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Separating the genetic and environmental drivers of body temperature during the development of endothermy in an altricial bird

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Abstract

When altricial birds hatch, they are unable to regulate their own temperature, but by the time they fledge they are thermally independent. Early-life conditions have been shown to be an important factor contributing to fitness. However, it is currently unknown to what extent body temperature during endothermy development is driven by genetic variation or by the early environment. We use thermal images of cross-fostered house sparrows (*Passer domesticus*) throughout the nestling period to separate genetic and environmental drivers of body temperature. We estimated negligible heritability of body temperature at all ages. We further found that there are effects from the natal environment that carry over into the late nestling stage. A correlation between the early- and mid-nestling periods was explained by the natal environment, and during this period body temperature and growth followed independent developmental trajectories. Furthermore, higher body temperature was under viability selection, independent of body mass. We, therefore, demonstrate that the natal environment influences future offspring phenotype via a novel measure; body temperature. Our study provides a novel investigation into the environmental and genetic drivers of body temperature variation in a wild bird, furthering our understanding of how traits evolve.

Keywords: endothermy, infrared thermography, nestling development, quantitative genetics

Introduction

Passerine birds are heterothermic endotherms, whose body temperature is influenced by both intrinsic and extrinsic factors, such as body condition (Nord et al., 2013), time of day (Barrett & Takahashi, 1995; Binkley et al., 1971) and exposure to stressors (Jerem et al., 2019). As adults, optimisation of body temperature has fundamental benefits for the individual, such as energy conservation (Tattersall et al., 2016) and improved ability to remain active (Torre-Bueno, 1976). Altricial birds start to develop their own body temperature regulation as nestlings and complete this development before fledging. Nestlings are therefore sensitive to fluctuations in their thermal condition (reviewed in Nord & Giroud, 2020) and to ambient temperature, which have both been shown to impact their survival (Andreasson et al., 2018; Bourne et al., 2020; Marques-Santos & Dingemanse, 2020). Previous studies on ambient temperature studied its effects at the brood level. We therefore know little about how an individual's body temperature is determined, and this is yet to be considered in an evolutionary context.

Early-life conditions affect the phenotype of developing individuals with effects persisting into adulthood (Metcalfe & Monaghan, 2001; Saino et al., 2018; Spagopoulou et al., 2020; Zwaan et al., 2020). To date, the literature on body temperature in birds has largely focussed on the adaptive response to environmental conditions, mostly in experimental studies. Very few studies have been conducted in the wild and most of the literature on body temperature in birds comes from studies on poultry that have been selected for production. The rate of endothermy development in wild nestling blue tits (*Cyanistes caeruleus*) has been shown to vary between individuals and with brood size (Andreasson et al., 2016), and nestlings in experimentally heated nests were better able to thermoregulate at later nestling ages (Page et al., 2022).

Early environments, such as the nest condition, may affect the thermal characteristics of juvenile birds, with future fitness implications. Prehatching (e.g., egg yolk composition) and posthatching (e.g., parental incubation behaviour) conditions have been shown to affect nestling phenotypes, such as growth (Mousseau, 1998; Nord & Nilsson, 2011; Saino et al., 2003). However, we do not know what determines an individual's development of body temperature regulation, and if the drivers of body temperature regulation are the same or separate from the drivers of growth, especially in the wild.

Metabolic rate is a trait that is studied more commonly than body temperature, but both probably share physiological mechanisms. Metabolic rate is a key trait for determining an individual's energy expenditure (Biro & Stamps, 2010).

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As body temperature is the result of metabolic heat production, this can be considered an indicator of an individual's metabolic state. There is evidence that metabolic rate has a heritable component in captive zebra finches (Rønning et al., 2007) and wild blue tits, *Cyanistes caeruleus* (Nilsson et al., 2009). However, a recent study demonstrated that it is prenatal effects, rather than genetic effects, that drive metabolic rate variation in nestlings (McFarlane et al., 2021), which the previous studies were unable to disentangle. Metabolic rate has been shown to have an independent genetic basis from morphological and behavioural traits (Mathot et al., 2013), and also varies in how predictive it is of energy expenditure (e.g., Briga & Verhulst, 2017). The study of body temperature can help us better understand how energy expenditure, growth, and metabolic rate together determine physiological condition.

