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Published in:
Journal of Experimental Biology

DOI:
10.1242/jeb.220046

2020

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Winder, L., White, S., Nord, A., Helm, B., & McCafferty, D. J. (2020). Body surface temperature responses to food restriction in wild and captive great tits. *Journal of Experimental Biology*, *223*(8), Article jeb220046. https://doi.org/10.1242/jeb.220046

Total number of authors:
5

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RESEARCH ARTICLE

Body surface temperature responses to food restriction in wild and captive great tits

Lucy A. Winder[1,2,*], Stewart A. White[1], Andreas Nord[1,3], Barbara Helm[1,4] and Dominic J. McCafferty[1]

ABSTRACT

During winter at temperate and high latitudes, the low ambient temperatures, limited food supplies and short foraging periods mean small passerines show behavioural, morphological and physiological adaptations to reduce the risk of facing energy shortages. Peripheral tissues vasoconstrict in low ambient temperatures to reduce heat loss and cold injury. Peripheral vasoconstriction has been observed with food restriction in captivity but has yet to be explored in free-ranging animals. We experimentally food restricted both wild and captive great tits (*Parus major*) during winter months and measured surface temperatures of the bill and eye region using thermal imaging, to investigate whether birds show rapid local heterothermic responses, which may reduce their thermoregulatory costs when facing a perceived imminent food shortage. Our results of a continuously filmed wild population showed that bill temperature was immediately reduced in response to food restriction compared with when food was available *ad libitum*, an apparent autonomic response. Such immediacy implies a 'pre-emptive' response before the bird experiences any shortfalls in energy reserves. We also demonstrate temporal variation in vasoconstriction of the bill, with bill temperature gradually rising throughout the food restriction after the initial drop. Eye-region temperature in the wild birds remained at similar levels throughout food restriction compared with unrestricted birds, possibly reflecting the need to maintain steady circulation to the central nervous and visual systems. Our findings provide evidence that birds selectively allow the bill to cool when a predictable food supply is suddenly disrupted, probably as a means of minimising depletion of body reserves for a perceived future shortage in energy.

KEY WORDS: Thermoregulation, Thermoneutral zone, Heterothermy, Thermal imaging, Winter

INTRODUCTION

Winter in seasonal habitats is often challenging for small endotherms as severe weather increases thermoregulatory costs while limited food supply and short foraging periods potentially constrain acquisition of resources to meet these increased costs. It follows that individuals must respond to winter conditions, by morphological, behavioural and physiological adaptations, to avoid facing energetic shortfalls. The thermoneutral zone (TNZ), where heat loss is offset by basal metabolic heat production, for most passerines is 15–35°C (Gavrilov and Dolnik, 1985). In winter at higher latitudes, small birds routinely experience environmental temperatures well below thermoneutrality and therefore to maintain body temperature, metabolic heat production must increase (Scholander et al., 1950; Dawson et al., 1983). A first defence to minimise heat loss is morphological adaptations (e.g. increased insulation from feathers) and behavioural responses (e.g. seeking shelter, ptiloerection) (Nord et al., 2011; Shipley et al., 2019). Physiological adaptations in small endotherms are aimed at increasing heat production (Swanson and Vézina, 2015) and insulation via local or global heterothermy (e.g. Johnsen et al., 1985; Ruf and Geiser, 2015). These responses operate at different temporal scales as seen by long-term seasonal acclimatisation (Swanson and Vézina, 2015) or through instantaneous responses when there are sudden changes in weather (Marsh and Dawson, 1989).

Reduction in peripheral temperature by shunting blood flow to the core (local heterothermy) can lead to significant energy savings in variable environments (Hagan and Heath, 1980; Steen and Steen, 1965; Tattersall et al., 2016). In birds, the legs, bill and eyes are usually unfeathered and are, therefore, key regions of heat transfer. Counter-current vascular arrangements, and sphincteric contractions in major vessels in and around birds' legs, allow the normally uninsulated region to remain at, or close to, ambient temperature (Johansen and Bech, 1983; Midtgård, 1981; Steen and Steen, 1965). This reduces heat loss and prevents cold injury. The bill is highly vascularised but uninsulated, and is known to play a role in thermoregulation particularly in large-billed species in hot climates, though recent work highlights the role of the bill also in cold environments and in small-billed species (Schraft et al., 2019; reviewed by Tattersall et al., 2017). In line with this, bill size declines with decreasing minimum winter temperature (Danner and Greenberg, 2015; Friedman et al., 2017; Symonds and Tattersall, 2010). It is, therefore, a realistic expectation that there will be thermoregulatory responses in the bill (as well as in other peripheral tissues) to manage energetically challenging situations, such as cold snaps and food shortage. Additionally, reduced circulation to the head region might lower evaporative heat loss through uninsulated regions such as the eyes and respiratory heat loss through the nasal passages (Midtgård, 1984). However, while local heterothermic responses carry energetic benefits, the resultant lower tissue temperature in appendages such as the legs and bill, and other peripherally located structures such as the eyes, may reduce ease of locomotion, foraging or sensory perception. Therefore, the use of local heterothermy may be subject to a trade-off between environmental conditions, energetic state and food availability. For example, a study of Muscovy ducklings (*Cairina moschata*) showed cold-acclimated birds had a more stable bill temperature, with evidence of vasoconstriction of the bill, when fasting for

