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RESEARCH ARTICLE

Acute stress and restricted diet reduce bill-mediated heat dissipation in the song sparrow (*Melospiza melodia*): implications for optimal thermoregulation

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ABSTRACT

We used thermal imaging to show that two environmental factors – acute stress and diet – influence thermoregulatory performance of a known thermal window, the avian bill. The bill plays important roles in thermoregulation and water balance. Given that heat loss through the bill is adjustable through vasoconstriction and vasodilation, and acute stress can cause vasoconstriction in peripheral body surfaces, we hypothesized that stress may influence the bill's role as a thermal window. We further hypothesized that diet influences heat dissipation from the bill, given that body condition influences the surface temperature of another body region (the eye region). We measured the surface temperature of the bills of song sparrows (*Melospiza melodia*) before, during and after handling by an observer at 37°C ambient temperature. We fed five birds a restricted diet intended to maintain body mass typical of wild birds, and we fed six birds an unrestricted diet for 5 months prior to experiments. Acute stress caused a decrease in the surface temperature of the bill, resulting in a 32.4% decrease in heat dissipation immediately following acute stress, before recovering over approximately 2.3 min. The initial reduction and subsequent recovery provide partial support for the hemoprotective and thermoprotective hypotheses, which predict a reduction or increase in peripheral blood flow, respectively. Birds with unrestricted diets had larger bills and dissipated more heat, indicating that diet and body condition influence bill-mediated heat dissipation and thermoregulation. These results indicate that stress-induced vascular changes and diet can influence mechanisms of heat loss and potentially inhibit optimal thermoregulation.

KEY WORDS: Thermal window, Bird, Thermal imaging, Body condition, Disturbance, Thermovascular physiology

INTRODUCTION

Recent research highlights the importance of the bill for heat dissipation and water conservation at high ambient temperatures. This research has provided important insights into the evolution of the bill and its role as a thermal window. The toco toucan's (*Ramphastos toco*) massive bill provides an example of both heat loss through the bill and the degree to which heat loss can be regulated in response to ambient temperature (Tattersall et al., 2009). Dissipating heat from the bill provides advantages over

evaporative cooling behaviors such as gaping and panting, which can lead to dehydration and are less efficient when humidity is high and reduces the rate of evaporation (Gerson et al., 2014; van Dyk et al., 2019). The evolutionary significance of bill-mediated heat dissipation (BMHD) is supported by interspecific trends between bill size and latitude (Symonds and Tattersall, 2010), bill size and ambient temperature (Greenberg et al., 2012a; Ryding et al., 2021), and bill size and humidity (Gardner et al., 2016), as well as intraspecific relationships between bill size and both ambient temperature and humidity (Danner and Greenberg, 2015; Greenberg and Danner, 2012; Greenberg et al., 2012a). A difference in bill size between two subspecies of song sparrow (*Melospiza melodia*) inhabiting thermally different habitats conferred advantages in the form of BMHD and water conservation for the subspecies inhabiting the more thermally challenging habitat (Greenberg et al., 2012b), further suggesting the evolutionary significance of the bill as an exaptation with important functions in heat dissipation and water conservation. Indeed, birds' bills have become a flagship example of how increasing thermal challenges caused by climate change can select for larger thermal windows in endotherms (Ryding et al., 2021).

Changes in bill temperature, and therefore heat loss through the bill, are thought to result in part from modulating blood flow through vasoconstriction and vasodilation, as evidenced indirectly by positive correlations between bill temperature and ambient temperature in observational (Tattersall et al., 2018) and experimental studies (Greenberg et al., 2012b; Tattersall et al., 2009). When ambient temperatures are high, the bill is vasodilated and its surface temperature is raised above that of the surrounding air, causing it to dissipate heat to the surrounding environment (reviewed in Tattersall et al., 2017). Conversely, when ambient temperatures are low and the bill is vasoconstricted, the surface of the bill is kept cool to reduce the amount of heat that is lost to the environment. Exposure of the bill to the environment can also be modulated via postural changes (Pavlovic et al., 2019; Ryeland et al., 2017).

Stress can affect the temperature of body surfaces important to avian thermoregulation, with acute stress causing an immediate decrease in temperature of the bill, comb and eye region (Herborn et al., 2015; Tabh et al., 2021), and chronic stress causing a long-term increase in comb, face and eye region temperature (Herborn et al., 2018). The surface temperature of the eye has also been linked to changes in cloacal temperature caused by handling-induced stress (Ikkatai and Watanabe, 2015). The surface temperature of the region surrounding the eye has been shown to be a predictor of circulating glucocorticoid levels, another indicator of stress, in wild blue tits (*Cyanistes caeruleus*; Jerem et al., 2018), though this association was only observed after acute activation of the hypothalamic–pituitary–adrenal axis in a captive study of house sparrows (*Passer*

domesticus; Ouyang et al., 2021). The temperature of the eye region has also been shown to respond to stress, with variation caused by ambient temperature and sex (Robertson et al., 2020a), as well as social hierarchy (Robertson et al., 2020b). The latter two examples provide evidence for the recent 'thermoprotective hypothesis', which proposes that stress-induced changes in peripheral temperature act to offset the energetic costs of a stress response by providing a thermoregulatory benefit. In contrast, the 'hemoprotective hypothesis' states that peripheral vasoconstriction following stress serves to reduce blood loss if the animal is injured (Jerem et al., 2015). If bird bills decline in temperature in response to acute stress, as predicted by the hemoprotective hypothesis, this would suggest that the bill's role as a thermal window may be compromised. If the thermoregulatory function of the bill is compromised, it could place birds inhabiting hot environments at elevated risk of heat stress when experiencing acute stress. However, this has not been tested at high temperatures, and it is not well known whether bill temperature declines by a sufficient amount or over a long enough duration to influence thermoregulation in a meaningful way.

Body condition is another factor known to affect the surface temperature of birds. Jerem et al. (2018) found that the eye region of birds with lower body condition was cooler than that of birds with higher body condition. If this pattern is reflected in the bill, then diet may be another environmental factor that can influence how effectively the bill functions for thermoregulation.