Using a wild population of house sparrows, subjected to a partial cross-fostering experiment, we aim to separate genetic and environmental effects on body temperature during development. There is some evidence in captive chickens (*Gallus gallus domesticus*) that body surface temperature is heritable (Loyau et al., 2016). However, heritability needs to be determined in wild systems to understand trait evolution and population ecology. Altricial nestlings are easily cross fostered between broods, and so provide the ideal opportunity to decompose variation in body temperatures into genetic, pre- and postnatal parental (or nest) effects (Winney et al., 2015). Here, we first decompose the variation in body temperature through ontogeny into genetic, natal environment, and rearing environment effects, covering a period of pre- and postendothermy development. We also determine, at a range of nestling ages, whether body temperature is under selection independently of growth. Our study shows that early-life conditions influence an individual's phenotypes using a noninvasive measure of individual quality: body surface temperature.

Materials and methods

Study population

Data for this study comes from a long-term study of a closed population of house sparrows (*Passer domesticus)* on Lundy Island in the Bristol Channel (51°100 N, 4° 400 W), monitored since 1996. LAW collected the thermal data for this study during the breeding season in 2018 and 2019. LAW cross-fostered nestlings in 2018 and 2019 at 2 days posthatching (day first chick observed in nest = day 1). Where possible, we used a triad approach, where up to three broods matched by their hatching date had nestlings swapped between them. As many nestlings were cross-fostered as possible—broods of equal size had all nestlings cross-fostered and broods of differing size had the number of chicks in the smallest clutch cross-fostered. If only one brood was at age two on a given day, then no cross-fostering occurred. 16 nestlings were removed from the dataset as they hatched significantly later than their siblings in the same brood (nestlings in a given brood generally hatch within 24 hr of each other). Social parents of the focal birds were identified from unique colour ring combinations and a British Trust for Ornithology metal ring. A genetic pedigree was assembled using 13 microsatellite loci obtained from blood samples (Dawson et al., 2012 as described in Schroeder et al., 2015). All blood sampling procedures were performed under a UK Home Office licence.

Thermal image collection

Surface temperature has previously been shown to correlate linearly with core temperature in birds (Giloh et al., 2012; Hill et al., 1980). The use of noninvasive temperature measurements via thermal imaging of surface temperature can therefore be used to determine an individual's thermal state (McCafferty, 2013; Nord et al., 2016). Eye-region temperature is the hottest surface region of passerine birds (Jerem et al., 2015). There is also evidence that eye-region temperature remains relatively stable when birds are faced with a perceived risk of an energetic shortfall, suggesting the eye region offers a reliable surface correlate of core temperature (Winder et al., 2020). Here, we use eye-region temperature (or maximum head temperature in very young birds, see below) measurements throughout the nestling period to determine to what extent body temperature is driven by natal and rearing conditions.

LAW visited each hatched brood on four occasions, when the nestlings were 2 (n = 695 individuals, 231 broods), 5 (n = 577 individuals, 216 broods), 10 (n = 516 individuals, 201 broods), and 12 (n = 487 individuals, 191 broods) days old. Four individuals were removed from the dataset as they hatched significantly later than the rest of their brood (these are not included in the sample sizes previously listed). House sparrow nestlings have been shown to develop endothermy by 9.5 days posthatching (Dunn, 1975). Therefore, this age range captures a near-poikilothermic (i.e., body temperature which varies with the environment) stage through to that of thermal independence. We limited our visits to the morning to minimise the effect of time of day. On each visit, LAW obtained a thermal image of each nestling, as follows. We temporarily removed all nestlings from the nest to allow measurement. LAW then took a thermal image of the right side of each bird's head using a C3 FLIR camera (FLIR Systems, Wilsonville, OR). Birds within a nest were thermally photographed in a randomised order, though order did not affect body temperature readings (data not shown) and so was not included in the final statistical models described below. The air temperature and relative humidity were also recorded at the time of image capture. Individual birds were identified from a toenail clipped on day 2.

Temperature extraction

JHG and EW extracted the nestling maximum head temperature (hereafter referred to as body temperature, for simplicity) from each image using the Thermimage package (Tattersall, 2017) in R version 3.6.2 (R Development Core Team, 2009) and by selecting the hottest pixel in the image of the bird's head (see Jerem et al., 2015). As the eye is highly vascularised and lacks feathers, this region closely correlates with core temperature, with maximum head temperature being shown to indicate physiological condition (Jerem et al., 2019). The hottest pixel was usually on the eye region of the bird, however, when birds were very young, tissues were not differentiated in our thermal images and so the hottest pixel on the bird's head was used. In some cases, the hottest pixel was not on the bird but instead in the background of the image (e.g., when birds were in poor health and colder than the environment) and, therefore, JHG and EW extracted the maximum head temperature identified in FLIR Tools by drawing a temperature selection box exclusively around the bird's head. The atmospheric temperature and relative humidity (from recordings taken at the time of measurement) were corrected for during image extraction in either Thermimage or FLIR Tools.

