than that of similarly aged individual tree swallow nestlings (approx. 20–30 ms in Leonard & Horn, 2006). There are several possible reasons for this difference in call length, including the presence of nestmates, differences in ambient noise levels (Leonard & Horn, 2005), and/or differences in nest cavity size across studies (Fairhurst et al., 2013). It is important to note that durations of calls measured on spectrograms are also influenced by the software and parameters used to generate the spectrograms, making it difficult to compare across studies.

Because this was an observational study, we cannot rule out the potential effect of temperature during our behavioural observations on our measure of nestling body mass taken the following day (McCarty & Winkler, 1999; Eeva et al., 2002; Dawson et al., 2005). Indeed, brood-average body mass in this study was weakly associated with the average morning temperature the previous day ($p = 0.04$, $R^2 = 0.14$; $N = 24$ nests). However, day 3 temperature was not the only factor affecting body mass, as we recorded small and large nestlings over the same range of temperatures on day 3 (mass < 6.8 g, range 12.2–29.3°C; mass > 6.8 g, range 12.8–29.2°C). Moreover, extrapolating from McCarty (2001) and Dawson et al. (2005), even a 20°C difference in temperature on day 3 could account for, at most, a range of about 0.7 g in mass the following day, much smaller than the 3.8 g range of variation observed (5.0–8.8 g; see Appendix A). Thus, in our study population, there was considerable variation in offspring mass independent of the temperature during our observations.

In summary, we show here that typical ambient temperature flux can constrain the ability of small nestlings to beg and alter the function of begging calls (Figure 4). When ambient temperatures were cold, the nestlings that were in the best condition with the highest body mass begged the most intensely, whereas the reverse was true at warmer temperatures. At moderate ambient temperatures, there was no significant difference in begging intensity between the size classes. This indicates that nestling begging calls are not a straightforward signal of quality or need (Mock et al., 2011). Instead, these signals are weather-dependent signals of offspring state, and parents may need to integrate multiple dynamic cues to determine the appropriate response (Dawson et al., 2005; Ouyang et al., 2015). Our results therefore provide an example and mechanism for how context-dependent dynamics of begging signal function can occur (Bro-Jørgensen, 2010). Moreover, we show how environmental quality can influence the function of begging calls even within a single species (Caro et al., 2016). Further studies are needed to understand the physiological links between environmental conditions, such as temperature, and the diversity of begging signal functions both within and across species.

Acknowledgements

References

Ardia, D.R., Cooper, C.B. & Dhondt, A.A. (2006a). Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range. — J. Avian Biol. 37: 137-142.

Ardia, D.R., Perez, J.H. & Clotfelter, E.D. (2006b). Nest box orientation affects internal temperature and nest site selection by Tree Swallows. — J. Field Ornithol. 77: 339-344.

Bengtsson, H. & Rydén, O. (1983). Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. — Behav. Ecol. Sociobiol. 12: 243-251.

Bioacoustics Research Program (2014). Raven Pro: interactive sound analysis software (version 1.5) (computer software). — The Cornell Lab of Ornithology, Ithaca, NY, available online at http://www.birds.cornell.edu/raven.

Brasso, R.L. & Cristol, D.A. (2008). Effects of mercury exposure on the reproductive success of tree swallows (*Tachycineta bicolor*). — Ecotoxicology 17: 133-141.

Bro-Jørgensen, J. (2010). Dynamics of multiple signaling systems: animal communication in a world in flux. — Trends Ecol. Evol. 25: 292-300.

Budden, A.E. & Wright, J. (2001). Begging in nestling birds. — Curr. Ornithol. 16: 83-118.

Caro, S.M., Griffin, A.S., Hinde, C.A. & West, S.A. (2016). Unpredictable environments lead to the evolution of parental neglect in birds. — Nature Commun. 7: 10985.

Choi, I. & Bakken, G.S. (1990). Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. — Phys. Zool. 63: 965-986.

Dakin, R., Lendvai, Á.Z., Ouyang, J.Q., Moore, I.T. & Bonier, F. (2016). Plumage colour is associated with partner parental care in mutually ornamented tree swallows. — Anim. Behav. 111: 111-118.