We experimentally tested how acute stress and diet influence heat exchange, and therefore thermoregulation, through the bill. Specifically, we used thermal imaging to monitor the effect of acute stress on the surface temperature of the bill, the eye and the eye region. Measuring the surface temperature of the eyeball provided a way to compare measurements of the bill, a known adjustable thermal window (Tattersall et al., 2017), with the temperature of a distinct surface that is not thought to function as an adjustable thermal window. We collected data at high ambient temperature in summer, when the bill is most likely to be used as a thermal window, with the goal of investigating the impact of acute stress on bill-mediated heat dissipation. We also tested the effect of diet, and by extension body mass, by feeding birds either an unrestricted diet or a restricted diet that was intended to maintain body mass typical of wild birds. The goal of this sampling approach was to test the hypothesis that peripheral vasoconstriction caused by acute stress can temporarily override the avian bill's thermoregulatory role and that diet may influence this response. We pose three predictions associated with this primary hypothesis. (1) Stress-induced peripheral vasoconstriction will cause bill temperature and heat dissipation to decrease. (2) Because of its thermoregulatory role, the bill (but not other regions) will return to, and then stabilize at, pre-stress temperature and heat dissipation following acute stress. (3) Birds with greater access to food will be more effective at thermoregulating through peripheral heat exchange, as indicated by higher BMHD.

To our knowledge, this is the first study to test the combined effects of heat stress, acute stress and diet simultaneously on the use of the bill as a thermal window. Our results provide novel evidence that acute stress can inhibit a bird's ability to thermoregulate via the bill, and that birds depend on their diet to maximize the efficacy of the bill as a thermoregulatory trait. Our findings also contribute to two broad and actively developing theories in the field of avian thermal biology: first, that birds can regulate bill temperature through vasoconstriction and vasodilation, and second, that thermal imaging can help identify acute stress. Support for prediction 1

would provide evidence for the long-standing hemoprotective hypothesis, whereas support for prediction 2 would provide evidence for the emerging thermoprotective hypothesis.

MATERIALS AND METHODS
Study species
The song sparrow has become a focal species for studies of heat dissipation from the bill. Song sparrows are a polytypic species (Patten and Pruett, 2009), and bill morphology is related to ambient temperature and humidity, suggesting that the bill has evolved, at least in part, for thermoregulation (Danner and Greenberg, 2015; Danner et al., 2017; Greenberg and Danner, 2012; Greenberg et al., 2012a). We studied two subspecies of song sparrow: the eastern song sparrow [*Melospiza melodia melodia* (Wilson 1810)] and the Atlantic song sparrow (*Melospiza melodia atlantica* Todd 1924).

Capture and care
We captured 11 immature male song sparrows with mist nets in November and December of 2012. These birds hatched in summer 2012 and were estimated to be between 3 and 6 months old when captured. We aged birds based on a combination of growth bar alignment on flight feathers and skull pneumatization (Pyle, 1997). We determined sex in the field based on wing length following Pyle (1997) and confirmed sex with genetic methods following Danner et al. (2013). We identified subspecies based on plumage (Danner et al., 2016) and range. We captured eastern song sparrows in marshes in Anne Arundel and Prince Georges Counties, MD, USA, and Atlantic song sparrows in marshes at Delaware Seashore State Park, DE, USA. Birds were maintained individually in finch breeder cages with two perches at uneven heights, *ad libitum* water, and food as described in Smith et al. (2018). Initially, all birds were provided with the same diet, which consisted of unrestricted access to Vita Sunscription® Canary diet (Vitakraft Sunseed Inc., PO Box 33, Bowling Green, OH, USA) and four mealworms per day. To test for potential dietary effects on bill growth and function, we subjected birds to one of two diet treatments for 5 months prior to thermography (details in Smith et al., 2018): six of the 11 individuals continued to receive the same unrestricted diet as previously; the remaining five birds were fed a restricted amount of the same diet, which was intended to maintain body mass typical of wild birds. The birds on the restricted diet maintained a body mass slightly higher than that of wild birds of the same subspecies during summer months (Tables S1 and S2), which makes it unlikely that they experienced more chronic stress from food limitation than would be typical in the wild. The birds on the unrestricted diet maintained higher mass than birds on the restricted diet. All capture, care and research described here was approved by the Smithsonian National Zoological Park and Conservation Biology Institute Animal Care and Use Committee (IACUC #12-31).

Morphological measurements
We measured the bill length, width and depth at the anterior edge of the nares with a precision of 0.01 mm with digital calipers. We then calculated the bill surface area of each individual (Table S3) using the areacone() function in Thermimage (https://CRAN.R-project.org/package=Thermimage). The bill surface area was calculated as an elliptical cone using the depth and width of the beak as the two axes of the ellipsis. The base of the cone was excluded. Our measurement of bill surface is of the distal portion of the bill (i.e. anterior tip to the nares) and therefore provides a conservative

estimate of total heat loss from the bill. We measured bills on 8 or 12 August 2013. We weighed birds on 26 August 2013.

Thermography

Prior to trials each day, we heated a climate-controlled room to 37°C. We transferred birds to clean trial cages, which we covered with translucent white cloth to reduce visual stimulation. The trial cages had the same dimensions as the housing cages, but contained a single perch, allowing lateral images to be collected more consistently (Greenberg et al., 2012b). We moved the individually caged birds into the climate-controlled room for separate trials. Inside the room, we placed the trial cage on a rack in front of a table that held a thermal imaging camera (FLIR T-300, resolution of 320×240 pixels). We provided the birds with a 10 min habituation period, followed by a 5 min pre-stress period. In total, this allowed birds at least 15 min to adjust to their new surroundings. Following these methods, we performed thermography trials on the 11 birds over 2 days: 28 and 29 August 2013. We tested six individuals of subspecies *M. m. melodia* and five of subspecies *M. m. atlantica*.