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Received 10 December 2019; Accepted 27 February 2020

relatively long periods, than birds that were kept in thermoneutrality (Tattersall et al., 2016). A recent study on blue tits (*Cyanistes caeruleus*) found that low periorbital temperature was correlated with low body condition (Jerem et al., 2018). Local heterothermy has also been shown to be a response to fasting in several other bird species, and this probably explains why in some studies core body temperature remains constant but, nevertheless, energy savings are made (Hohtola, 2012). There is now a need to experimentally test predictions from this work on wild models in their natural environment.

In this study, we experimentally tested the effects of environmental conditions on peripheral body temperature of wild and captive great tits (*Parus major*) in winter, using thermal imaging. In both settings, we temporarily manipulated access to food and recorded the dynamics of the birds' eye and bill temperatures before, during and after food restriction. We predicted that peripheral body temperatures would decrease in response to food restriction, and more so when ambient temperature was lower. We expected to reliably record body surface temperature in uninsulated areas of the body, specifically the bill and eye region, which are likely key areas of heat exchange. We did not record responses to food restriction in the uninsulated legs, because previous work in our population has shown that wild parids (including great tits) maintain stable low leg temperatures in winter, even when fed *ad libitum*. By contrast, bill temperature is consistently maintained well above ambient (A.N., A. Huxtable, H. Reilly and D.J.M., in preparation).

MATERIALS AND METHODS

The study used great tits, *Parus major* Linnaeus 1758, in two populations of separate subspecies: one captive (ssp. *newtoni*) and one wild (ssp. *major*). In both populations, we compared food-restricted birds with unrestricted control birds. The wild study consisted of continuous filming on days with and without a food restriction experiment (treatment or control days). For the captive study, filming occurred before and after a food restriction event and two consecutive days before the food restriction day. The air temperature range was between −10 and +2°C in the captive study, and +2 and +13°C in the wild study, below the TNZ of great tits (Broggi et al., 2005).

Captive study

Fourteen wild great tits were captured (by A.N.) whilst roosting in nest boxes at night near Vomb, Sweden (55°39′N, 13°33′E) and were immediately transferred to four outdoor aviaries (6.0×3.0×2.5 m; width×length×height) at Stensoffa Ecological Field Station, Sweden (55°42′N, 13°27′E), where they were ringed for identification and kept in mixed-sex groups from October 2012 to January 2013 and handled as described in Nord et al. (2016). The aviaries contained both a covered and non-covered area, perches and nest boxes for the number of individuals in each aviary. The birds were left for 2 weeks to acclimate to the aviaries before the start of the experiment. All procedures on the captive birds were approved by the Malmö/Lund Animal Ethics Committee (permit no. M236-10). Catching and ringing of birds was licensed by the Swedish Ringing Centre (licence no. 475), and the use of radio transmitters was permitted by the Swedish Post and Telecom Authority (permit no. 12-9096).

Thermal videos were taken at 3 Hz of birds at the feeders at 1.4 m distance using a SC640 FLIR camera (FLIR® Systems, Inc.) with a FOL 76 mm lens on three consecutive days (1–3 December). On days 1 and 2, food remained available *ad libitum* throughout the day (including while filming). On day 3, food was restricted for 3 h (mean±s.e.m.: 3 h 17 min±8 min) staggered by an hour between aviaries, with the first restriction beginning in the first aviary at 09:00 h (local time) and in the last aviary at 13:00 h. Water was freely available in heated trays (that prevented freezing) throughout the experiment. Thermal imaging took place before the food restriction (data also include the 2 days prior to the food restriction) and after the food restriction period and lasted for 1 h (mean±s.e.m.: 54±14 min) at each aviary (for day 2, aviary 4, filming lasted for 4 h 29 min). A video camera (Panasonic model HC-V720, Hamburg, Germany) was used to film the feeder so individual birds could be identified from unique colour ring combinations (birds were also fitted with subcutaneous PIT tags and radio transmitters for other research projects; see Nord et al., 2016).

Air temperature (accuracy ±0.5°C, resolution 0.0625°C) was recorded continuously from the centre of the aviary (iButton DS1922-L, Maxim Integrated Products, San Jose, CA, USA; accuracy ±0.5°C). Relative humidity was recorded by a weather station at Lund University, 17 km from the study site.

Wild study

Data for the wild study were collected in an oak (*Quercus robur*) woodland surrounding the Scottish Centre for Ecology and the Natural Environment on Loch Lomond, Scotland, UK (56°3′N, 04°33′W), between January and March 2017. A bird feeder containing peanut granules (Haith's, Grimsby, UK) was provided 2 months prior to the start of the experiment to attract resident birds.