Dawson, R.D., Lawrie, C.C. & O'Brien, E.D. (2005). The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. — Oecologia 144: 499-507.

Dawson, W.R. & Evans, F.C. (1957). Relation of growth and development to temperature regulation in nestling field and chipping sparrows. — Phys. Zool. 30: 315-327.

Dor, R. & Lotem, A. (2009). Heritability of nestling begging intensity in the house sparrow (*Passer domesticus*). — Evolution 63: 738-748.

Dunn, E.H. (1975). The timing of endothermy in the development of altricial birds. — Condor 77: 288-293.

Eeva, T., Lehikoinen, E., Rönkä, M., Lummaa, V. & Currie, D. (2002). Different response to cold weather in two pied flycatcher populations. — Ecography 25: 705-713.

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. — Anim. Behav. 70: 967-971.

Evans, R.M. (1994). Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. — Behaviour 129: 13-34.

Fairhurst, E.N., Horn, A.G. & Leonard, M.L. (2013). Nest acoustics and begging call structure in nestling tree swallows. — Anim. Behav. 85: 913-923.

Gerhardt, H.C. (1978). Temperature coupling in the vocal communication system of the gray tree frog, *Hyla versicolor*. — Science 199: 992-994.

Gillooly, J.F. & Ophir, A.G. (2010). The energetic basis of acoustic communication. — Proc. Roy. Soc. Lond. B: Biol. Sci. 277: 1325-1331.

Godfray, H.C.J. (1991). Signalling of need by offspring to their parents. — Nature 352: 328-330.

Grafen, A. (1990). Biological signals as handicaps. — J. Theor. Biol. 144: 517-546.

Grodzinski, U. & Lotem, A. (2007). The adaptive value of parental responsiveness to nestling begging. — Proc. Roy. Soc. Lond. B: Biol. Sci. 274: 2449-2456.

Grodzinski, U., Hauber, M.E. & Lotem, A. (2009). The role of feeding regularity and nestling digestive efficiency in parent–offspring communication: an experimental test. — Funct. Ecol. 23: 569-577.

Hussell, D.J.T. (1983). Age and plumage color in female tree swallows. — J. Field Ornithol. 54: 312-318.

Kilner, R.M. & Johnstone, R.A. (1997). Begging the question: are offspring solicitation behaviours signals of need? — Trends Ecol. Evol. 12: 11-15.

Leech, S.M. & Leonard, M.L. (1996). Is there an energetic cost to begging in nestling tree swallows (*Tachycineta bicolor*)? — Proc. Roy. Soc. Lond. B: Biol. Sci. 263: 983-987.

Lendvai, Á.Z., Akçay, C., Ouyang, J.Q., Dakin, R., Domalik, A.D., St John, P.S., Stanback, M., Moore, I.T. & Bonier, F. (2015). Analysis of the optimal duration of behavioral observations based on an automated continuous monitoring system in tree swallows (*Tachycineta bicolor*): is one hour good enough? — PLoS ONE 10: e0141194.

Leonard, M. & Horn, A.G. (1996). Provisioning rules in tree swallows. — Behav. Ecol. Sociobiol. 38: 341-347.

Leonard, M.L. & Horn, A.G. (1998). Need and nestmates affect begging in tree swallows. — Behav. Ecol. Sociobiol. 42: 431-436.

Leonard, M.L. & Horn, A.G. (2001a). Acoustic signalling of hunger and thermal state by nestling tree swallows. — Anim. Behav. 61: 87-93.

Leonard, M.L. & Horn, A.G. (2001b). Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). — Behav. Ecol. Sociobiol. 49: 170-175.

Leonard, M.L. & Horn, A.G. (2001c). Dynamics of calling by tree swallow (*Tachycineta bicolor*) nestmates. — Behav. Ecol. Sociobiol. 50: 430-435.

Leonard, M.L. & Horn, A.G. (2005). Ambient noise and the design of begging signals. — Proc. Roy. Soc. Lond. B: Biol. Sci. 272: 651-656.