At the end of the 15 min period at the trial temperature, we took the first 10 s thermal image sequence recorded at 6.3 frames s^{-1}, hereafter called 'time −1'. A researcher then entered the climate-controlled room, opened the cage and quickly captured the bird by hand, careful not to touch the bill. We then immediately took another 10 s thermal image sequence, hereafter called 'time 0'. The researcher then held the bird by the legs in what is known as 'photographer's grip' for the next ~10 min (Fig. 1). We took a 10 s thermal image sequence once per minute, called 'time 1' to 'time 10', until the trial ended.

We collected one data point for each minute in the thermal image sequences using ExaminIR version 1.30.0 (FLIR). The data were not always collected at the exact minute mark because of the birds' movement and resulting position in the camera's view, but were consistently collected within 5 s of the minute mark, and were selected as close to the minute mark as possible. We prioritized frames where the tip of the bird's bill was pointing 90 deg to the left or right and where the bird was still (i.e. no motion blur present in the frame), from within each 10 s sequence. We drew separate region of interest (ROI) polygons around the bird's bill, eyeball and eye region to obtain the average or maximum surface temperature (T_s) for each ROI. For the bill and eye, we recorded average T_s to allow comparison between those features. For the eye region, we recorded the maximum T_s to allow comparison with data from Robertson et al. (2020a) and to minimize bias towards cooler temperature measurements that could result from higher evaporation from the eye surface at high temperatures. If the bird was exhaling, the camera detected the nares as hotter or cooler (depending on the temperature treatment) than the surrounding bill. Therefore, we avoided the nares when drawing ROI of the bill because they would be more indicative of internal body temperature than of T_s of the bill. For eyeball measurements, we did not include the skin immediately around the eye. If the eye was closed during the selected frame, we collected data for the eye from the nearest preceding or following frame when the eye was open. For eye region measurements, the polygons encompassed the warm region surrounding the eye, from which we extracted the maximum temperature to match methods from Robertson et al. (2020a); we also avoided the bill when drawing eye region ROI to ensure that the maximum temperature was measured from the eye
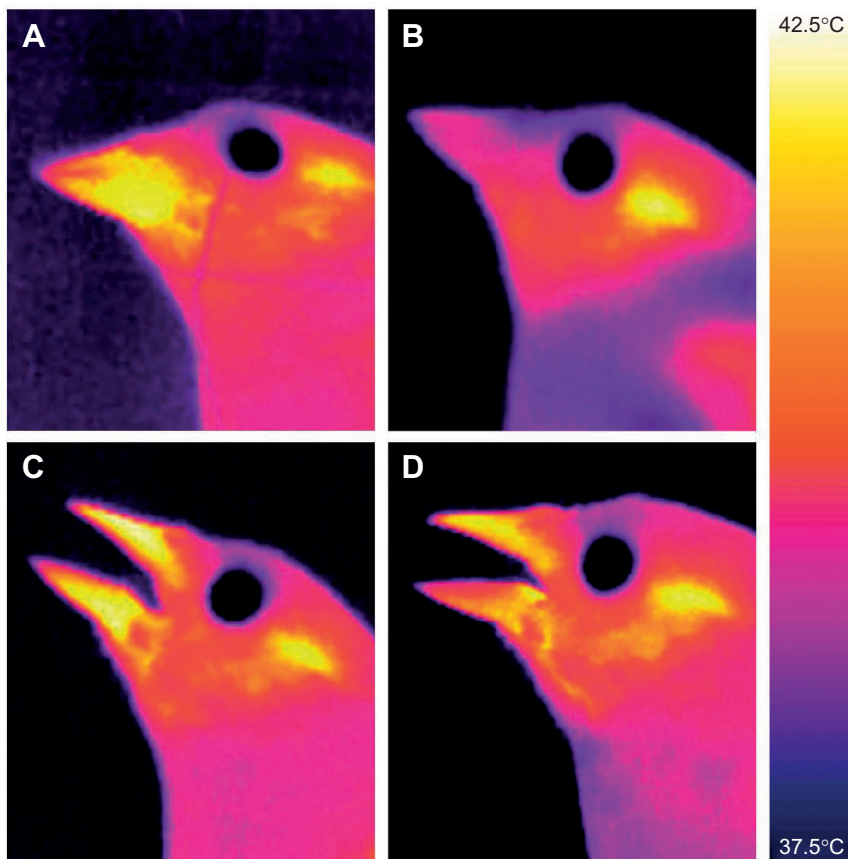

Fig. 1. Thermal images of a song sparrow (*Melospiza melodia*) during a trial at 37°C ambient temperature. Images in A–D were taken at times −1, 0, 5 and 10, respectively. Notice that the bill is warm at time −1 (before handling), cools at time 0 (immediately after capture), and is warmer again at times 5 and 10.

region, and not from the bill, which was often warmer at the high ambient temperature. Bill ROI had 273.94±20.39 pixels (mean±s.e.m.), eye ROI had 37.71±1.97 pixels and eye region ROI had 686.46±34.78 pixels.

To ensure that the high temperature treatment was above the thermoneutral zone, we scanned each 10 s sequence from start to finish for the presence of gaping, which we considered to be present during the minute if gaping was observed at all during the 10 s clip. All but one of the individuals gaped, and gaping was observed in 72.44% of the image sequences at 37°C.

After collecting average T_s of the bill in each frame using ExaminIR, we exported the data to R version 4.0.4 (http://www.R-project.org/) and converted to convective (qconv) and radiative (qrad) heat transfer (W m^{-2}) using the R package Thermimage (https://CRAN.R-project.org/package=Thermimage), which follows equations from Blaxter (1989) and Gates (2003). We assumed an emissivity of 0.96 following Tattersall (2016). Relative humidity was assumed constant at 50% for all experiments. Kinematic viscosity and conductivity of air were assumed fixed. The experiments were conducted indoors and wind speed was undetectable (0 km h^{-1}) during all trials, as measured by a portable anemometer (Kestrel 4000) placed within 1 m of the bird. We therefore applied the type="forced" argument within the qconv() function with an estimated wind speed of 0.1 m s^{-1} as reasoned in Greenberg et al. (2012a,b). For surface reflectivity, we used a value of 0.05 (Tattersall et al., 2018). We then multiplied area-specific heat transfer by the surface area of the bill of each individual (m^2) and summed the resulting area-specific qconv and qrad to obtain the amount of BMHD (W) taking place instantaneously during each frame. Finally, we multiplied by 1000 to convert BMHD from W to mW.