Nineteen great tits were then caught by mist netting around the feeder from January to February 2017, and were fitted with a British Trust for Ornithology (BTO) ring on the right leg and a passive integrated transponder (PIT) tag (EM4102 PIT Tag, Eccel Technology, Leicester, UK), used for identification, on the left leg. A custom-built PIT tag recorder (University of Glasgow Bioelectronics Unit, Glasgow, UK) was attached to the feeder in order to identify birds visiting at a given time. All procedures were approved by BTO ringing permits, and by a UK Home Office Licence.

Thermal video was collected from food-restricted and control birds at 7.5 Hz using a FLIR AX5 thermal camera from 0.7 m distance, on nine days between 10 February and 2 March 2017. Food was restricted on five of those days (14, 16, 21, 23 February and 2 March 2017) for 3 h (mean±s.e.m.: 2 h 43 min±6 min) between 10:00 h and 13:20 h. On these days, thermal videos were taken for 1 h before the food restriction, 3 h during the food restriction and 1.5 h after the food restriction (with the exception of 16 February, when due to equipment failure filming occurred only after food restriction). Each food restriction was considered as a stand-alone event as at least one control day separated each day of food restriction. For the remaining four control days (10, 13, 15 and 20 February 2017), where there was no food restriction, filming occurred continuously at the feeder. A dummy camera was deployed 5 days prior to filming to habituate birds to the presence of the camera and was subsequently returned each day after thermal imaging was completed. Air temperature was measured using a thermocouple attached to the feeder (Tinytag Talk 2, Gemini Data Loggers, Chichester, UK). Relative humidity data were available from a MiniMet Automatic Weather Station (Skye Instruments, Powys, UK), within 200 m of the thermal camera.

Thermal image analysis

Individual thermal images (sample sizes shown in Table 1) were extracted and analysed from the thermal videos using FLIR Tools

Table 1. Sample sizes in the experiment

Group		No. of individuals	No. of images
Wild	Food-restricted days	19 (6 female, 8 male, 5 unknown sex)	126
	Control days	46 (41 unknown ID; of known: 3 female, 2 male)	55
Captive	Before food restriction	15 (4 female, 11 male)	99
	After food restriction	17 (5 female, 12 male)	52

Unidentified individuals were used on control days as equipment failure limited our sample size (see 'Thermal image analysis' in Materials and Methods).

4.1. Images were selected where a clear lateral view of the head was shown. When a bird visited the feeder, a unique PIT tag code was recorded with the time of visit. The time could be compared with the thermal imaging video to identify individuals in the wild study. We only analysed one image per bird within a 10 min period so each image could be considered as an independent visit to the feeder. As many birds in the wild study could not be identified when visiting the feeder, we used 41 images from unknown birds. To prevent repeated measurements of the same bird, we only used images of unknown individuals that were ≥10 min in time apart. For the wild experiment, the entire video was used. For the captive study, we randomly selected an aviary to be filmed for 1 h at the feeder from 08:00 h to 12:00 h (before food restriction) and 12:30 h to 15:30 h (after food restriction), so that despite using a single camera, all aviaries were filmed on each day.

For each image, the emissivity was set as 0.98 (Best and Fowler, 1981; McCafferty, 2013). Both the atmospheric and reflected temperatures during image analysis were set as the hourly mean air temperature obtained from the weather station during recording. Relative humidity equalled the mean for each recording session.

Mean bill temperature (hereafter referred to as bill temperature) was measured from the mean surface temperature of a straight line fitted from the base of the nostril to the tip of the bill (Fig. 1). Maximum eye region temperature (hereafter referred to as eye temperature) was taken by fitting a rectangle across the head which was large enough to encompass the periorbital ring, where the maximum temperature of the head is typically recorded (see Jerem et al., 2015). Image focus was recorded as a three-level factor. Each image was ranked as 'good' when all edges of the bill were clearly defined in the image, 'medium' when either the tip or base of the bill was not clearly defined, and 'poor' when the edges of the entire bill were undefined. Though images were selected for quality and lateral view of the head, in some images, the head of the bird was slightly turned to one side. As the length of the line along the bill varies depending on the angle of the head, distance from the camera and individual size of the bird, the pixel length of the bill was recorded as a continuous variable as a proxy of position of the bird (hereafter referred to as position index).

Statistical analyses

All statistical analyses were conducted using R version 3.3.2 (http://www.R-project.org/). Generalised linear mixed effect models (GLMM) were used to analyse bill and eye region temperatures for both datasets using the lme4 package (Bates et al., 2015).