Leonard, M.L. & Horn, A.G. (2006). Age-related changes in signalling of need by nestling tree swallows (*Tachycineta bicolor*). — Ethology 112: 1020-1026.

Leonard, M.L., Fernandez, N. & Brown, G. (1997). Parental calls and nestling behavior in tree swallows. — Auk 114: 668-672.

Leonard, M.L., Horn, A.G., Gozna, A. & Ramen, S. (2000). Brood size and begging intensity in nestling birds. — Behav. Ecol. 11: 196-201.

Marques, P.A., Leonard, M.L., Horn, A.G. & Contasti, A. (2011). How nestling tree swallows (*Tachycineta bicolor*) integrate their responses to hunger and signalling by nestmates. — Ethology 117: 163-170.

Marsh, R.L. (1980). Development of temperature regulation in nestling tree swallows. — Condor 82: 461-463.

Martín-Gálvez, M., Pérez-Contreras, T., Soler, M. & Soler, J.J. (2011). Benefits associated with escalated begging behaviour of black-billed magpie nestlings overcompensate the associated energetic costs. — J. Exp. Biol. 214: 1463-1472.

McCarty, J.P. (1996). The energetic cost of begging in nestling passerines. — Auk 113: 178-188.

McCarty, J.P. (2001). Variation in growth of nestling tree swallows across multiple temporal and spatial scales. — Auk 118: 176-190.

McCarty, J.P. (2002). The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in tree swallows. — J. Field Ornithol. 73: 9-14.

McCarty, J.P. & Winkler, D.W. (1999). Relative importance of environmental variables in determining the growth of nestling tree swallows *Tachycineta bicolor*. — Ibis 141: 286-296.

Mengelkoch, J.M., Niemi, G.J. & Regal, R.R. (2004). Diet of the nestling tree swallow. — Condor 106: 423-429.

Mock, D.W., Dugas, M.B. & Strickler, S.A. (2011). Honest begging: expanding from signal of need. — Behav. Ecol. 22: 909-917.

Nieuwenhuis, R., Pelzer, B. & te Grotenhuis, M. (2015). influence.ME: tools for detecting influential data in mixed effects models. — R package version 0.9-6. R Foundation for Statistical Computing, Vienna, available online at https://cran.r-project.org/web/packages/influence.ME/index.html.

Ouyang, J.Q., Lendvai, Á.Z., Dakin, R., Domalik, A.D., Fasanello, V.J., Vassallo, B.G., Haussmann, M.F., Moore, I.T. & Bonier, F. (2015). Weathering the storm: parental effort and experimental manipulation of stress hormones predict brood survival. — BMC Evol. Biol. 15: 219.

Parker, G.A., Royle, N.J. & Hartley, I.R. (2002). Begging scrambles with unequal chicks: interactions between need and competitive ability. — Ecol. Lett. 5: 206-215.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. (2015). nlme: linear and nonlinear mixed effects models. — R package version 3.1-120. R Foundation for Statistical Computing, Vienna, available online at https://cran.r-project.org/web/packages/nlme/index.html.

R Core Team (2014). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna. Available online at http://www.R-project.org.

Rector, M.E., Walsh, C.J., Kouwenberg, A., Fitzsimmons, M.G. & Storey, A.E. (2014). Signals of need and quality: Atlantic puffin chicks can beg and boast. — Behav. Ecol. 25: 496-503.

Rose, A.P. (2009). Temporal and individual variation in offspring provisioning by tree swallows: a new method of automated nest attendance monitoring. — PLoS ONE 4: e4111.

Royle, N.J., Hartley, I.R. & Parker, G.A. (2002). Begging for control: when are offspring solicitation behaviours honest? — Trends Ecol. Evol. 17: 434-440.

Ryan, M.J. (1988). Constraints and patterns in the evolution of anuran acoustic communication. — In: The evolution of the amphibian auditory system. Wiley, New York, NY, p. 637-677.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A. & Bolker, B. (2015). glmmADMB: generalized linear mixed models using AD model builder. — R package version 0.8.0. R Foundation for Statistical Computing, Vienna, available online at http://glmmadmb.r-forge.r-project.org/.