Statistical analysis

We analyzed our data using linear mixed effects modeling in the R package lme4 (Bates et al., 2015). Specifically, we modeled four response variables: mean bill temperature (T_{bill}, °C), mean BMHD (mW), mean eye temperature (T_{eye}, °C), and maximum temperature of the eye region ($T_{eye-region}$, °C). We included the bird's assigned identification number (bird ID) as a random intercept in all models to account for interindividual variation, and we constructed all null models using only the random intercept of bird ID. We first tested whether subspecies influenced the response variables by comparing AICc values of linear models with the subspecies variable to the null model (bird ID). The criteria we set for subspecies to be included as an effect in the model structure was for the subspecies model to rank better (lower AICc) than the null model, and for the null model to be non-competitive (ΔAICc>2). Subspecies was not supported as an effect in any of the model sets (i.e. the null model never had ΔAICc>2); therefore, we did not include subspecies as a fixed effect in the final model structure for any of the response variables. We collected data for both diet and mass, which we expected to be strongly correlated (i.e. we expected birds fed an unrestricted diet to be heavier than those fed a restricted diet). We therefore included only one of these variables (diet or mass) as a fixed effect in the model structure for each response variable. We selected the variable by comparing a model with diet to one with mass and using the variable that had greater explanatory power (lower AICc); both models also contained the random intercept of bird ID. Based on this selection process, mass was better supported for all response variables except for maximum $T_{eye-region}$. Therefore, we included mass as a fixed effect in the final model structure for T_{bill}, BMHD and T_{eye}, and we included diet as a fixed effect in the model structure for $T_{eye-region}$.

Table 1. Linear mixed effects models describing mean bill temperature (T_{bill}) during three time frames

Time frame	Model	K	AICc	ΔAICc	AICc weight
−1 to 0	Time	4	63.72	0	0.52
	Time+mass	5	64.47	0.75	0.35
	Time×mass	6	66.47	2.75	0.13
0 to 2	Time+mass	5	95.63	0	0.47
	Time	4	95.86	0.22	0.42
	Time×mass	6	98.65	3.02	0.10
3 to 13	Time×mass	6	108.54	0	0.83
	Time	4	112.48	3.94	0.12
	Time+mass	5	114.67	6.13	0.04

Time −1 is before acute stress, time 0 is the initiation of acute stress, and positive values are after the initiation of acute stress.

To capture the stress response pattern, we created segmented models based on known and calculated changes in slope. The first segment from time −1 to 0 was specified *a priori* for all three model sets because of the expected change in temperature elicited by handling at time 0. For models of time 0–13, we determined the presence of changes in slope (i.e. breakpoints) using a simple linear regression [function lm() in base R] in conjunction with the R package segmented (https://cran.r-project.org/web/packages/segmented/index.html). After finding the breakpoint, we then fitted separate mixed effects models for each segment of time, as determined by the breakpoints. We modeled the fixed effects of time and mass (or diet in the case of $T_{eye-region}$), and we specified bird ID as a random intercept to account for repeated measures in each model. Model support was determined using AICc (Burnham and Anderson, 2002) and the R package AICcmodavg (https://CRAN.R-project.org/package=AICcmodavg). We assessed the fit of top models by calculating the conditional Nakagawa's R^2 using function tab_model() in the package sjPlot (https://CRAN.R-project.org/package=sjPlot). We reported marginal Nakagawa's R^2 for one model set (BMHD from time −1 to 0). We visually represented findings from our models by plotting raw data for T_{bill}, BMHD, T_{eye} and $T_{eye-region}$ over time with model predictions from top models using package ggplot2 (Wickham, 2016). We plotted predictions based on diet treatment or, when mass was a better predictor, mean mass per diet treatment.

RESULTS

Of the 11 individuals, 10 exhibited a reduction in bill temperature at the onset of acute stress. The top-ranked model from time −1 to 0 for T_{bill} included time (Table 1; R^2=0.670), and there was a competitive model that included time with mass as non-interactive fixed effects. Model-averaged parameter estimates (±s.e.) show that T_{bill}

Table 2. Linear mixed effects models describing bill-mediated heat dissipation (BMHD) during three time frames

Time frame	Model	K	AICc	ΔAICc	AICc weight
−1 to 0	Time+mass	5	101.70	0	0.74
	Time×mass	6	104.64	2.94	0.17
	Time	4	105.84	4.14	0.09
0 to 2	Time+mass	5	150.87	0	0.73
	Time×mass	6	153.96	3.09	0.16
	Time	4	154.67	3.80	0.11
3 to 13	Time×mass	6	276.82	0	0.92
	Time+mass	5	282.91	6.09	0.04
	Time	4	283.50	6.69	0.03

Time −1 is before acute stress, time 0 is the initiation of acute stress, and positive values are after the initiation of acute stress.

Table 3. Parameter estimates that describe surface temperature and heat dissipation in relation to time and diet

Model set		Time	Mass	Diet (unrestricted)	Time×mass
T_{bill}	−1 to 0*	−2.55±1.98	0.17±0.10	–	–
	0 to 2*	0.85±0.54	0.26±0.14	–	–
	3 to 13	0.53±0.19	0.17±0.08	–	−0.03±0.01
BMHD	−1 to 0	−4.86±0.85	0.63±0.19	–	–
	0 to 2	2.07±0.39	0.88±0.29	–	–
	3 to 13	1.37±0.50	0.75±0.23	–	−0.07±0.02
T_{eye}	−1 to 0	−1.45±0.16	–	–	–
	0 to 7*	−0.10±0.12	0.13±0.05	–	0.006±0.007
	7 to 13*	0.45±0.76	0.41±0.30	–	−0.05±0.03
Max. $T_{eye-region}$	−1 to 0	–	–	–	–
	0 to 13*	−0.004±0.009	–	0.41±0.18	–