Captive

Bill temperature and eye region temperature were both modelled using air temperature, position index and treatment (factorial: before/after food restriction). Bird ID with a first order autoregressive (AR1) covariance structure and the aviary ID were

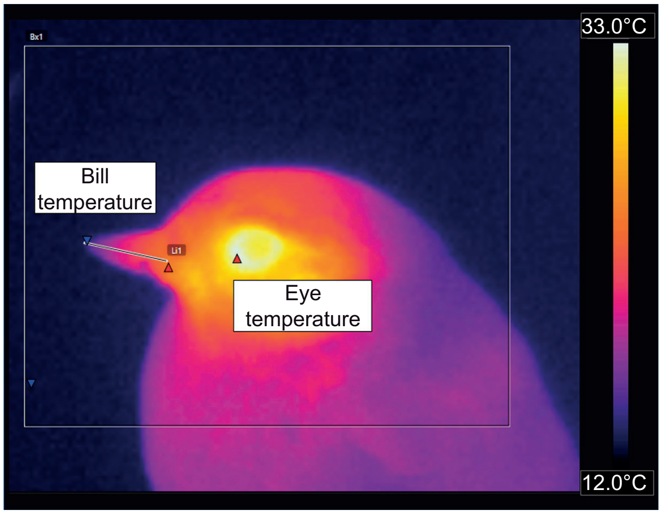

Fig. 1. Data extraction from a thermal image of a great tit at the feeder. Lateral image. Bill temperature was extracted by drawing a line from the base of the nostril to the tip of the bill. Eye region temperature was extracted by drawing a box around the head to select the hottest pixel inside the box, which was consistently found on the unfeathered periorbital ring.

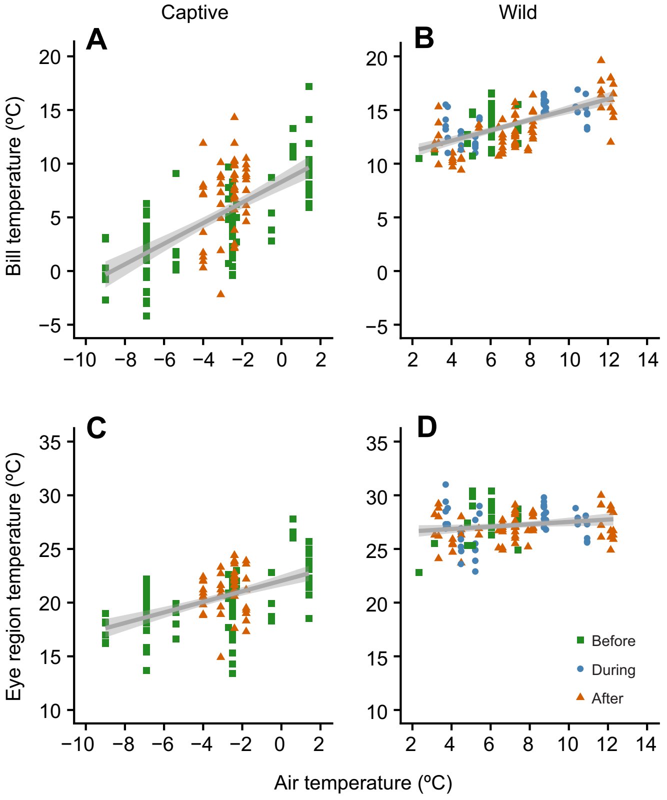

Fig. 2. The relationship between bill (top) and eye region (bottom) temperature and air temperature for captive and wild great tits. (A,C) Captive birds (*n*=151 images of 18 birds, 15 before and 17 after food restriction) and (B,D) wild birds [*n*=181 images of 60 (including 41 unknown) birds, 14 individuals were measured before food restriction, 33 during food restriction and 37 after food restriction]. Lines are slopes from linear models of bill and eye region temperature against air temperature. Shaded regions are 95% confidence intervals.