Smith, H.G. & Montgomerie, R. (1991). Nestling American Robins compete with siblings by begging. — Behav. Ecol. Sociobiol. 29: 307-312.

Stamps, J., Clark, A., Arrowood, P. & Kus, B. (1989). Begging behavior in budgerigars. — Ethology 81: 177-192.

Trivers, R.L. (1974). Parent–offspring conflict. — Am. Zool. 14: 249-264.

Winkler, D.W., Luo, M.K. & Rakhimberdiev, E. (2013). Temperature effects on food supply and chick mortality in tree swallows (*Tachycineta bicolor*). — Oecologia 173: 129-138.

Wright, J. & Leonard, M.L. (2002). The evolution of begging: competition, cooperation and communication. — Kluwer Academic Publishers, Dordrecht.

Zeileis, A., Grothendieck, G., Ryan, J.A. & Andrews, F. (2015). zoo: S3 infrastructure for regular and irregular time series (Z's ordered observations). — R package version 1.7-11. R Foundation for Statistical Computing, Vienna, available online at https://cran.r-project.org/web/packages/zoo/index.html.

Appendix A

A.1. *Missing visits*

To evaluate potential causes of the 21 missing visits that were observed but that could not be detected in our audio recordings, we examined binomial GLMMs of the proportion of a parent's visits that were missing in relation to each the following predictors: parental sex, brood size, date of the observation period, time of day of the observation period, average ambient temperature during the observation period, and offspring mass. These models included nest as a random effect to account for repeated measures of the same brood. Only parental sex was significantly associated with the proportion of missing visits (sex: $z = 2.84$, $p = 0.004$; all others: $p > 0.29$, $N = 45$ parents at 24 nests), suggesting that the odds of missing a male visit were about 6 times greater than the odds of missing a female visit (odds ratio 6.5 (95% CI 1.8, 23.4)).

To assess whether missing visits might have biased our estimates of begging rate or length, we also modeled the proportion of each parent's visits that could not be detected in the audio recordings in relation to the average per capita begging rate and the average begging call length experienced by that parent, again with nest as a random effect. There was no significant association between the proportion of visits that were missing and average per capita begging rate ($z = 1.36$, $p = 0.18$) or average begging call length ($z = 1.59$, $p = 0.11$), indicating that parents with more missing visits did not have especially high (or low) measures of brood begging rate. Thus, there was no evidence to suggest that missing visits biased our estimates of brood begging signals. The only significant predictor of the proportion of a parent's missing visits was parent sex. A possible explanation for this difference is that males may be more likely to enter the nest without the arrival sound used to locate visits in the audio recordings.

We did not attempt to quantify any begging calls that did not occur during observed visits, because there was no way to tell from the audio recordings alone whether a parent was in fact present and interacting with the nestlings.

A.2. Time of day

Because temperature is highly correlated with time of day (see main text Figure 1), we repeated our analyses with time of day in place of temperature. In no case was the resulting model a better fit than the original model (delta AICc 2.9–8.6). This supports our interpretation that the relationships described in the main text are the result of temperature.

A.3. Mass and temperature

To evaluate the potential influence of day 3 ambient temperature on day 4 body mass, we compared the range of body masses we observed to the expected effect of temperature on growth rate. The range of body masses observed was 5.0–8.8 g (mean 6.8 g; $N = 24$ nests). Extrapolating from Dawson et al. (2005), a 10°C difference in temperature would have yielded at most a difference in the growth rate constant, k, of 0.075. Solving the growth curve equation in McCarty (2001), using an average value of $k = 0.50$ from McCarty (2001) to represent typical conditions and an asymptotic mass of 21.7 g, a nestling with a body mass of 4.6 g on day 3 would have grown to 6.8 g on day 4 (the average we observed). If the temperature was 10°C

colder, the same nestling might have grown to only 6.4 g instead. If the temperature was 10°C warmer, the same nestling might have grown to 7.1 g instead. Therefore, even an extreme difference in temperature of 20°C can only explain a difference of about 0.7 g in body mass the following day, much smaller than the 3.8 g range of body masses observed (5.0–8.8 g).