Parameter estimates (±s.e.) come from top or averaged competing (*) models. T_{bill}, mean bill temperature; BMHD, mean bill-mediated heat dissipation; T_{eye}, mean eye temperature; $T_{eye-region}$, maximum eye region temperature. Parameter estimates for time are given in °C min^{-1} for models of T_{bill}, T_{eye} and $T_{eye-region}$, and in mW min^{-1} for models of BMHD. Parameter estimates for mass are given in °C g^{-1} for models of T_{bill} and T_{eye}, and in mW g^{-1} for models of BMHD. Parameter estimates are given to 2 decimal places or to 3 decimal places for those <0.01.

declined by 2.55±1.98°C from time −1 to 0 (Table 3). The top-ranked model from time −1 to 0 for BMHD included time and mass as non-interactive fixed effects (Table 2; marginal R^2=0.692), and there was no competitive model. Model-averaged parameter estimates show that BMHD declined by 4.86±0.85 mW from time −1 to 0 (Table 3), a difference of 32.39% from before acute stress. Model-averaged parameter estimates indicate that mass had a positive effect on heat dissipation of 0.63±0.19 mW g^{-1} (Table 3).

Segmented regressions identified breakpoints for T_{bill} and BMHD at 2.251 and 2.236 min, respectively. The top-ranked models for T_{bill} and BMHD from time 0 to 2 both included time and mass as non-interactive fixed effects (Tables 1 and 2; R^2=0.782 and 0.779). Model-averaged parameter estimates show that T_{bill} and BMHD increased by 0.85±0.54°C min^{-1} and 2.07±0.39 mW min^{-1}, respectively (Table 3). Mass also had a positive effect on both T_{bill} and BMHD of 0.26±0.14°C g^{-1} and 0.88±0.29 mW g^{-1}, respectively (Table 3).

The top-ranked models for T_{bill} and BMHD from time 3 to 13 both included time and mass as interactive fixed effects (Tables 1 and 2; R^2=0.603 and 0.747). Model-averaged parameter estimates show that T_{bill} and BMHD increased by

0.53±0.19°C min^{-1} and 1.37±0.50 mW min^{-1}, respectively (Table 3). Mass had a positive effect on both T_{bill} and BMHD of 0.17±0.08°C g^{-1} and 0.75±0.23 mW g^{-1}, respectively (Table 3). Lastly, the interaction between time and mass had a slight negative effect on both T_{bill} and BMHD of −0.03±0.01°C g^{-1} min^{-1} and −0.07±0.02 mW g^{-1} min^{-1}, respectively (Table 3), resulting in slopes near zero for restricted birds, and steeper negative slopes for unrestricted birds (Figs 2 and 3).

The segmented regression identified a breakpoint for T_{eye} at 7 min. The top-ranked model for T_{eye} from time −1 to 0 included time as a fixed effect (Table 4; R^2=0.809), and model-averaged parameter estimates show that T_{eye} decreased by 1.45±0.16°C min^{-1} from time −1 to 0 (Table 3). The top-ranked model for T_{eye} from time 0 to 7 included time and mass as non-interactive fixed effects (Table 4 R^2=0.357). The top-ranked model for T_{eye} from time 7 to 13 included time and mass as interactive fixed effects (Table 4 R^2=0.706). After the initial decrease in temperature at the onset of acute stress, the slopes for T_{eye} remained negative but became shallower (Table 3, Fig. 4). The interaction detected in the models from minutes 7 to 13 suggests that the slope for birds with unrestricted diets was steeper than that for birds with restricted diets; however, further testing would be
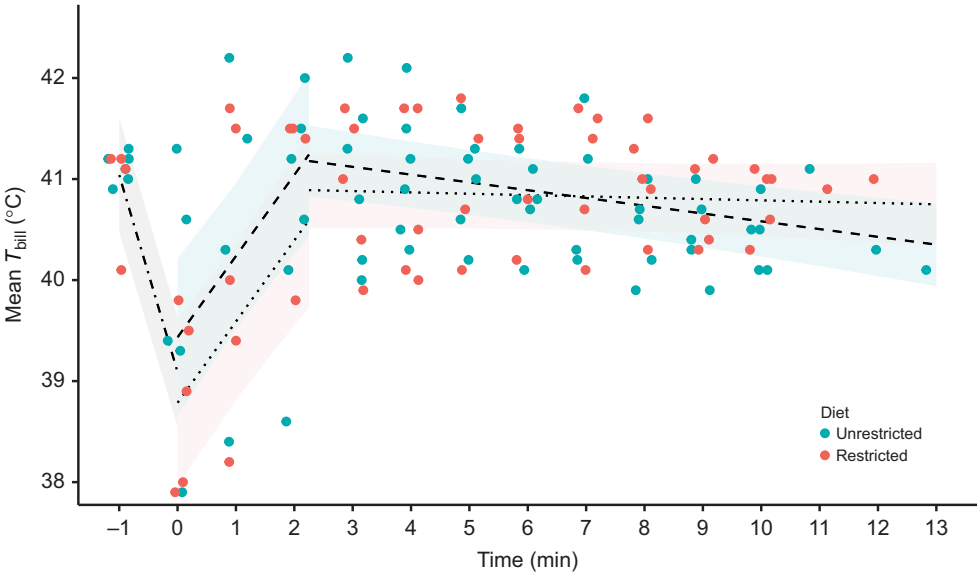

Fig. 2. Mean bill temperature (T_{bill}) across time in 11 trials at 37°C. Lines are predictions (±95% confidence interval, CI) from top-ranked models, which describe the two diet treatments combined from minute −1 (prior to stress) to minute 0 (start of the stressor; R^2=0.67), and each diet treatment separately from minutes 0 to 2.2 (R^2=0.78) and following the breakpoint identified at minute 2.2 (R^2=0.60). Raw data are jittered for clarity.