Table 2. Model outputs of bill temperature for wild and captive great tits

Model	Parameter	Estimate	(predicted means)	s.e.	*F*-value	d.f.	*P*
Bill temperature							
Captive	Intercept	−0.12		1.42	220.51	1, 130	**<0.0001**
T_{bill}~T_{air}+*treatment category*+*position index*	Air temperature	0.83		0.08	142.83	1, 130	**<0.0001**
	Treatment: before*/after food restriction	1.79	(Before: 4.32±0.39) (After: 6.11±0.45)	0.50	14.69	1, 130	**0.0008**
	Position index	0.32		0.06	30.39	1, 130	**<0.0001**
Wild							
T_{bill}~T_{air}+*treatment category*+*position index*	Intercept	7.26		0.88	5055.80	1, 61	**<0.0001**
	Air temperature	0.62		0.09	106.38	1, 61	**<0.0001**
	Treatment: before*/during/after food restriction	During: −1.20 After: −0.09	(Before: 14.01±0.28) (During: 12.71±0.22) (After: 13.92±0.27)	(During) 0.31 (After) 0.35	20.64	1, 61	**<0.0001**
	Position index	0.17		0.05	9.69	1, 61	**0.0028**
Wild	Intercept	24.67		7.43	6708.43	1, 68	**<0.0001**
T_{bill}~T_{air}+*treatment category*+*time*+*position index*+treatment category×time+treatment category×time^2	Air temperature	0.42		0.05	107.25	1, 68	**<0.0001**
	Treatment: food-restricted*/food-available day	−6.88		15.43	3.31	1, 68	0.0731
	Time of day	−3.31		1.29	0.01	1, 68	0.9177
	Position index	0.23		0.05	24.31	1, 68	**<0.0001**
	Treatment×time of day	1.63		2.72	3.11	1, 68	0.0823
	Treatment×time of day^2	Food restricted: 0.15 Food available: 0.07		0.06 0.1	3.78	2, 68	**0.0279**
Eye region temperature							
Captive	Intercept	19.42		1.07	6117.29	1, 107	**<0.0001**
T_{eye}~T_{air}+*treatment category*+*position index*	Air temperature	0.49		0.06	78.66	1, 107	**<0.0001**
	Treatment: before*/after food restriction	0.78	(Before: 20.03±0.29) (After: 20.81±0.34)	0.37	5.52	1, 107	**0.04652**
	Position index	0.10		0.04	5.08	1, 107	**0.02868**
Wild	Intercept	22.25		0.90	40,586.53	1, 61	**<0.0001**
T_{eye}~T_{air}+*treatment category*+*position index*	Air temperature	0.44		0.08	42.31	1, 61	**<0.0001**
	Treatment: before*/during/after food restriction	During: −0.64 After: −0.92	(Before: 27.61±0.26) (During: 26.97±0.18) (After: 26.69±0.24)	(During) 0.32 (After) 0.36	6.74	1, 61	**0.0023**
	Position index	0.16		0.06	7.67	1, 61	**0.0074**
Wild	Intercept	20.97		7.5	38,927.14	1, 68	**<0.0001**
T_{eye}~T_{air}+*treatment category*+*time*+*position index*+treatment category×time+treatment category×time^2	Air temperature	0.1		0.05	5	1, 68	**0.0286**
	Treatment: food-restricted*/food-available day	31.66		14.78	1.53	1, 68	0.22
	Time of day	0.35		1.3	2.19	1, 68	0.1434
	Position index	0.25		0.05	24.15	1, 68	**<0.0001**
	Treatment×time of day	−5.5		2.61	0.27	1, 68	0.6062
	Treatment×time of day^2	Food restricted: −0.02 Food available: 0.22		0.06 0.1	2.52	2, 68	0.088

For the captive study, filming occurred before and after a food restriction event and two consecutive days before the food restriction day (included in the control group) (see Materials and Methods). The models used are described in the table with the response variable and fixed effects (all models were mixed effects and details of random effect can be found in Materials and Methods). Interactions are represented by '×' between variables. Estimates are the change in the response variable (i.e. surface temperature) per unit increase in the parameter, or for categorical variables, per unit increase when the baseline equals zero. *Baseline levels for categorical variables. For interactions, the estimates give the change in slope from the regression of the response for each treatment level compared with the baseline treatment level. Bold indicates significance.

tested as random effects in separate models. However, aviary ID did not improve model fit in any case and was removed from all models. Predicted means (±standard error) of the bill and eye region temperatures for each treatment in the model described were calculated using the predictmeans package (version 1.0.1; https://CRAN.R-project.org/package=predictmeans).

Wild

We tested effects of food restriction in two ways. Firstly, we tested treatment effects in a model with surface temperature as the dependent variable and 'time' (i.e. before, during or after food restriction) as a categorical explanatory variable. We calculated predicted means (±standard error) of surface temperature from the described model for each of these 'times' using the predictmeans package (version 1.0.1; https://CRAN.R-project.org/package=predictmeans). Tukey HSD *post hoc* tests were used to compare differences between food restriction treatments in both wild and captive birds, using the *stats* package (version 3.5.2; http://www.R-project.org/). In both tests, we confined the after food restriction period to 1.5 h from the end of food restriction to mirror the timing of the captive experiment.

Secondly, we also used continuous body surface temperature data from before, during and after food restriction. Bill temperature and eye region temperature were both modelled using, as fixed effects, air temperature, position index and the interaction between treatment/control day and time of day as both linear and quadratic terms along with their main effects. Bird ID with a covariance structure (AR1 covariance structures) and focus level were random factors. Focus level did not improve fit and was removed from the model.

RESULTS

Bill and eye region temperature were linearly related to air temperature regardless of food restriction treatment in both experiments (bill: captive: $P<0.0001$, wild: $P<0.0001$, Fig. 2A and B, respectively; eye region: captive: $P<0.0001$, wild: $P=0.03$, Fig. 2C and D, respectively; Table 2).

The position index also accounted for significant variation in the observed bill temperature for captive ($P<0.0001$; Table 2) and wild great tits ($P<0.0001$; Table 2).

