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Comment and Opinion

What does infrared thermography tell us about the evolutionary potential of heat tolerance in endotherms?

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Abstract

Anthropogenic climate change affects wild animal populations through increasing average temperatures and more frequent extreme climatic events. Endotherms have evolved the capacity to regulate their body temperature but little is still known about how they can physiologically adapt to the pace of global warming. Adaptive responses would require that heat-tolerance mechanisms, such as the capacity to withstand high body temperatures and regulate evaporative water loss, exhibit sufficient heritable genetic variation for selection to act upon. Unfortunately, the quantitative genetics of these traits in endotherms remains poorly understood. In a recent study using infrared thermography (IRT) on semi-captive ostriches, Svensson et al., (Heritable variation in thermal profiles is associated with reproductive success in the world's largest bird. Evolution Letters, 8(2), 200–211.) sought to address this knowledge gap by measuring relative heat exchange from the head and neck and assessing the link between among-individual variation in heat dissipation and reproductive fitness. We discuss how IRT serves as a valuable tool for non-invasive data collecting, highlighting its potential for field studies of the evolutionary potential of thermal tolerance. Nevertheless, interpreting IRT data is not as straightforward as it may seem and thus must be conducted carefully. For instance, body parts from which surface temperatures are measured need to be unequivocally identified as sources of dry heat exchange in order to inform on thermoregulation—something lacking in the mentioned study. Furthermore, there is still no conclusive evidence that surface temperatures reflect core body temperatures in endotherms. Critical underlying mechanisms of the heat response, such as evaporative cooling, must also be considered. Assumptions stemming from uncertain proxies of thermoregulation can obscure our understanding of the endothermic adaptation of heat-tolerance traits to rapid global warming. These considerations emphasize that, while IRT can be a valuable tool for developing quantitative genetic approaches to estimate the evolutionary potential of heat tolerance in endotherms—particularly for species most vulnerable to warming, its application warrants careful planning.

Keywords: adaptation, climate change, evolutionary physiology

Anthropogenic climate change has consistently been a major source of perturbance to life on Earth for decades (Bennett et al., 2021), leading to long-term increases in average temperatures accompanied by more frequent, intense, and prolonged heat waves and extended dry seasons (henceforth referred to as warming; IPCC, 2023). To understand and predict the potential for adaptation in animals facing the challenges of a warmer world, we need to assess whether traits involved in tolerance to short- and long-term warming, possess sufficient heritable genetic variation such that natural selection can act upon them, and we need to measure the direction and strength of selection (Boyles et al., 2011; Hoffmann & Sgrò, 2011). The additive genetic variance associated with these heat-tolerance traits determines their heritability and the potential for natural selection to disseminate genes associated with higher tolerance across generations (Lynch & Walsh, 1998). Heat-tolerance traits are commonly reported as mean population-specific values and the amount of variation among individuals is rarely considered (Herrando-Pérez et al., 2019), particularly in endotherms (Palacio & Clark, 2023). However, among-individual variation, not the population mean, will determine the chances of a population to endure warming and persist in the long run (Humanes et al., 2022; Palacio & Clark, 2023).

While quantitative genetic parameters in wild endotherms have been quantified for many morphological and life-history traits in a context of warming (e.g., Berteaux et al., 2004; Husby et al., 2011; Teplitsky & Charmantier, 2019), current estimations on traits relevant to heat tolerance are virtually absent. To predict adaptive thermoregulatory responses of endotherms to warming, we need more data on the individual variation in the way high ambient (T_a) and core body (T_b) temperatures are tolerated across environmental gradients (Boyles et al., 2011). For this, it is essential to understand the genetic architecture of informative heat-tolerance traits, such as the dynamics of water evaporation for cooling (onset and rate of rapid evaporative water loss, EWL) and the maximum tolerable T_a ($T_a$max) and T_b ($T_b$max) before damage to the organism occurs (Cabello-Vergel et al., 2022; Freeman et al., 2022). Despite these information needs, a review

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published a decade ago revealed that, from all heritability estimations in wild vertebrates, only 2.6% concerned physiological traits in general, and none were traits directly involved in heat tolerance (Postma, 2014). An updated version of this review found that heritability estimates of physiological traits had increased by only 1.5%, with still no estimations on heat-tolerance traits (Young & Postma, 2023). Similarly, studies on repeatable among-individual variation (i.e., repeatability) have focused on average T_b in endotherms not stressed by heat (e.g., Tapper et al., 2021).