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Table 4. Linear mixed effects models describing mean eye temperature (T_{eye}) during three time frames

Time frame	Model	K	AICc	ΔAICc	AICc weight
−1 to 0	Time	4	33.90	0	0.66
	Time+mass	5	36.14	2.24	0.22
	Time×mass	6	37.26	3.36	0.12
0 to 7	Time+mass	5	250.00	0	0.64
	Time×mass	6	251.43	1.43	0.32
	Time	4	255.74	5.74	0.04
7 to 13	Time×mass	6	77.67	0	0.40
	Time+mass	5	77.87	0.21	0.36
	Mass	4	80.21	2.55	0.11

Time −1 is before acute stress, time 0 is the initiation of acute stress, and positive values are after the initiation of acute stress.

Table 5. Linear mixed effects models describing maximum temperature of the eye region ($T_{eye-region}$) during two time frames

Time frame	Model	K	AICc	ΔAICc	AICc weight
−1 to 0	Null (bird ID)	3	34.28	0	0.60
	Time	4	36.40	2.12	0.21
	Diet	4	37.22	2.95	0.14
0 to 13	Diet	4	83.91	0	0.51
	Time+diet	5	85.87	1.96	0.19
	Null (bird ID)	3	86.15	2.24	0.17

Time −1 is before acute stress, time 0 is the initiation of acute stress, and positive values are after the initiation of acute stress.

necessary to ascertain whether this pattern would persist or is an artifact of the cluster of unrestricted birds with high T_{eye} at minutes 7 and 8.

The segmented regression identified a breakpoint for maximum $T_{eye-region}$ at 9.89 min, which is near the end of the distribution and was likely caused by the dearth of data after 10 min; this breakpoint was not used and the data were therefore only subset at the *a priori* determined breakpoint at 0 (Fig. 5). The top-ranked model for maximum $T_{eye-region}$ from time −1 to 0 was the null model (Table 5; R^2=0.156), indicating a negligible effect of acute stress on the eye region in this dataset. The top-ranked model for maximum $T_{eye-region}$ from time 0 to 13 included diet as the only fixed effect (Table 5; R^2=0.568), with birds on unrestricted diets having 0.41±0.18°C higher maximum $T_{eye-region}$ than birds on restricted diets (Table 3).

DISCUSSION
As a consequence of climate change and human population growth, birds globally are increasingly facing heat stress (Albright et al., 2017; Conradie et al., 2019, 2020) and anthropogenic disturbance (Matuoka et al., 2020). The intersect of these two challenges has not been extensively studied, and their interaction may therefore be underappreciated. Using thermal imaging to monitor the effect of acute stress during a thermoregulatory challenge, we found evidence that the peripheral vasoconstriction caused by acute stress can temporarily override the avian bill's thermoregulatory role.

Prediction 1: acute stress will cause bill temperature and heat dissipation to decrease
Supporting our first prediction, bill temperatures during trials at 37°C decreased after acute stress, resulting in a reduction in heat loss of 4.86±0.85 mW, or 32.4%. A similar vascular response to the initial reduction measured in T_{bill} and T_{eye} here has been observed in rabbits (Roatta et al., 2009), where blood flow to the orofacial region, measured by a perivascular flow probe, decreased after test subjects were exposed to a range of stressors. Both results are consistent with the hemoprotective hypothesis, which predicts that blood flow is shunted away from the periphery during stressful experiences. Additionally, if the reduction in temperature from acute stress is indeed caused by blood shunting, then our results also support the theory that birds regulate bill temperature through vasoconstriction and vasodilation.

Prediction 2: the bill will return to, and then stabilize at, pre-stress temperature and heat dissipation
While T_{bill} recovered, T_{eye} remained stable and lowered after the initial reduction in temperature caused by acute stress. Maximum $T_{eye-region}$ did not change notably over the entire experiment. The bill rewarmed to pre-stress temperatures or higher at 2.2 min after capture, supporting our second prediction that surface temperature of the bill, but not other regions, would return to and then stabilize at pre-stress conditions following acute stress. The lack of recovery to pre-stress temperatures in the eye and of any change in the eye region indicates that the vasculature of these regions is less versatile than that of the bill during a stress response.
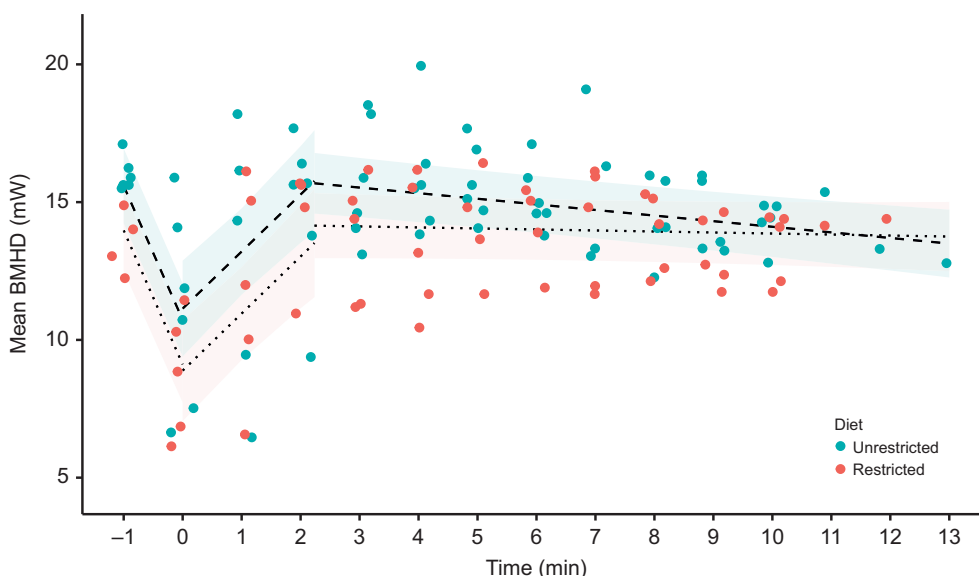

