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Journal: Proceedings of the Royal Society B

Manuscript: rspb20131436

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Cite this article: Burness G, Huard JR, Malcolm E, Tattersall GJ. 2013 Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail. *Proc R Soc B* 2013;1436.
<http://dx.doi.org/10.1098/rspb.2013.1436>

Received: 4 June 2013

Accepted: 2 July 2013

Subject Areas:

physiology, ecology, environmental science

Keywords:

ontogeny, thermal window, phenotypic plasticity, Allen's rule

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.1436> or via <http://rspb.royalsocietypublishing.org>.

Post-hatch heat warms adult beaks: irreversible physiological plasticity in Japanese quail

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Across taxa, the early rearing environment contributes to adult morphological and physiological variation. For example, in birds, environmental temperature plays a key role in shaping bill size and clinal trends across latitudinal/thermal gradients. Such patterns support the role of the bill as a thermal window and in thermal balance. It remains unknown whether bill size and thermal function are reversibly plastic. We raised Japanese quail in warm (30°C) or cold (15°C) environments and then at a common intermediate temperature. We predicted that birds raised in cold temperatures would develop smaller bills than warm-reared individuals, and that regulation of blood flow to the bill in response to changing temperatures would parallel the bill's role in thermal balance. Cold-reared birds developed shorter bills, although bill size exhibited 'catch-up' growth once adults were placed at a common temperature. Despite having lived in a common thermal environment as adults, individuals that were initially reared in the warmth had higher bill surface temperatures than cold-reared individuals, particularly under cold conditions. This suggests that blood vessel density and/or the control over blood flow in the bill retained a memory of early thermal ontogeny. We conclude that post-hatch temperature reversibly affects adult bill morphology but irreversibly influences the thermal physiological role of bills and may play an underappreciated role in avian energetics.

1. Introduction

Bills are emblematic structures in avian evolution [1], evolving rapidly in response to extrinsic factors. In Darwin's finches of the Galápagos Islands, for example, bills have evolved in response to local environmental conditions, and provide an excellent example of character displacement [2,3]. The avian bill plays an important role in feeding [3], communication [4], respiration [5], evaporation [6], sensory perception [7] and mounting evidence suggests that it may also play a parallel role in body temperature regulation [8–10]. A thermoregulatory role for bills has been demonstrated in numerous bird taxa, with bills routinely responsible for heat exchange representing 5–60% of basal heat production [10–12], depending on their size and regulation over blood flow. Furthermore, as homeotherms, birds require physiological control over heat distribution throughout their body, not only for heat retention during cold exposure, but also to facilitate the loss of internally generated heat (e.g. from activity, digestion; [5,13]). Surface areas of bodies through which heat exchange can occur should thus be subject to selective forces that minimize energetic costs of thermoregulation [14].

Allen's rule is an eco-geographical hypothesis, relating climate to body size proportion in endotherms [15–17], and has been established within and among numerous avian groups [9,18–20]. The rule proposes that protruding morphological features, such as limbs, digits and ears, vary in proportion to body mass, and to the environmental temperatures in which the animal normally resides. The amount of heat a protruding body part can exchange with its environment depends on the area that is exposed to the environment [10–14], as well as the

nature of the underlying blood flow [12,13,21]. By adjusting the size of extremities to the prevailing temperature, thereby modifying the surface area to body mass ratios, thermal maintenance costs are reduced [14,22]. Conventionally, it has been suggested that extremity size is a favourable, heritable trait [15]. Renewed interest in eco-morphological patterns has provoked studies to question this claim, speculating that although extremity sizes are heritable, phenotypic plasticity may play a role [9,16,18,22,23]. For example, bill size in sparrows exhibits strong seasonality [8,24], demonstrating that not only some extremities are plastic in size, but are also reversibly plastic.

Previous research has shown that environmental temperature plays a key role in shaping bill size [25–27], that strong clinal trends in bill size exist across latitudinal/thermal gradients [9] and that bill size (at least in sparrows) is larger in the summer compared with the winter [8,24]. All of the above suggest that ontogenetic effects of environmental temperature on bill size are likely prevalent, that bill size is plastic and that this plasticity is reversible. Although variation in bill morphology is comparatively well studied [8,24–27], the underlying physiological processes governing heat loss and retention (i.e. blood flow regulation) are not, and it remains entirely unknown how plastic or reversible such processes are. If growth rates and extremity size are reversibly plastic, but physiological control over peripheral heat loss is not, then the adult physiological responses will exhibit a mismatch between form and function.