Data analysis

LAW performed all statistical analyses for this study with guidance from JLP, who also reviewed the analysis code. LAW determined the heritability of body temperature for each age (2, 5, 10, and 12 days) in separate "animal models", which use the relatedness structure of a pedigree to estimate additive genetic effects (Henderson, 1988; Kruuk, 2004). Our pruned pedigree contained 1,242 individuals for the age 2 dataset with 1,143 maternities and 1,159 paternities (see Supplementary Information S1 for further pedigree statistics and for the other ages). We included fixed effects of air temperature (at time of image capture; continuous), year (two-level factor), and brood size (at given age; continuous) in the models. In addition to additive genetic effects, we estimated random effects of the natal brood (brood in which the nestling was born into), the rearing brood (brood in which the nestling was raised) and date. As the additive genetic effect variance at all ages was low, *p*-values were calculated to determine if there was statistical support for this effect. Random effects of rearing brood were not included in the model for day 2, as temperature measures were taken at the point of cross-fostering. All covariates were mean-centred to aid interpretation. We also calculated evolvability (Houle, 1992) of body temperature at each age; to do this we used the same models described above but converted body temperature from (°C) to Kelvin (traits need a true 0 to calculate evolvability).

To account for selective disappearance when estimating the variance components of body temperature (i.e., there is a potential to underestimate variances at later ages when viability selection is acting on the traits), LAW then modelled body temperature (for all ages combined) using a multivariate linear mixed effects model (Hadfield, 2008; Hadfield et al., 2013), in a character state approach. This approach uses data augmentation to estimate data for missing individuals at older ages through their values at younger ages. It also means that we did not have to make any assumption about the function by which temperature changes over age. We included a fixed effect of age (categorical), as well as brood size (at given age; continuous), air temperature (continuous), and year (categorical), which were treated separately for each age inside the model. Date of image capture was modelled as random effects in the model. We modelled natal brood and residual effects with 4 × 4 unstructured covariance matrixes, specifying a variance for each age, and the covariances between ages. We modelled rearing brood effects for ages 5, 10, and 12 with a 3 × 3 unstructured covariance matrix. We did not have sufficient power to model genetic effects in this analysis, most likely due to the very low genetic variance across ages. When natal brood is separated from the rearing brood in our models, the genetic variance will be confounded with the natal brood effects; however, given the small additive genetic effects in the models for each age separately, the additive genetic effect will be negligible. We repeated this analysis but included a fixed effect of body mass (again separately for each age) to determine to what extent body temperature is an independent trait from body mass.

The analyses described above were run in MCMCglmm version 2.36 (Hadfield, 2010) using R version 4.4.0 (R Development Core Team, 2009). The burn-in period was 45,000 for all analyses and a chain length of 195,000 iterations and a thinning interval of 150. Parameter expanded priors were used for the random effect variances (V = 1, nu = 1, alpha.mu = 0, and alpha.V = 1,000), and inverse wishart priors were used for the residual variances (V = 1 and nu = 0.002 for the univariate models, and V = 1e-6 and nu = 5 for the multivariate models). *p*-Values were deemed statistically significant if the 95% credible intervals do not overlap zero. To infer statistical support for the genetic component in the day 2 univariate model, JLP generated a null distribution of posterior medians for the univariate models at each age via simulation following Pick et al. (2023). *p*-Values were generated as the proportion of samples from the null distribution that were greater than the posterior median estimated from the real data. The minimum detectable heritabilities (posterior medians) were 0.072, 0.081, 0.151, and 0.107 for days 2, 5, 10, and 12, respectively. When model estimates are presented, we use the posterior median (unless otherwise stated).

LAW analysed whether body temperature predicts survival to the next age using generalised linear mixed-effect models with a binomial error distribution in lme4 (Bates et al., 2015), using the BOBYQAO optimiser. For age 12, survival was determined by whether an individual was sighted as an adult (i.e., over winter or during the following breeding season). All ages were analysed in separate models, and included fixed effects of body temperature, body mass, and year, and random effects of natal brood (all ages) and rearing brood (age 5, 10, and 12 only). *p*-Values were estimated from likelihood ratio tests, comparing nested models.