Fig. 3. Mean bill-mediated heat dissipation (BMHD) across time in 11 trials at 37°C. Lines are predictions (±95% CI) from top-ranked models, which describe each diet treatment separately from minute −1 (prior to stress) to minute 0 (start of the stressor; R^2=0.69), minutes 0 to 2.2 (R^2=0.78) and following the breakpoint identified at minute 2.2 (R^2=0.75). Raw data are jittered for clarity.
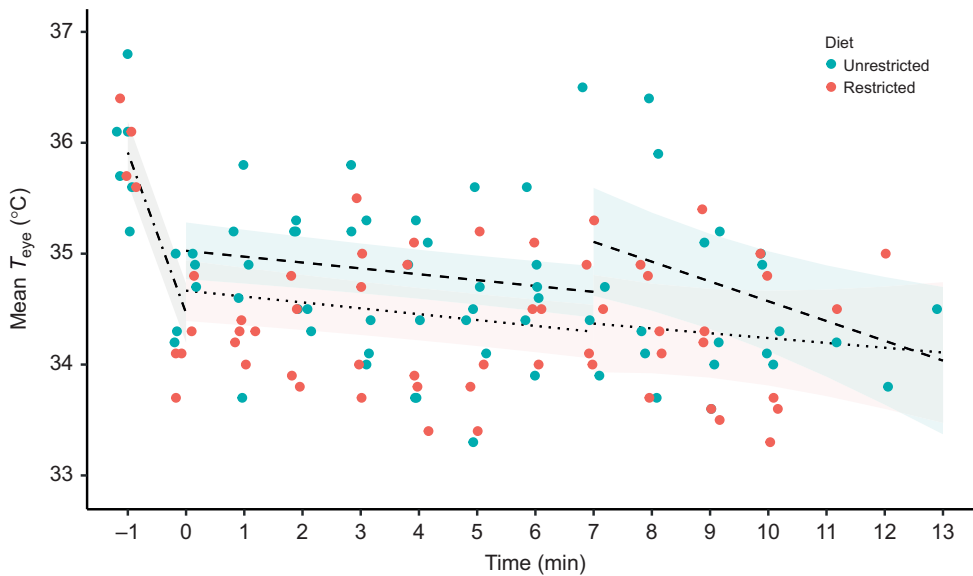
Fig. 4. Mean eye temperature (T_{eye}) across time in 11 trials at 37°C. Lines are predictions (±95% CI) from top-ranked models, which describe the two diet treatments combined from minute −1 (prior to stress) to minute 0 (start of the stressor; R^2=0.81), and each diet treatment separately from minutes 0 to 7 (R^2=0.36) and following the breakpoint identified at minute 7 (R^2=0.71). Raw data are jittered for clarity.

The higher vascular versatility of the bill and, more specifically, its ability to return to pre-stress levels of temperature and heat dissipation, supports the idea that the bill has evolved partly as an exaptation for heat dissipation. These results also provide support for the emerging thermoprotective hypothesis, which predicts an increase in peripheral blood flow at the onset of acute stress to aid in heat dissipation. While our study found support for the thermoprotective hypothesis only in the bill, the eye region of black-capped chickadees (*Poecile atricapilus*) has been found to function thermoprotectively (Robertson et al., 2020a), suggesting that selective pressure on peripheral vasculature varies between species.

Prediction 3: birds with greater access to food will be more effective at thermoregulating through peripheral heat exchange

T_{bill} was higher in the heavier birds (i.e. those with greater access to food in this study) over two of the three time periods (the recovery and post-recovery periods), and the BMHD of heavier birds was higher over all three time periods. Supporting our third

prediction, the presence and effect of body mass as a fixed effect in two of the three top models for T_{bill} and all three top models for BMHD indicates that heavier birds were more effective at thermoregulating through peripheral heat exchange at high ambient temperatures. The presence of mass in some models describing BMHD but not T_{bill} is likely a result of mass influencing bill size, which is incorporated in BMHD values because they are area specific, but not in T_{bill} values because they are measures of surface temperature only; in other words, the effect of mass is higher on BMHD than on T_{bill} because mass likely influenced bill size.

Unexpectedly, we found that T_{bill} and BMHD of birds on the unrestricted diet rose to higher than pre-stress conditions at ~2.3 min; we hypothesize that those birds temporarily directed more blood to the bill to dump excess heat that was generated during the initial stage of the acute stress response. The absence of the compensatory elevated heat dissipation in restricted diet birds, and its presence in unrestricted diet birds, suggests that diet and body condition play an important role in determining the versatility and effectiveness of BMHD.
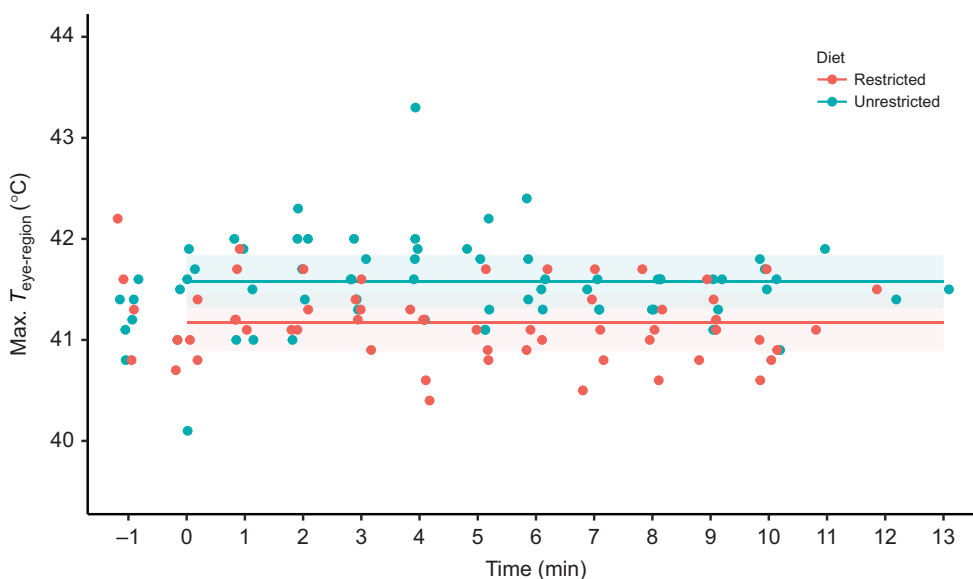

Fig. 5. Maximum temperature of the eye region ($T_{eye-region}$) across time in 11 trials at 37°C. Lines are predictions (±95% CI) from the top-ranked model, which describes each diet treatment separately from minute −1 (prior to stress) to minute 13 (R^2=0.57). No predictions are plotted from time −1 to 0 because the null model (random intercept of bird ID) was the most supported model during this time. The models did not identify a change in temperature following the stressor at minute 0. Raw data are jittered for clarity.