In this study, we tested whether the effects of temperature during early development on extremity growth manifest in a manner consistent with Allen's rule. Importantly, we addressed the functional consequence of early rearing environment on adult bill surface temperature as an index of heat loss to test whether bill radiator function covaries with bill size changes. As a model, we used Japanese quail, *Coturnix japonica*, for multiple reasons. As precocial young, they can be raised at different temperatures from an early age, without parental influence over temperature (i.e. via brooding). Although they have small bills relative to their body size, as one of the only thermal windows available to quail, we expect underlying blood flow to the bill to maximize heat loss under heat stress. As generalist feeders, quail would be less constrained by bill size and shape-specific requirements of foraging than in many other species, and thus would be better able to respond to temperature variation. Finally, robust relations between bill size and environmental temperatures have been observed in their phylogenetic lineage (order Galliformes) [9,28]. We hypothesized that the temperature of the rearing environment would influence adult morphology, and that in particular bill morphology, a site of heat exchange, would be a plastic trait. We predicted that individuals raised in warm environments would develop larger bills than individuals raised in the cold. If the bill indeed acts as a radiator of body heat, we predicted that birds raised in warm environments would exhibit warmer bills than birds raised at cold temperatures due to coevolution of bill morphology and physiology. In contrast to studies of bills, biogeographic studies of the tarsus (or limb, more specifically) have shown it to be little influenced by latitude and environmental temperature [9]. As such, we predicted that in contrast to the bill, tarsus length of quail would not be affected by rearing temperature.

2. Material and methods

(a) Species and husbandry

Japanese quail ($n = 40$) were obtained at hatch (day 0) from Cro Quail Farms, Ltd. (St. Anne's, Ontario, Canada), and transported for 3 h to Trent University. During transportation birds were kept in Styrofoam incubators held at approximately 35°C ($\pm 5^\circ\text{C}$), and upon arrival were placed in a single brooder held at 37°C ($\pm 5^\circ\text{C}$). On day 5 post-hatch, individuals were randomly assigned to one of two identical, walk-in environmental chambers (2.94 × 2.79 × 2.35 m), and placed in flight cages (45 × 45 × 90 cm) at densities of 10 per cage. On day 20 post-hatch, cages were divided in half and density was reduced to three individuals per side of the cage. On day 25, all birds were single-housed to prevent aggression. Because cages were stacked, to ensure all individuals had equal access to light, individuals were rotated between the upper and lower cages, every 5 days, beginning on day 25. Individuals had ad libitum access to food and water. For the first 30 days, individuals were fed Master Feed Turkey Starter (24% protein) and were then switched to Mazuri Feed Adult Breeder Diet (21% protein), phased in over a period of 7 days.

(b) Experimental treatments

On day 5 post-hatch, when birds were placed into an environmental chamber, they were randomly assigned to one of two (cold versus warm) treatments: 15°C or 30°C ($\pm 2^\circ\text{C}$). Twenty birds were assigned to each treatment group. Both chambers were initially set at 37°C. On day 6 post-hatch, the temperature of the chambers was decreased to 35°C ($\pm 2^\circ\text{C}$). Temperature was then decreased over the subsequent 5 days at a rate of either 2.5°C or 0.5°C per day, until day 11 when the appropriate environmental temperatures had been reached (15°C or 30°C, respectively). Using different cooling rates was necessary to ensure both treatments started the experimental phase concurrently (i.e. to reach their equilibrium temperatures by day 11). Individuals remained at their respective temperatures until day 51. Individuals were then removed from the environmental chambers, randomized, and held in two rooms in the animal care facility at $ca\ 19 \pm 2^\circ\text{C}$ until they reached 130 days of age. In this way, we could test whether individuals converged on a common morphology when placed in a common environment.