Results

Variance explaining body temperature at each age

To reliably estimate the environmental and genetic variance components explaining body temperature at each age, we accounted for air temperature, which as expected was significantly positively correlated with surface body temperature at all ages (Table 1). As our study took place over two consecutive years, we also accounted for differences in the environmental conditions between years, by including year as a two-level factor in the model. In 2019, birds were warmer at ages 2 and 5 compared to those recorded in 2018 (although this was not statistically supported). However, birds were cooler at ages 10 (not significant) and 12 compared to 2018 (Table 1).

We found that body temperature had a small (and not statistically supported) heritability at all ages [Age 2, $h^2 = 0.02$ (95% CrI: 0.00–0.13, $p = .333$); Age 5, $h^2 = 0.06$ (95% CrI: 0.00–0.21, $p = .105$; Age 10, $h^2 = 0.03$ (95% CrI: 0.00–0.19, $p = .562$); Age12, $h^2 = 0.01$ (95% CrI: 0.00–0.08, $p = .990$); Figure 1, Table 1]. We calculated evolvability (I_A) of body temperature (in Kelvin) to be 0.000003 (95% CrI: 0.000000001–0.00001) for age 2, 0.000004 (95% CrI: 0.00000001–0.00001) for age 5, 0.000003 (95% CrI: 0.000000002–0.00001) for age 10, and 0. 0.0000004 (95% CrI: 0.0000000007–0.000002) for age 12. At early ages (ages 2 and 5), body temperature was driven by the current conditions that the individual experienced in the nest (i.e., the combined natal and rearing brood effect for age 2 and rearing brood for age 5). At age 10, when the nestlings become thermally independent, temperature was not driven by their

Table 1. Variance components of body temperature by age. Values for fixed effects and random effect variances are the posterior median (95% credible intervals). Statistically significant values (pMCMC < 0.05) are in bold.

	Age (days)			
	2	5	10	12
Fixed				
Intercept	**30.79 (30.12–31.35, $p < .001$)**	**34.24 (33.75–34.72, $p < .001$)**	**37.65 (37.11–38.17, $p < .001$)**	**38.56 (38.28–38.82, $p < .001$)**
Air temperature	**0.55 (0.45–0.64, $p < .001$)**	**0.44 (0.37–0.52, $p < .001$)**	**0.22 (0.14–0.29, $p < .001$)**	**0.19 (0.14–0.25, $p < .001$)**
Year (2019)	0.64 (−0.12–1.47, $p = .134$)	0.51 (−0.04–1.17, $p = .10$)	−0.47 (−1.11–0.12, $p = .142$)	**−0.54 (−0.92– −0.14, $p = .006$)**
Brood size	−0.04 (−0.39–0.30, $p = .818$)	**0.61 (0.33–0.91, $p < .001$)**	**0.33 (0.09–0.58, $p = .006$)**	−0.06 (−0.23–0.11, $p = .538$)
Random				
Genetic	0.20 (0.00–1.12, $p = .333$)	0.27 (0.00–1.08, $p = .105$)	0.15 (0.00–1.12, $p = .562$)	0.02 (0.00–0.20, $p = .990$)
Natal brood	5.25 (4.18–6.59)	0.18 (0.00–0.76)	1.76 (0.85–3.09)	0.16 (0.00–0.55)
Rearing brood		2.37 (1.58–3.34)	0.03 (0.00–0.35)	0.06 (0.00–0.38)
Date	1.04 (0.29–2.15)	0.38 (0.00–1.43)	0.74 (0.10–1.70)	0.26 (0.00–0.75)
Residual	1.85 (1.38–2.19)	1.55 (1.03–1.92)	2.72 (2.12–3.34)	1.80 (1.50–2.15)