In a recent contribution to *Evolution Letters*, Svensson et al., (2024) used infrared thermography (IRT) to measure individual variation in surface temperature (T_s) of the head and neck of semi-captive ostriches (*Struthio camelus*) in South Africa, its heritability and selection acting on it. Svensson et al., (2024) revealed that female ostriches that kept a head T_s lower than that of the neck during hot days had higher egg-laying rates and that this effect was more prominent in subspecies originating from more thermally-variable sites, suggesting evolutionary changes in the thermal physiology of ostriches. To our knowledge, the work by Svensson et al., (2024) is the first attempt to assess the evolutionary implications of geographically-driven, among-individual variation in the heat-tolerance response of an endotherm and we commend it for its novelty. Until now, the genetic basis of physiological adaptation to local climatic heterogeneity in an endotherm had only been assessed for a cold-tolerance trait, that is, the maximum thermogenic metabolism in the dark-eyed Junco (*Junco hyemalis*) (Stager et al., 2021). In addition, although IRT has been used in the past to explore geographic variation in heat dissipation in endotherms (Greenberg et al., 2012), it was unknown whether this variation was heritable and whether it had adaptive potential.

Estimating the heritable variation and adaptive potential of heat-tolerance traits is indeed crucial to understanding how endotherms will cope with climate change, and the study by Svensson and colleagues is a step in the right direction. However, we would like to offer our perspective on why basing conclusions about heat tolerance solely on measurements of T_s, as done by Svensson et al., (2024), may not fully capture the physiological response of endotherms to heat. Traditionally, heat tolerance traits are measured in a laboratory under controlled conditions through elaborate experiments that can last several hours and typically test only a limited number of individuals at a time (Wu et al., 2024). Collecting a sufficiently large sample size to accurately estimate heritability can be time-consuming under these conditions. In contrast, the ease with which T_s can be measured, along with the minimal equipment needed and the non-invasive nature of data collection, has made IRT an attractive alternative for assessing heat stress in endotherms (McCafferty, 2012). Yet, there are several concerns and precautions that need to be considered when applying IRT to measure heat tolerance, particularly when it comes to assessing the biological implications of the T_s data collected. Below, we discuss the challenges of using T_s to quantify heat tolerance and we offer a broad perspective on the potential and limitations of IRT to assess the evolutionary responses of endotherms to warming.

The strength of IRT in thermal physiology lies in its ability to correctly identify body regions that function as sources of heat retention, dissipation, or gain (Figure 1). These so-called "thermal windows" are bare, well-vascularized areas that facilitate dry heat exchange through the surface of the body (McCafferty et al., 2011). Thermal windows are fully functional at high T_a if they become hotter than the environment by allowing heat to radiate from them up to a T_a threshold, beyond which passive heat dissipation is no longer possible (McCafferty et al., 2011; McQueen et al., 2023). In contrast, body parts such as the fur or feather coat efficiently insulate the skin from fluctuating T_a and reflect the thermal environment the animal is exposed to on their external surface (McFarland et al., 2020). One way to identify thermal windows is to compare heat transfer from the same body regions and at the same T_a between animal skins and live animals (Tattersall et al., 2018; Ward et al., 2008). Regions that show the largest deviations in T_s between the dead and live animals can be considered thermal windows. For example, beak T_s of dead specimens of Darwin's finches (*Geospiza* spp.) under natural environmental conditions closely followed the T_a gradient, reaching maximum T_s as high as 55 °C, while that of live birds never exceeded 44 °C, which confirms that heat transfer from the beak is under physiological control (Tattersall et al., 2018). In contrast, T_s of densely feathered body parts only differed by a modest 4 °C between live and dead animals (Tattersall et al., 2018). The legs