On day 1 post-hatch, all birds were banded and data collection began. Body mass was measured using a top loading balance (Sartorius, LE2202S, ± 0.01 g). Culmen length (distally, from the bill tip to where the forehead feathers began to cover the bill), bill width (across the proximal edge of nares), bill depth (at edge of feathers) and tarsus length (from the notch of the intertarsal joint to the proximal base of the toes) were measured using digital callipers (± 0.01 mm). For the following 30 days, data were collected between 09.00 and 12.00 every other day. After day 30, data collection occurred every 5 days, until post-natal day 51, when all individuals were expected to have stopped increasing in structural size based on previous research [29]. Following day 51, measurements were taken at less frequent intervals until 123 days post-hatch. To assess repeatability [30,31], measurements were performed in duplicate on 36 individuals at 123 days of age. Two individuals had a deformed bill by 123 days of age and could not be included in repeatability estimates of culmen length. Tarsus and culmen lengths had high, and significant repeatability (tarsus: $r = 0.90$, $F_{35,36} = 18.921$, $p < 0.0001$; culmen: $r = 0.89$, $F_{33,34} = 17.428$, $p < 0.0001$), while width and depth were moderately, but significantly repeatable ($r = 0.60$, $F_{35,36} = 3.905$, $p < 0.0001$; depth: $r = 0.53$, $F_{35,36} = 3.217$, $p < 0.001$). All morphological measurements were performed by J.R.H.

(c) Thermal imaging

Adult birds between day 120 and 130 were imaged using an infrared thermal imaging camera (Mikron Model 7515) to assess differential surface temperatures over the body surface, with a particular focus on the bill, since the limbs were not readily visible without manipulation and risking handling-induced artefacts. A subsample of birds from each treatment group ($n = 8$ for each of the cold and warm group) was examined at the three experimental temperatures (15°C, 22°C and $30 \pm 2^\circ\text{C}$), over a period of 3 days (one temperature per day). On the day prior to experimentation, birds were transferred from the animal holding facility to a temperature-controlled environmental chamber, held at 22°C. On the morning of experimentation, the temperature in the environmental chamber was changed to one of the 3 experimental temperatures (chosen randomly) and food was withheld. Four hours later, birds were imaged from a distance of 40–50 cm. With the thermographer blinded to bird identity and origin, multiple images were captured from each bird and a minimum of three images from each bird were analysed for the following: average bill temperature, maximum eye (peripalpebral region) temperature and average feather temperature over the rest of the body as done previously [10], using MikrospecRT software. Regions of interest were drawn on the captured images and the average values for the pixel population obtained. All thermographic images were captured and analysed by G.J.T. Raw data for morphological measurements and thermal imaging are available via the Dryad data depository (<http://dx.doi.org/10.5061/dryad.gs661>).

(d) Statistical analysis

To explore the effect of environmental temperature on bill size, we first used a principal component analysis (PCA) to collapse the morphological data into a single uncorrelated axis. The first principal component axis (PC1) was extracted from the covariance matrix of \log_{10} -transformed bill length, width and depth. PC1, when extracted from \log -transformed data, is a commonly used index of size [32]. We performed a single PCA including all chicks between 5 and 123 days of age, following Miller [32]. Day 5 was the age at which individuals were placed in the environmental chambers, and day 123 was the last day on which bill measurements were made. PC1 explained 81.8% of the variance among measurements, with culmen, bill depth and bill width having loadings of 0.88, 0.42 and 0.23, respectively.

We used linear mixed models (LMM) to examine the effect of temperature on morphological variables of interest. An LMM is often recommended for analysis of repeated-measures data, particularly if there are any missing data points [33,34]. Prior to all analyses, we \log_{10} -transformed data for tarsus length and body mass. The identity of each individual quail was included as a random factor. Experimental treatment (15°C or 30°C), sex and age were included as fixed factors, and all models were fitted using a restricted maximum-likelihood function in JMP v. 10.0 (JMP, v. 10. SAS Institute Inc., Cary, NC, USA, 2012). We initially included all two-way interaction terms, which if non-significant ($p > 0.10$, following the study of Bowers *et al.* [35]) were deleted from models and the analysis was re-run. The interaction between age and experimental treatment was of interest *a priori* and was always retained in the model. To test for an effect of rearing environment on final bill and tarsus size (at post-natal day 123), we performed an analysis of covariance with treatment, sex and their interaction as main effects, and either PC1 scores (as index of bill size) or tarsus length as a dependent variable. In some analyses of morphological data, the distribution of residuals was not normally distributed owing the presence of possible outliers. Exclusion of these outliers improved the distribution of residuals, but as inclusion or removal did not change our conclusions, we retained all data in analysis.