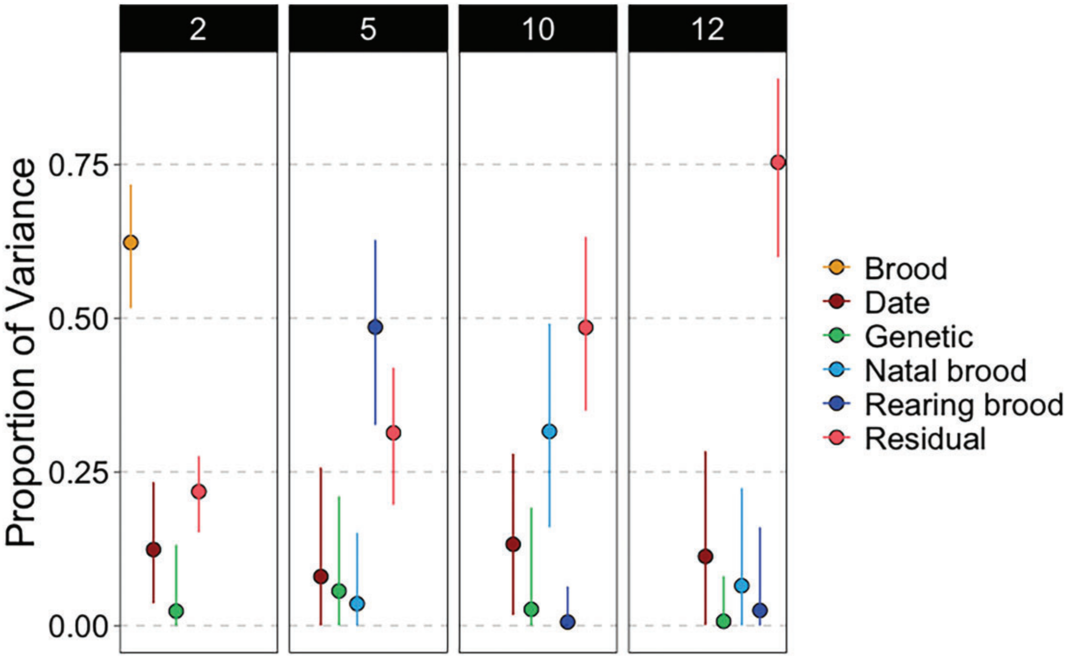

Figure 1. The proportion of variance in body temperature at each age (2, 5, 10, and 12 days posthatching) over the nestling period for the random effects in the model. Points are the proportion of variance from posterior medians and whiskers represent the 95% CrI's. Note that birds were cross-fostered at age 2 and brood is the combination of rearing and natal brood (which are both the same at this age).

current environment (rearing) but by their prior natal environment. The amount of residual variation in body temperature increased as the nestlings aged, suggesting that environmental variables not captured in our models became increasingly determinative of body temperature. By age 12, only a small proportion of variation was driven by the rearing brood (and negligible variation was driven by genetic or the natal environment) and most variation was explained by residual variation (Table 1, Figure 1).

Covariance in body temperature across ages

We found that chicks that hatched in the same nest who have higher temperatures just after hatching (2 days) also have higher temperatures at later ages (5 and 10 days) (Table 2). This relationship weakened slightly when body mass was included in the model, but remained significant between ages 2 and 10 (Table 3). However, by age 12 the correlation with earlier ages disappears (Tables 2 and 3; although note the large confidence intervals for these estimates, likely driven by the

Table 2. Posterior medians (95% credible intervals) for the random effects of the model of body temperature by age. Variances (95% credible intervals) are on the diagonal. Covariances are below the diagonal and correlations (95% credible intervals) are above the diagonal. Significant medians and correlations are in bold.

	2	5	10	12
Natal brood:				
2	5.61 (4.57, 6.98)	**0.53 (0.13, 0.95)**	**0.31 (0.10, 0.52)**	−0.03 (−0.92, 0.88)
5	**0.64 (0.07, 1.28)**	0.27 (0.02, 0.82)	0.51 (−0.23, 0.97)	−0.21 (−0.95, 0.93)
10	**1.05 (0.35, 1.86)**	0.35 (−0.11, 0.95)	2.06 (1.09, 3.15)	0.09 (−0.89, 0.96)
12	−0.01 (−0.37, 0.34)	−0.01 (−0.23, 0.12)	0.02 (−0.28, 0.46)	0.04 (0.00, 0.45)
Rearing brood:				
2	/	/	/	/
5	/	2.47 (1.79, 3.24)	0.63 (−0.64, 0.99)	0.33 (−0.86, 0.97)
10	/	0.27 (−0.11, 0.90)	0.10 (0.00, 0.55)	0.41 (−0.92, 0.97)
12	/	0.08 (−0.15, 0.43)	0.01 (−0.06, 0.18)	0.04 (0.00, 0.32)
Residual:				
2	2.01 (1.77, 2.32)	**0.15 (0.05, 0.25)**	0.07 (−0.04, 0.18)	−0.04 (−0.15, 0.06)
5	**0.27 (0.09, 0.47)**	1.71 (1.46, 1.99)	**0.14 (0.01, 0.26)**	0.09 (−0.04, 0.23)
10	0.17 (−0.10, 0.44)	**0.31 (0.03, 0.58)**	2.88 (2.42, 3.51)	**0.15 (0.02, 0.27)**
12	−0.09 (−0.30, 0.13)	0.17 (−0.07, 0.42)	**0.35 (0.05, 0.67)**	1.92 (1.59, 2.25)

Table 3. Posterior medians (95% credible intervals) for the random effects of the model of body temperature by age. The model included an interaction term between age and body mass. Variances (95% credible intervals) are on the diagonal. Covariances are below the diagonal and correlations (95% credible intervals) are above the diagonal. Significant medians and correlations are in bold.