In the captive study, bill temperature was 1.8±0.5°C greater after food restriction ($P=0.0008$; Fig. 3A, Table 2). In the wild study, bill temperature was significantly lower during food restriction than both before and after (mean±s.e.m. before: 14.0±0.3°C, during: 12.7±0.2°C, after: 13.9±0.3°C; combined effect: $P<0.0001$; Fig. 3B, Table 2). Eye region temperature in captive birds was

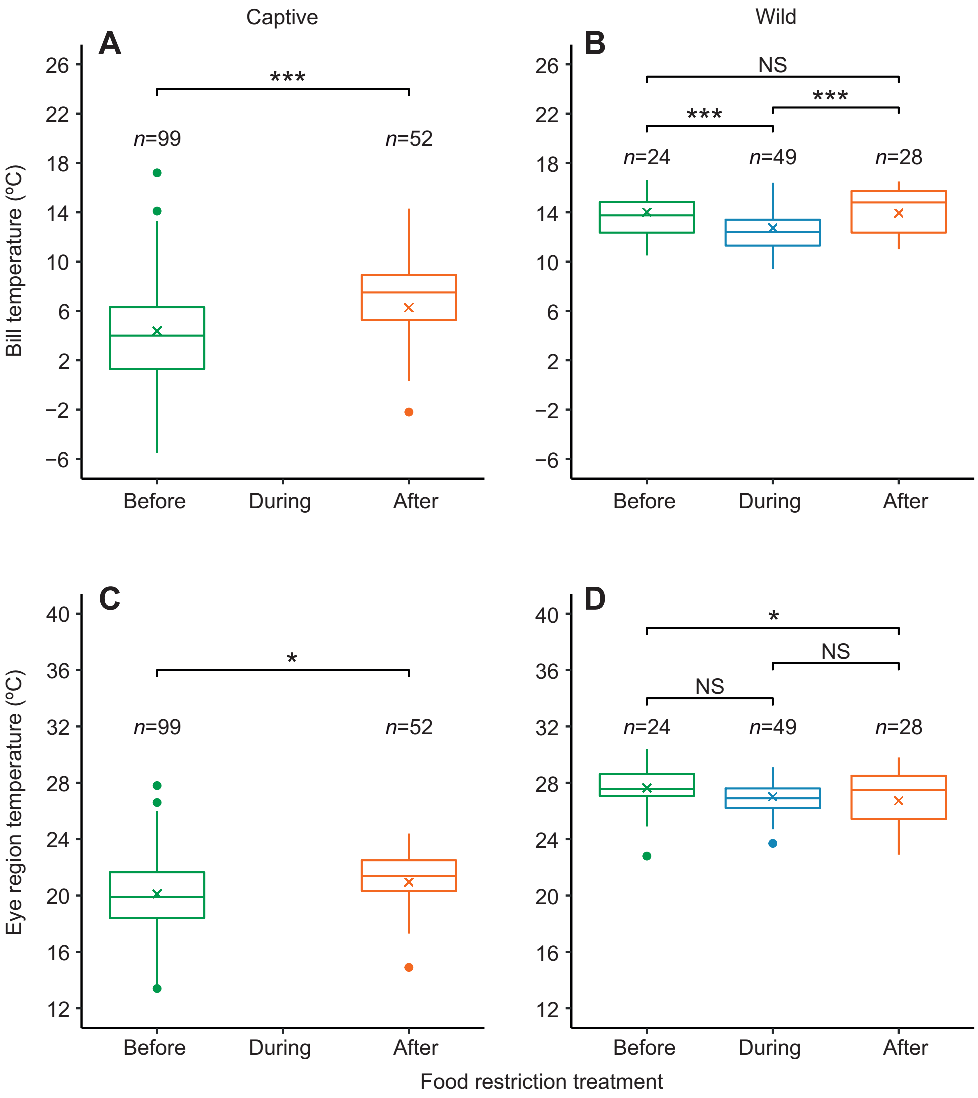

Fig. 3. Bill (top) and eye region (bottom) temperature before, during and after food restriction for wild and captive great tits. Only data for food-restricted days are shown. The wild study is confined to 1.5 h from the end of the food restriction to maintain a similar time frame to that in the captive study. Boxes are first and third quartiles and whiskers extend to the lowest and highest observation within 1.5 times the interquartile range. Observations outside of this range are shown as solid circles. The mean is indicated by a cross in each box. Significance values are from Tukey HSD. Significance is indicated by brackets with asterisks indicating significance level (*$P<0.05$, ***$P<0.0001$). Sample size above each plot indicates the number of images used. (A,C) In the captive experiment, 15 individuals were measured before food restriction and 17 after food restriction. (B,D) In the wild experiment, 11 individuals were measured before food restriction, 17 during food restriction and 9 after food restriction.