In analysis of thermal imaging data, we also used an LMM. Each experimental quail ($n = 8$ per treatment) was measured

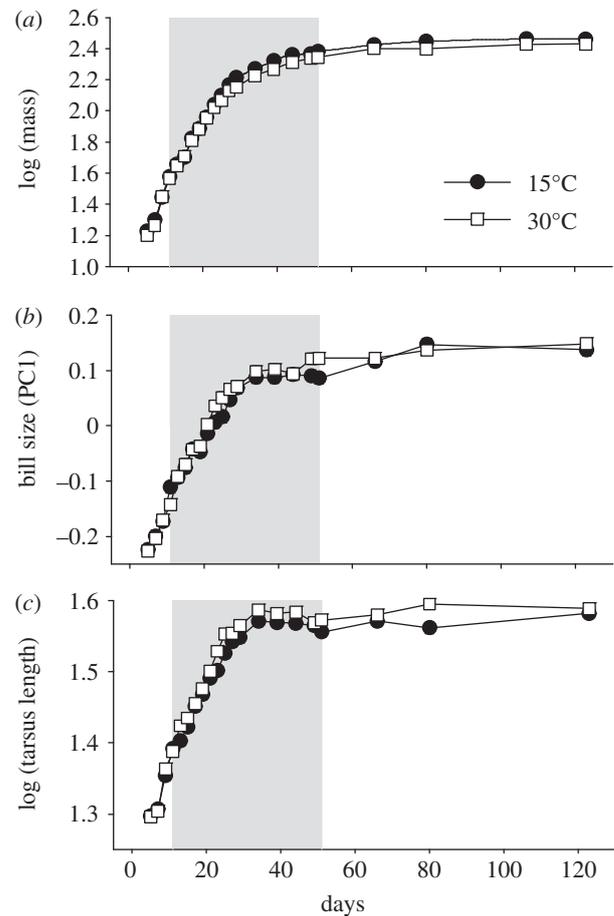


Figure 1. Summary of morphometric measurements from quail raised at warm (30°C) and cold (15°C) temperatures from 5 to 51 days post-hatch (grey shaded area). (a) \log_{10} (body mass), (b) bill size (PC1 score) and (c) \log_{10} (tarsus length). Plotted values are least-squares means ± 1 s.e.m.

under three different ambient temperatures. Independent variables included experimental treatment (i.e. whether an individual had been raised at 15°C or 30°C), sex and ambient temperature (15°C, 22°C or 30°C), plus all two-way interactions as fixed factors, and quail identity as a random factor. A single data point for bill temperature with a very low studentized residual (-3.55) was omitted as an outlier, as this bird had recently drunk water and its bill was wet.

3. Results

(a) Temperature effects on body mass

Individuals gained mass throughout the experiment (age: $F_{21,691} = 4422.83$, $p < 0.0001$) and did so at temperature-specific rates, as inferred from a significant interaction between experimental treatment and age (treatment \times age: $F_{21,691} = 2.55$, $p = 0.0002$; figure 1a). Although individuals in each treatment were of similar body mass when the experiment began, by *ca* day 23, individuals held at 15°C were becoming heavier than individuals held at 30°C. Males and females also diverged in body mass with age, as indicated by a significant interaction term (sex \times age: $F_{21,691} = 1.93$, $p = 0.008$). There were no independent statistical effects of treatment ($F_{1,76.77} = 2.12$, $p = 0.150$) or sex ($F_{1,76.77} = 1.87$, $p = 0.176$) on body mass. To explore these results further, we restricted our analysis to the time period when individuals were housed at a common temperature (days 51–123). During this period, individuals continued to gain mass (age: $F_{4,130.1} = 83.01$, $p < 0.0001$) and did so at sex-specific rates

(sex \times age: $F_{4,130.1} = 11.26$, $p < 0.0001$) with individuals originally housed at 15°C remaining *ca* 1% heavier from day 51 onwards (treatment: $F_{1,55.65} = 7.54$, $p = 0.008$), suggesting small, but persistent effects of early environmental temperature on body mass.