	2	5	10	12
Natal brood:				
2	5.16 (4.19, 6.39)	0.39 (−0.42, 0.94)	**0.30 (0.07, 0.51)**	−0.06 (−0.80, 0.77)
5	0.25 (−0.12, 0.83)	0.10 (0.00, 0.48)	0.43 (−0.69, 0.96)	−0.16 (−0.95, 0.93)
10	**0.82 (0.17, 1.47)**	0.14 (−0.17, 0.57)	1.54 (0.78, 2.53)	0.07 (−0.94, 0.95)
12	−0.03 (−0.39, 0.28)	0.00 (−0.17, 0.08)	0.01 (−0.26, 0.39)	0.07 (0.00, 0.47)
Rearing brood:				
2	/	/	/	/
5	/	1.98 (1.43, 2.67)	0.41 (−0.88, 0.98)	0.30 (−0.77, 0.97)
10	/	0.09 (−0.18, 0.53)	0.04 (0.00, 0.39)	0.33 (−0.90, 0.98)
12	/	0.09 (−0.15, 0.40)	0.01 (−0.04, 0.19)	0.06 (0.00, 0.34)
Residual:				
2	1.80 (1.59, 2.06)	0.04 (−0.06, 0.14)	0.01 (−0.10, 0.11)	−0.08 (−0.19, 0.03)
5	0.06 (−0.09, 0.24)	1.44 (1.24, 1.68)	0.05 (−0.07, 0.16)	0.05 (−0.10, 0.17)
10	0.03 (−0.21, 0.25)	0.09 (−0.13, 0.32)	2.54 (2.13, 3.13)	0.09 (−0.03, 0.22)
12	−0.15 (−0.36, 0.05)	0.07 (−0.15, 0.28)	0.20 (−0.06, 0.50)	1.81 (1.51, 2.16)

low variances in this component at this age). We also found that nestlings raised together were no more likely to have similar temperatures at later ages (Tables 2 and 3), suggesting that body temperature is an individual-based trait.

Selection on body temperature

Nestling body temperature had a positive effect on their survival to the next age, independent of body mass (Figure 2, Table 4; although this was only statistically significant at ages 2 and 10). However, body temperature at age 12 did not predict survival to adulthood, though only 12 (out of 487) individuals survived to adulthood (estimate = −0.28 ± 1.66, Table 4, Figure 2). Body mass also predicted survival but only at ages 2 and 5 (Table 4).

Discussion

Our study provides a crucial step in the understanding of the drivers of a key physiological trait in birds, body temperature. We found low heritability of body temperature at all ages, though this did not have statistical support at any age. Our results also show that the natal brood explained a substantial amount of variance in body temperature after being cross-fostered and after endothermy developed. A notable finding of this work was that variation in body temperature and its effect on survival were, to a degree, independent from body mass. Our results provide a crucial step in understanding the drivers of a key physiological trait in birds—body temperature.

A key finding of this work is that early-life effects predicted body temperature at later nestling ages. The combination of low heritability and variation explained by the natal brood provided evidence that the prehatching effects have a profound impact on the physiology of nestlings during their development. Possible mechanisms for this could be either parental incubation effects or investment in egg quality (for example, through investment in proteins or hormones). Environmental conditions during development have been shown to affect nestling physiology, morphology and survival (Mueller et al., 2019; Nord & Giroud, 2020; Nord & Nilsson, 2011; Ospina et al., 2018). However, nestlings can compensate for negative early-life conditions (Bize et al., 2006; Metcalfe & Monaghan, 2001). This could, in part, explain why, by age 12, variance explained by the natal and rearing environments was low (though see below where we discuss selective disappearance). At age 10, after endothermy has developed, the natal