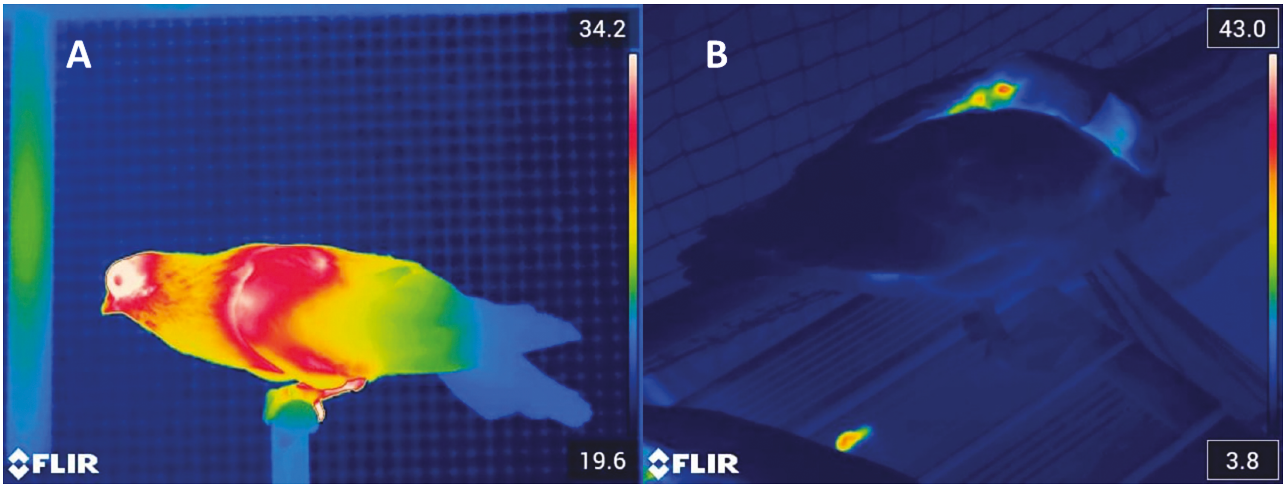

Figure 1. Examples of infrared thermal images of a pigeon (*Columba livia*) inside an indoor cage (A) and of a Canada goose (*Branta canadensis*) in an outdoor aviary during winter (B), captured with a thermographic camera (model FLIR T530). Thermal images can be used to identify featherless areas of the body where heat loss and retention occur, such as the eye region, the beak, and the tarsus. Both pictures show the temperature scale in degrees Celsius on the right side. Photos kindly provided by Andrea Ferretti$^{(c)}$.

are also considered efficient thermal windows. In fact, a recent study involving 14 bird species deemed the tarsus more efficient for heat exchange than the beak because it appeared to control vasoconstriction more tightly at both hot and cold T_a (McQueen et al., 2023). Once thermal windows are identified, their thermoregulatory function can be assessed by collecting IRT images in succession across a range of naturally fluctuating T_a (Soravia et al., 2022; van de Ven et al., 2016). In van de Ven et al., (2016), T_a thresholds were identified that indicated when the beak of southern yellow-billed hornbills (*Tockus leucomelas*) started transferring heat (at T_a = 32 °C) and when it stopped (T_a = 43 °C).

Identifying body structures that are truly involved in heat exchange, and how they function along gradients of T_a, is therefore critical to assigning biological meaning to T_s measurements (McCafferty et al., 2011; McFarland et al., 2020; Soravia et al., 2022; Szafrańska et al., 2020). In their study, where the difference between head and neck T_s was used, Svensson et al., (2024) do not explicitly test whether the head of the ostrich acts as a thermal window during high heat exposure but they do confirm that the neck does not function as such and that it reflects environmental T_a. Considering what we just reported about defining thermal windows and their functionality, uncertainty on whether a body region acts as a thermal window or not can be problematic because the body part in question may simply neither regulate heat exchange nor play a relevant role in heat transfer and tolerance. Svensson et al., (2024) also averaged T_s from polygons covering different areas within the head to estimate head T_s in their analysis. When estimating T_s of the head as a whole, T_s from areas considered thermal windows would be combined with T_s from regions that are not, complicating the understanding of what "head T_s" is actually measuring. On the contrary, it would be more practical and informative to simply analyze the maximum T_s value from a specific target area within the head. For example, Szafrańska et al., (2020) found that this target area consistently corresponded to the featherless periorbital region in zebra finches (*Taeniopygia guttata*) in thermal images of the whole head. It is worth noting that the region within the head from which T_s will be measured needs to be carefully chosen, because some regions can be more prone to measurement errors than others. For example, past studies have shown that T_s measurements of the periorbital region are more affected by shifts in the angle of orientation of the head and by increasing focal distance than others such as the beak (Playà-Montmany & Tattersall, 2021; Tabh et al., 2021). Finally, it is intriguing that the T_s of the ostrich leg were not considered in Svensson et al., (2024), especially since the thermal images captured may have provided a good angle (see e.g., Figure 1B in Svensson et al., 2024) and the role of the legs in heat exchange has already been explored using IRT in this species. Phillips & Sanborn, (1994) suggested that the ostrich leg was involved in the regulation of heat transfer given that it showed a high degree of variation in T_s along a gradient of T_a.