(b) Temperature effects on bill size

Bill size (PC1) increased over the course of the experiment (age: $F_{20,676} = 352.69$, $p < 0.0001$). There was a significant interaction between treatment and age, indicating that bill growth rate differed with rearing temperature (treatment \times age: $F_{20,676} = 1.76$, $p = 0.022$). Individuals had similar-sized bills until *ca* 17 days of age, at which point those held at 30°C developed larger bills than those housed at 15°C (figure 1b). Across the entire age range (5–123 days of age), bill size did not differ with treatment (treatment: $F_{1,246.3} = 0.01$, $p = 0.909$), but differed with sex (sex: $F_{1,32.95} = 4.82$, $p = 0.035$). When individuals were placed at a common environmental temperature (51–123 days of age), the bill continued to grow (age: $F_{3,98.36} = 11.63$, $p < 0.0001$) and across this time range individuals initially held at 30°C had bill PC1 scores that were *ca* 40% larger than individuals initially held at 15°C (treatment: $F_{1,90.52} = 7.17$, $p = 0.009$). However, bill growth rate also depended on the previous rearing temperature (treatment \times age: $F_{3,98.36} = 3.29$, $p = 0.024$); the bills of individuals originally held at 15°C where changing size more rapidly than individuals originally held at 30°C. Females had significantly larger bills than males over this time period (sex: $F_{1,32.59} = 5.98$, $p = 0.020$). By the final day of measurement (123 days of age) bill size no longer differed with treatment (2-way ANOVA, treatment: $F_{1,31} = 0.91$, $p = 0.347$) or sex (2-way ANOVA, Sex: $F_{1,31} = 3.96$, $p = 0.056$). Actual measurements of bill size are reported in the electronic supplementary material, table S1.

(c) Temperature effects on tarsus length

Tarsus length increased between 5 and 123 days of age (age: $F_{20,678} = 535.11$, $p < 0.0001$). Growth rates were similar between individuals held at 15°C and 30°C (treatment \times age: $F_{20,678} = 1.43$, $p = 0.100$; figure 1c). Tarsus length did not differ with treatment or sex (treatment: $F_{1,169.9} < 0.01$, $p = 0.947$; sex: $F_{1,32.99} = 2.69$, $p = 0.111$). When quail were housed at a common temperature (between 51 and 123 days of age), tarsi continued to grow (age: $F_{3,100.4} = 5.88$, $p = 0.001$), but the growth rate was similar between treatments (treatment \times age: $F_{3,100.4} = 2.63$, $p = 0.054$). During this time period, tarsus length did not differ between individuals raised at 30°C and 15°C (treatment: $F_{1,83.64} = 3.09$, $p = 0.082$), nor did it differ with sex (sex: $F_{1,33.16} = 3.53$, $p = 0.069$). On the final day of measurement (123 days of age), tarsus length did not differ with treatment, but females had longer tarsi than males (2-way ANOVA, treatment: $F_{1,33} = 0.862$, $p = 0.360$; sex: $F_{1,33} = 8.22$, $p = 0.007$).

(d) Temperature effects on surface temperatures

Bill temperature increased with increasing ambient temperature (ambient temperature: $F_{2,24.85} = 97.86$, $p < 0.0001$). On the whole, birds that developed in a hot environment had bill temperatures 7.4°C higher than individuals that developed in cold environments (treatment: $F_{1,31.32} = 25.61$, $p < 0.0001$). There was a significant interaction between developmental temperature and ambient temperature, such that individuals

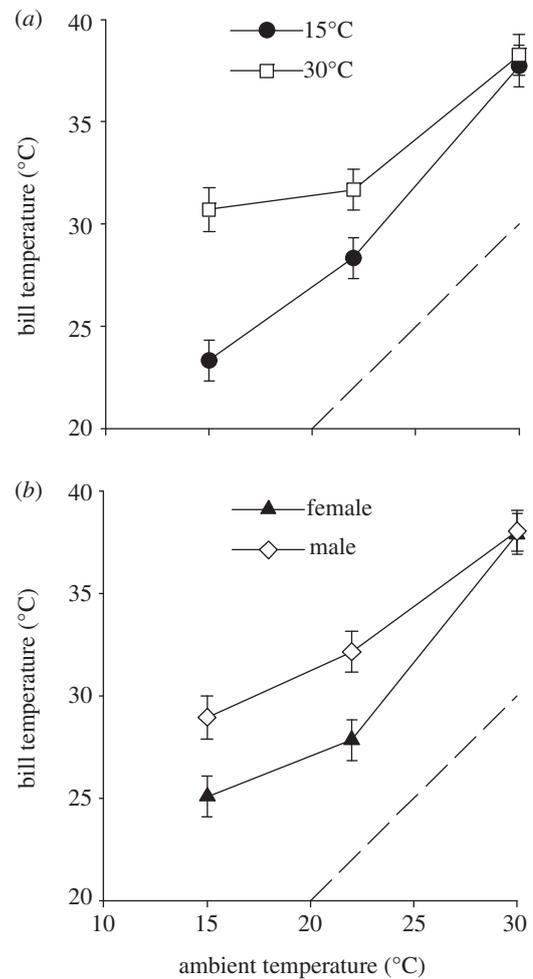


Figure 2. Bill surface temperatures of adult Japanese quail raised at warm (30°C; $n = 8$) and cold (15°C; $n = 8$) conditions, tested at 15°C, 22°C and 30°C measured at 120–130 days of age. (a) Data arranged by developmental temperature, (b) data arranged by sex. Plotted values are least-squares means ± 1 s.e.m. from LMMs.