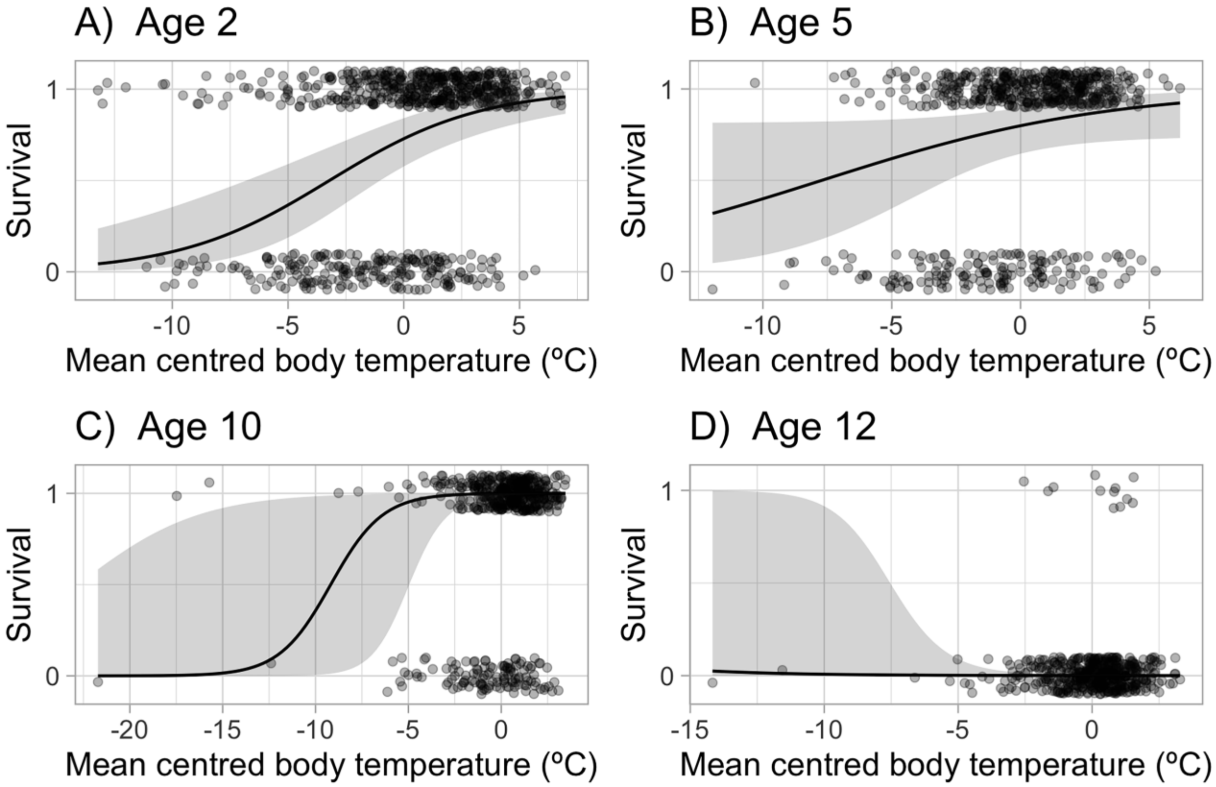

Figure 2. Survival given mean centred maximum head temperature (°C) for nestlings aged (A) 2, (B) 5, (C) 10, and (D) 12 days old. Points show the raw data and are jittered to aid interpretation. Solid lines are survival predictions from models and shaded regions are the 95% confidence intervals.

brood explained more variation in body temperature than the current environment—the rearing brood. This was the case when body temperature was modelled for each age individually and additionally when selective disappearance was accounted for, where body temperature was largely explained by covariances associated with natal brood effects between ages 2–5 and 2–10.

However, when body mass, as well as selective disappearance, were accounted for, early-stage body temperature did correlate with mid-stage nestling temperature (i.e., ages 2–10 only) but the effects of natal and rearing brood could not be separated for these ages. This does still, importantly, show that early-life effects had significant carry-over effects to the later stages of the nestling period and that this occurred independently from the effects of growth, though further work is needed to determine if it is the natal parents or social parents that drive this variation. Thomson et al. (2017) found in blue tit (*Cyanistes caeruleus*) nestlings, a small effect of the nest of origin and heritability of body mass, and concluded that as nestlings age, body mass is driven more by the social parents. However, our results do not provide evidence for the same trend, as rearing brood explained little variation in any of our models, though this variation was confounded with that of the natal brood for the age 2 effects.