Implications for optimal thermoregulation

Greenberg et al. (2012b) found a difference of 33% in the amount of bill-mediated heat dissipation between two subspecies of song sparrow inhabiting thermally different habitats, suggesting the evolutionary significance of a change in heat dissipation of this magnitude. Here, we have shown that acute stress at high ambient temperatures in the same species can cause a comparable reduction in bill-mediated heat dissipation. Although our study focused on the bill and face, stress-induced cooling of other body surfaces could further diminish heat loss. We found that the eye region did not cool following stress, but our study was not designed to allow measurement of the body or legs. The cooling of the bill was temporary, lasting ~2.2 min after the onset of acute stress. It is unknown whether repeated stressors would cause similar cooling for surfaces.

An implication of reduced heat loss from a thermal window after acute stress is that birds experiencing thermally challenging conditions may be forced to thermoregulate less effectively when stressors are present. For example, the rise in metabolic rate associated with stress, coupled with the reduction in efficiency of a thermal window (shown here), may necessitate greater expenditure of resources to meet thermoregulatory demands than would be necessary in the absence of stress; whether these amplified thermoregulatory demands are met immediately through evaporative cooling (possibly increasing dehydration), or delayed (possibly causing hyperthermia), the intersection of stress and a thermal challenge poses a synergistic threat that could raise the cost of thermoregulation. Based on this relationship, we hypothesize that stress-induced reductions in heat dissipation can exacerbate the negative effects of high temperatures on reproduction and survival. For example, high temperatures have been shown to reduce cognitive and motor performance on tasks related to foraging (Danner et al., 2021) and mate choice (Coomes et al., 2019). High temperatures can also impose opportunity costs associated with breeding, such as reductions in singing rate and other territorial behaviors while birds seek shade or a reduction in activities that can generate heat (Luther and Danner, 2016), leading to lower reproductive success (Cunningham et al., 2021; van de Ven et al., 2020). Extreme hyperthermia and dehydration are also known to cause mass die-offs (McKechnie et al., 2021; Welbergen et al., 2008). We hypothesize that negative effects from a combination of heat and stress would be more likely to affect birds inhabiting hot environments that are also prone to disturbance, such as some beach-nesting birds (e.g. Snowden, 2018).

It is possible that in some cases birds may opt to maintain heat dissipation through the bill instead of responding to a threat by constricting blood flow, as shown by one bird that did not constrict blood flow to the bill during handling in our study. Other indicators of stress, such as breathing rate and internal body temperature, have been shown to be influenced by an individual bird's tendency towards shyness or boldness (Carere and Van Oers, 2004). Such interindividual variation may provide a basis for evolutionary pressure to act upon behaviorally influenced vascular changes during thermoregulation and stress, such as those predicted by the hemoprotective and thermoprotective hypotheses.

The need to balance synergistic challenges of acute stress and heat may have led to the evolution of a sequence of hemoprotective vasomotion followed by thermoprotective vasomotion. In our study, the shunting of blood away from surfaces may protect the animal from the immediate threat of blood loss, and the subsequent recovery and overcompensation in surface temperature might protect them against a more prolonged threat of overheating. When viewed under this framework, the differences in surface temperature changes among body regions might reflect the potential for blood loss or function for thermoregulation in each region. For example, the eyeball did not recover temperature in our study, suggesting that it is at greater threat of blood loss than of value for thermoregulation. It remains to be determined whether the putative switch from hemoprotection to thermoprotection is consistent in occurrence and timing across species, ambient temperatures and other body regions. The legs may be an important feature to study in the context of the thermo-vascular response to stress, given their lack of insulation as well as high vascularization and use for thermoregulation.

Our finding that acute exposure to stress can inhibit the thermoregulatory function of the avian bill contributes to the growing body of literature describing how the bill interfaces with the thermal environment. Specifically, it was previously described that the bill responds to temperature and provides water savings; we now provide evidence that these important functions of the bill can be compromised by acute stress. This highlights the importance of considering anthropogenic and other types of disturbance in systems where thermal stress is present. We also found that heavier birds with access to more food had higher temperatures and instantaneous rates of heat dissipation, suggesting that body condition influences thermoregulation via peripheral heat dissipation. If birds depend, in any capacity, on their diet for effective thermoregulation or the water savings provided by the bill, then this finding may provide conservationists with novel strategies for boosting the thermoregulatory capabilities of birds in the face of climate change, such as enacting efforts to improve food availability and reduce disturbance in regions where birds are expected to increasingly face heat stress (e.g. Albright et al., 2017; Conradie et al., 2019, 2020).

Applications

Our results highlight the value of thermal imaging for non-invasively monitoring thermo-vascular changes during an acute stress response. Thermal imaging may also provide a non-invasive alternative to blood analysis in research on acute stress. Ouyang et al. (2021) found evidence for a link between changes in eye region surface temperature and bloodborne indicators of stress. In addition to not requiring blood work, the thermal imaging of the vascular response can provide researchers with a continuous measure of physiological changes that take place during the stress response, as opposed to the instantaneous measures provided by blood analysis. It should be noted that Ouyang et al. (2021) found there is a threshold of stress required for detection by thermal imaging. Therefore, depending on the variables of interest and the level of stress experienced by the bird, thermal imaging may provide a continuous and less invasive alternative to blood work.

Because acute stress and diet can influence surface temperatures of the bird, it is necessary for researchers to control or account for these variables in thermographic studies. To account for handling stress, researchers should collect thermal images after the T_s of the body ROI has recovered to pre-stress temperature, which can be determined experimentally (e.g. here, 2.2 min after stress for the bill, and >10 min after stress for the eyeball). Additional research is needed to determine whether changes in surface temperature in relation to acute stress and food vary among species or in relation to ambient temperatures.

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