which developed in hot temperatures had warmer bills when measured in the cold, than did individuals which developed in the cold (figure 2a; treatment \times ambient temperature: $F_{2,24.85} = 8.78$, $p = 0.001$). The importance of developmental temperature on adult bill temperature decreased with increasing ambient temperature, such that all individuals had similar bill temperatures at 30°C, irrespective of developmental temperature (figure 2a). Overall, males had significantly higher bill temperatures than females (sex: $F_{1,31.32} = 7.07$, $p = 0.012$; figure 2b). At low ambient temperatures, males had warmer bills than females, but the two sexes converged with warming ambient temperatures (sex \times ambient temperature: $F_{2,24.85} = 4.07$, $p = 0.030$). Heat loss from the bill was estimated to account for *ca* 1.9–2.9% of total body heat loss (see the electronic supplementary material). Both feather and eye temperature increased with ambient temperature (feather: $F_{2,30} = 1186.74$, $p < 0.001$; eye: $F_{2,30} = 214.30$, $p < 0.001$), but neither was affected by developmental temperature or sex (each, $p > 0.30$, see the electronic supplementary material).

4. Discussion

We tested whether the bill and tarsus of Japanese quail exhibit plasticity in growth and function in response to the post-hatch thermal environment. Our results suggest that at least some of

253 the variation in limb size and morphology that has tradition-
 254 ally been ascribed to evolutionary adaptation to prevent heat
 255 loss in the cold results from phenotypic plasticity [16,22,26].
 256 Importantly, quail that initially developed in the warmth had
 257 greater bill surface temperatures when measured in the cold,
 258 than did individuals that initially developed in the cold. This
 259 suggests that there is a physiological inability of birds reared
 260 in the warmth to avoid heat loss from thermal windows such
 261 as the bill at cold temperatures.

262 The mechanisms of bill bone growth and development are
 263 well studied [36,37], with the bone morphogenic protein (BMP)
 264 pathway playing an important role in determining size and
 265 shape [38]. In mice, decreased temperatures promote apoptosis
 266 in chondrocytes [16], which is one possible explanation for the
 267 development of shorter limbs; the temperature sensitivity of
 268 bill growth may share similar mechanisms. Importantly, the
 269 nature of the vasculature of the bill may contribute to an
 270 environmental matching of bill size; adult birds exposed to
 271 cool temperatures may vasoconstrict portions of their bill
 272 to conserve heat. In juveniles, however, the need for nutrient
 273 delivery to the growing bill conflicts with the need for heat con-
 274 servation [10]. Obligatory vasodilation in juveniles resulting
 275 from growing tissues would result in heat held within the
 276 blood to be exposed to cool ambient temperatures. This low
 277 ambient temperature exposure would reduce the temperature
 278 of the blood within the growing tissue [16]; therefore, the devel-
 279 opment of a smaller bill may result from the inherent thermal
 280 plasticity of bill growth and development. The reduction in
 281 heat loss via the overall effect on bill size would then be a con-
 282 sequence of the smaller surface area in the mature bird that
 283 was raised in the cold. Once individuals were placed in an
 284 intermediate thermal environment, there was a continuation
 285 of bill growth, but a convergence upon a common bill size.
 286 Because bill size is determined by both growth and ram-
 287 photheca wear [39], changes in bill size during the return to
 288 common temperature may involve processes in addition to
 289 bone growth and development.