Our findings also show that the drivers of body temperature are fundamentally different to those of body mass, despite being correlated (Supplementary Information S2). Previous studies have shown that nest temperature affects survival (Andreasson et al., 2018; Berntsen & Bech, 2016). Our study, importantly, goes beyond the collective nest effect and explores body temperature at the individual level. Determining the survival effects of body temperature at the individual level also allowed us to separate this effect from other physiological effects that might impact survival. We concluded that selection acts on body temperature; body temperature predicts survival to the next age, with warmer birds being more likely to survive. The selection on body temperature was independent of body mass, showing the selection effect of body temperature was not simply a result of larger nestlings being selected for. Interestingly, at age 10, body mass did not significantly predict survival, but body temperature did. Numerous other studies have shown that lower nestling body mass is associated with reduced survival (e.g., Monrós et al., 2002; Tinbergen & Boerlijst, 1990; and Ronget et al., 2018, however also see Linden et al., 1992). However, few studies have assessed selection of body mass across ontogeny. Hadfield et al. (2013), showed that selection of larger blue tit nestlings remained strong across ontogeny. Sauve et al. (2024), however, found that selection on larger body masses was stronger in early ontogeny than later. This is consistent with our study, which also showed stronger selection on body mass earlier in the nestling period.

This demonstrates the potential for body temperature to be a key indicator of individual quality during the nestling period. By age 12, this trend disappeared, possibly because by this age the cooler, poor-quality nestlings had already died (i.e., selective disappearance). It is also possible that, after fledging, that many other extrinsic factors lead to the death of an individual and, therefore, the body temperature becomes negligible in explaining mortality. Indeed, very few individuals survived to adulthood, and so the results of survival to adulthood should be treated with caution. Body temperature therefore indicates the quality of a nestling that is independent of growth, although this may not translate into adulthood. It

Table 4. Model outputs for survival to the next age class predicted by body temperature at each age. Survival for age 12 was determined by being resighted as an adult. *p*-Values are from likelihood ratio tests.

	Estimate	SE	*z*	*p*
Age 2				
Fixed				
(Intercept)	0.99	0.35	2.86	.004
Body temperature	0.31	0.07	4.25	<.001
Body mass	0.91	0.19	4.83	<.001
Year (2019)	3.49	0.66	5.26	<.001
Random	Variance	SD		
Natal brood	8.88	2.98		
Age 5				
Fixed				
(Intercept)	1.38	0.40	3.45	<.001
Body temperature	0.18	0.10	1.90	.054
Body mass	0.47	0.10	4.66	<.001
Year (2019)	3.65	0.70	5.23	<.001
Random	Variance	SD		
Natal brood	0.36	0.60		
Rearing brood	7.22	2.69		
Age 10				
Fixed				
(Intercept)	6.57	1.19	5.51	<.001
Body temperature	0.72	0.22	3.32	<.001
Body mass	0.11	0.09	1.25	.21
Year (2019)	5.16	1.90	2.71	<.001
Random	Variance	SD		
Natal brood	9.40	3.07		
Rearing brood	121.30	11.01		
Age 12				
Fixed				
(Intercept)	−7.84	1.66	− 4.72	<.001
Body temperature	−0.28	0.43	− 0.64	.45
Body mass	0.10	0.15	0.67	.50
Year (2019)	−18.84	34669.44	− 0.001	.12
Random	Variance	SD		
Natal brood	33.61	5.80		
Rearing brood	6.28	2.51		

would also be interesting, though challenging in terms of the sample size required, to follow these effects throughout adulthood to determine if there are subsequent fitness consequences of nestling body temperature.

Conclusion

Our results provide insight into what drives variation in body temperature throughout the nestling period and that body temperature is somewhat independent of the effects of growth. This study also demonstrates the importance of determining what drives variation in phenotypic traits in early life, as in the absence of cross-fostering, it would be difficult to separate rearing effects from prehatching incubation effects. Importantly, our study shows that the rearing environment explains very little of the variation in body temperature after endothermy has developed. We have also shown that body temperature is selected for independently of body mass and, therefore, body temperature could provide a useful tool for determining differences in individual quality.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Data and R code are available on Zenodo https://doi.org/10.5281/zenodo.17534342.

Author contributions

Lucy A. Winder (Conceptualization [lead], Data curation [equal], Formal Analysis [lead], Investigation [lead], Methodology [lead], Project administration [lead], Visualization [lead], Writing – original draft [lead], Writing – review & editing [equal]), Jacob Hogger Gadsby (Data curation [equal]), Eleanor Wellman (Data curation [equal]), Joel L. Pick (Formal Analysis [supporting], Methodology [supporting], Supervision [equal], Validation [equal], Writing – review & editing [equal]), Julia Schroeder (Data curation [supporting], Resources [equal]), Mirre J. P. Simons (Supervision [equal], Writing – review & editing [equal]), and Terry Burke (Supervision [lead], Writing – review & editing [equal])

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Conflict of interest

We have no conflict of interest to declare.

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