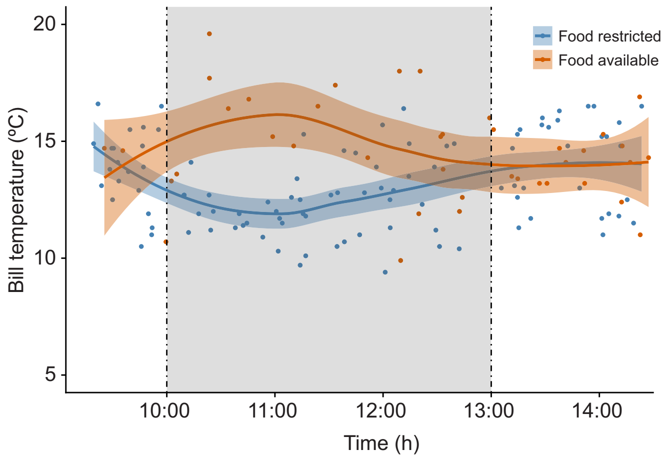

Fig. 4. Effects of food restriction on bill temperature for wild great tits. Food-restricted days are shown in blue (*n*=126 images, 19 birds) and days where food was available are shown in orange (*n*=55 images, 46 birds). The smooth curve line and 95% confidence intervals are fitted from locally estimated scatterplot smoothing. The grey shaded region indicates the food restriction period (variation in start and end time between days was <15 min).

higher after food restriction compared with before (before: 20.0±0.3°C, after: 20.8±0.3°C; *P*=0.04652; Fig. 3C, Table 2). For the wild study, eye region temperature was significantly lower after food restriction compared with before (before: 27.6±0.3°C, during: 27.0±0.2°C, after: 26.7±0.2°C; combined effect: *P*=0.0023; Fig. 3D, Table 2).

In the wild study, bill temperature was measured continuously from the start of recording and was found to vary temporally between food-restricted and food-available days (Fig. 4, Table 2). During food restriction, bill temperature was 1.3±0.3°C below bill temperature on food-available days at the corresponding time period when ambient temperature was accounted for (Fig. 4). After the initial decrease, however, the bill temperature of food-restricted birds increased throughout the food restriction period and was similar to that in birds on food-available days at the end of the observation period, unlike in the captive birds. Before and after food restriction temperatures were, thus, similar for food-restricted and food-available days.

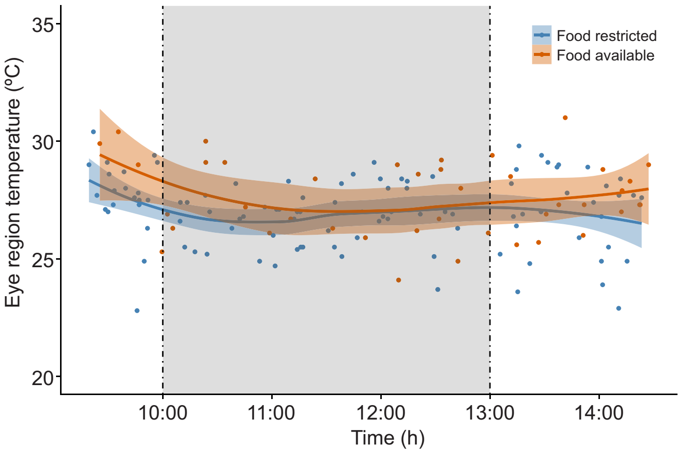

Fig. 5. Effects of food restriction on eye temperature for wild great tits. Food-restricted days are shown in blue (*n*=126 images, 19 birds) and days where food was available are shown in orange (*n*=55 images, 46 birds). The smooth curve line and the 95% confidence intervals are fitted from locally estimated scatterplot smoothing. The grey shaded region indicates the food restriction period (variation in start and end time between days was <15 min).

Eye region temperature in the wild study was not significantly influenced by food restriction (Fig. 5, Table 2), and the 95% confidence intervals overlapped between food-restricted and food-available days throughout the experiment. There was a general decrease in eye temperature throughout the experiment; however, as this was true for both food-restricted and food-available days, this trend was not driven by the food restriction event.

DISCUSSION

We found that the bill temperature of free-ranging great tits decreased significantly during periods of food restriction compared with periods when supplemented food was available to birds. As bill temperature returned to before-food restriction levels (or higher, in the case of the captive birds) on food-available days, we are confident that the reduction in bill temperature was a direct response to the removal of a reliable food source. The relative immediacy (the lowest temperature occurred in less than an hour from the beginning of the restriction) of the reduction in bill temperature indicates control of vasoconstriction by the bird, rather than a reduction in temperature due to lower metabolic heat production as a result of the lack of food. This is suggestive of a cautionary measure, as an autonomic response, to minimize subsequent energetic shortfalls, should the lack of food persist. The putative mechanism, constriction of the blood vessels that supply the bill (see Midtgård, 1984), reduces the tissue–skin gradient and hence heat loss rate. Tattersall et al. (2017) suggest that small birds are disproportionately more affected by heat loss from uninsulated regions compared with larger birds. Therefore, vasoconstriction of the bill is probably an important energy-saving response for small passerines in cold environments.