290 We used thermal imaging to explore the functional
 291 implications of a mismatching between developmental and
 292 adult environments. When individuals that developed in the
 293 warmth were imaged in the cold, they had higher bill tempera-
 294 tures than individuals that developed in the cold. In this sense,
 295 the bill of the quail performed similar to that of immature Toco
 296 toucans (*Ramphastos toco*) and wild-caught song sparrows
 297 (*Melospiza melodia*), which do not have the ability to reduce
 298 blood flow to the bill at cooler ambient temperatures [10,11].
 299 The mechanism underlying differences in heat loss across
 300 quail bills is not clear, although rearing temperature can alter
 301 the density of arterio-venous anastomoses (low-resistance
 302 shunt vessels), and epidermal thickness in the nasal mucosa
 303 of birds [40] and in the tail and feet of rodents [41]. As such,
 304 warm-raised animals have greater capacity for losing heat
 305 from their thermolytic organs [41]. Heat dumping from the
 306 bill may also result from vascular morphology, which unlike
 307 the counter-current system found in avian limbs, is not condu-
 308 cive to simultaneously exhibiting nutritive blood supply to
 309 tissues while conserving body heat [10,42]. Our results suggest
 310 that blood vessel density and/or the control over bill blood
 311 flow retains a memory of the thermal environment experienced
 312 during development.

313 Male quail exhibited higher bill surface temperatures than
 314 females (figure 2) and therefore higher heat loss from this
 315 thermal window. Previous work [43] in quail suggests that

males may have slightly elevated metabolic rates relative to
 females. Coupled with the similar eye surface temperatures
 between the sexes, suggestive of similar body temperatures,
 one interpretation is that male birds have higher metabolic
 rates and the elevated bill surface temperatures are simply
 a result of this greater source of heat production in the cold.

Individuals raised in the warmth had lower body mass
 than individuals raised in the cold, a result previously
 reported for laboratory-reared homeotherms [22]. A lower
 mass would decrease thermal inertia and augment heat dissi-
 pation (i.e. higher surface area-to-volume ratio, SA:VOL).
 Nevertheless, the trends in heat loss across the bill that we
 observed cannot be explained simply by mass. Smaller
 birds (warm-reared) may produce less total body heat by
 virtue of their size but lose more heat relative to that which
 is produced, due to higher SA:VOL. Based only on body
 SA:VOL, one would predict that smaller bodied home-
 otherms (i.e. those with a greater SA:VOL) would require
 less use of a thermal window [44]; this was not the case.
 Instead, warm-reared birds made more use of their thermal
 window by virtue of their higher bill surface temperatures.

The tarsus also displayed some evidence of temperature-
 dependent developmental plasticity. A weaker pattern for the
 tarsus than the bill is not surprising. Biogeographic studies of
 birds have shown that in contrast with the bill, the tarsus (or
 limb, more specifically) is influenced much less by latitude
 and environmental temperature [9]. Although we did not
 measure surface temperatures of the tarsus, at cool tempera-
 tures, quail tucked their legs beneath their bodies (e.g.
 electronic supplementary material, figure S1), whereas at
 warm temperatures the legs were outstretched (see the elec-
 tronic supplementary material, figure S1*d*). Because the bill
 is small in quail, it is possible that in this species the legs
 takes on a more prominent role in thermal balance than in
 other species.

With the exception of specialized structures such as wattles,
 combs and other naked surfaces in certain avian taxa, bills and
 limbs are the primary sites of exposed, un-feathered regions
 common to all birds. We showed that in quail, an individual's
 heat exchange across its bill surface, a major thermoregulatory
 organ in some birds, parallels the morphological trends in
 terms of thermoregulatory function, but also retains a signal
 of the environmental temperature experienced during devel-
 opment. A mismatching between developmental and adult
 temperatures may thus result in unavoidable heat loss or heat
 deficits via the bill when facing environmental temperatures
 different from ontogenetic temperatures. Understanding the
 role that temperature may play in shaping an individual's
 phenotype will allow for better predictions as to how birds
 will respond to increased climatic unpredictability [45].

The staff of the Animal Care Facility, Trent University, provided care
 for the animals.

Acknowledgements. We thank E. Chin for advice on rearing and handling
 of Japanese quail, T. Philips, P. Falls, M. Fullford, V. Marshall and
 A. Corkery for assistance during measurements, and A. Storm-Suke,
 Ray Danner, Philip Withers and two anonymous reviewers for reading
 previous versions of the manuscript.

Funding statement. Funding was provided to G.B. and G.J.T. by the
 Natural Sciences and Engineering Research Council (NSERC), the
 Canadian Foundation for Innovation, and the Ontario Innovation
 Trust. E.M. was supported by an NSERC-Undergraduate Student
 Research Award.

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