Conversely, we found no difference in eye region temperature when wild birds were food restricted compared with periods when food was available. This suggests that the bill temperature response was caused by local vasoconstriction, and not by reduced circulation to the entire head region. A possible reason for maintaining eye region temperature could be the close proximity of the eye to the brain, which must receive a continuous supply of warm blood to maintain function. Likewise, steady, high temperature in the eye region is probably of value for visual acuity, and hence beneficial for maintained foraging efficiency in a visually guided bird such as the great tit. The relatively long duration that the bill was at a lower temperature on food-restricted days compared with food-available days indicates that vasoconstriction of the bill was not driven by an acute stress response triggered by the experiment. If so, we would have expected to see a considerably faster return to the before food restriction values, based on the time line of the thermal response to an acute stressor in periorbital skin in the closely related blue tit (*Cyanistes caeruleus*) (Jerem et al., 2019). This provides evidence for selective vasoconstriction of the bill as opposed to a global drop in peripheral temperature as is expected in response to an acute stressor (e.g. Herborn et al., 2015; Nord and Folkow, 2019; Robertson et al., 2020).

The blood supply to the bill must also serve some purpose in functionality, otherwise it would remain permanently low when the bird is below the TNZ, even when food is plentiful. It follows that even though vasoconstriction of the bill probably reflects a first major defence against energetic shortfalls, it is conceivable that the bird will act to minimise periods of reduced bill function. This could explain why, in the wild, bill temperature gradually increased throughout the food restriction period following the initial drop.

This gradual increase in temperature throughout food restriction may, in part, occur through increased activity as birds tried to locate, and potentially ingest, alternative food sources. This is supported by surface temperature increases seen in non-manipulated wild birds throughout the morning, probably from activity-generated heat. Though no filming occurred during food restriction in the captive study, the significantly higher bill and eye temperatures in these birds after food restriction, compared with those before, is likely to be due to increased activity and/or metabolic heat production when birds were re-fed (Zhou and Yamamoto, 1997).

Bill and eye temperature of wild and captive great tits decreased with air temperature, which we believe was largely due to greater heat loss to the environment. Similar trends have been observed in other studies of birds at varying environmental temperatures (McCafferty et al., 2011; Robinson et al., 1976; Tattersall et al., 2016). It is important to note that the effect of air temperature on body surface temperature occurred regardless of whether food was being restricted at the time or not. Our data, and those of other studies, highlight the role of the bill in thermoregulation. Under low ambient temperatures, heat loss through the bill is reduced by vasoconstriction; conversely, at high ambient temperatures, there is increased circulation to the bill to facilitate heat loss (Tattersall et al., 2009; Wolf and Walsberg, 1996). This thermoregulatory role of the bill, consolidated by our data, should be taken into account when interpreting recently described adaptive changes in bill size, notably in great tits (Bosse et al., 2017; Danner and Greenberg, 2015; Friedman et al., 2017; Symonds and Tattersall, 2010; Tattersall et al., 2017).

Conclusion

We have shown that the bill plays a key role in the thermoregulatory response to a sudden drop in food availability in wild passerines. This is probably a pre-emptive response by the bird to prevent future energetic shortfalls by immediately reducing thermoregulatory costs. In addition, our results suggest that the level of vasoconstriction is flexible, as bill temperature increased throughout the food restriction period, possibly through active control to allow functionality of the bill to resume, or through increased activity to locate alternative food sources. This study gives novel insight into the thermoregulatory responses of birds to meet immediate changes to prospects of energy acquisition.

Acknowledgements

We thank Ruedi Nager, Marina Lehmann, Ross MacLeod and Jan-Åke Nilsson for assistance in data collection and for feedback throughout the project, Paul Jerem for crucial advice on experimental setup and comments on the manuscript, and Adam Wynne, Fanny Maillard, Güney Guüvenç and Jean Brustel for assistance in data collection. We would also like to thank staff of both Stensoffa and SCENE field stations for support throughout this study.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: L.W., S.W., A.N., B.H., D.M.; Methodology: L.W., S.W., A.N., B.H., D.M.; Validation: A.N., B.H., D.M.; Formal analysis: L.W., A.N., B.H.; Investigation: L.W.; Resources: S.W., D.M.; Data curation: L.W., D.M.; Writing - original draft: L.W., D.M.; Writing - review & editing: L.W., S.W., A.N., B.H., D.M.; Visualization: L.W.; Supervision: S.W., B.H., D.M.; Project administration: S.W., B.H., D.M.; Funding acquisition: A.N., B.H., D.M.

Funding

A.N. was supported by the Birgit and Hellmuth Hertz Foundation/Kungliga Fysiografiska Sällskapet i Lund (grant no. 2017-39034) and Vetenskapsrådet (grant no. 637-2013-7442). Data collection in Sweden was enabled by an ERASMUS Training Mobility Grant. L.A.W. was supported by a SCENE research bursary for the MRes Ecology and Environmental Biology at the University of Glasgow.

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