Another relevant consideration before using IRT to infer thermoregulatory dynamics is to thoroughly understand the relationship between T_s and T_b. Indeed, there is a lack of consensus on whether T_s can be effectively used as a proxy for T_b and its variation. For example, Svensson et al., (2024) argue that when head T_s remains lower than that of the neck, it is more tightly regulated and lowers the chances for the brain to overheat. However, to connect T_s with temperature regulation occurring inside the body, the relationship between exterior and interior temperatures should be well understood first (McFarland et al., 2020; Szafrańska et al., 2020). In fact, invasive measurements in free-ranging ostriches show that brain temperature is kept mostly constant and even stays higher than the more fluctuating arterial blood temperature in the neck during the day (Fuller et al., 2003). Other examples from the literature show that the capacity to predict T_b accurately from IRT is still poorly defined. In mallard (*Anas platyrhynchos*) ducklings, estimating T_b using T_s collected with IRT resulted in measurement errors of ≥1 °C (Bakken et al., 2005). van der Vinne et al., (2020) attempted to estimate T_b from maximum body T_s in laboratory mice but, after subsequent validations, T_s measurements could not accurately reflect the absolute T_b. In vervet monkeys (*Chlorocebus pygerythrus*), the initial positive association between T_s and T_b disappeared after accounting for variation in local climate, prompting the authors to discourage equating T_s to T_b (McFarland et al., 2020). Thus, complex thermoregulatory dynamics at the internal and external levels cannot be captured by the exclusive use of IRT. More studies that employ invasive and non-invasive methods jointly are vital to help estimate whether T_s can be validated against internal temperatures and improve its capacity to inform on heat tolerance in endotherms (Szafrańska et al., 2020).

An additional complication of relying solely on IRT measurements is that thermal windows are effective only up to a threshold T_a, above which they stop dissipating heat and can even become sources of heat gain (Soravia et al., 2022). This threshold T_a signals the point at which passive heat dissipation begins to decline in performance and EWL takes over as the main mechanism to regulate T_b in endotherms (McKechnie & Wolf, 2019; van de Ven et al., 2016). For example, threshold T_a in the thermal windows of three arid zone birds was around 35 °C in the highly-vascularized head of the bald ibis (*Geronticus eremita*), 38 °C in the eye region of pied babblers (*Turdoides bicolor*), and 41 °C in the beak of southern yellow-billed hornbills (Galván et al., 2017; Soravia et al., 2022; van de Ven et al., 2016). In fully-hydrated ostriches, this threshold is around 40 °C, above which all metabolically-produced heat can be dissipated through evaporative cooling (Crawford & Schmidt-Nielsen, 1967; Schmidt-Nielsen et al., 1969). Maximum daily T_a captured by weather stations in parts of the ostrich distribution exceeds 40 °C during the austral summer (Fuller et al., 2003), with microclimatic conditions likely being even harsher (Mitchell et al., 2024), meaning that ostriches frequently use EWL to dissipate heat. Therefore, any analysis of dry heat dissipation (as captured by IRT), along gradients of T_a that include extremely high levels of heat, would need to integrate estimations of heat loss via EWL. Respiratory EWL is key for the response to extreme T_a in ostriches (Schmidt-Nielsen et al., 1969), and endotherms in general, and this trait has been assessed in evolutionary studies to assess its adaptive potential in several species. For example, Tielemann et al., (2003) reported among-individual repeatabilities ranging from R = 0 to R = 0.7 in larks (Alaudidae) living along a gradient of aridity, indicating inter-specific differences in the level at which climate-related selection on EWL can operate.

Considering its timing, we believe that research such as the one by Svensson et al., (2024) will lead to exciting opportunities for future evolutionary studies involving thermoregulatory dynamics of endotherms in the face of warming. For instance, it has been suggested that the divergent selection observed in the beak size of song sparrow (*Melospiza melodia*) subspecies along the Atlantic coast of the United States results from thermal adaptation to local climates (Gamboa et al., 2022). It is, however, unknown whether such selective forces act on the capacity of the beak, a recognized thermal window in this species (Greenberg et al., 2012), to dissipate heat. In addition, previous studies have shown that some mammal and bird populations living in arid zones possess lower rates of increased EWL and lower $T_b$max than those from mesic habitats (Freeman et al., 2022; Gearhart et al., 2020). It would therefore be interesting to investigate whether heritable, among-individual variation exists in those traits along climate gradients within species distributions.

In summary, IRT has been a useful tool to collect large amounts of data rapidly and without affecting individuals, allowing researchers to identify thermal windows, quantify heat loss rates, and assess variation in threshold temperatures in passive heat dissipation performance. Such large-scale sampling is an important asset to initiate timely quantitative genetic analyses that will estimate the evolutionary potential of heat tolerance traits. Nevertheless, we believe it is important to consider that T_s data cannot yet be used as a proxy of T_b or internal organ functioning or to assess thermoregulation at T_a above the threshold of thermal window performance. We would like to underscore that there is great potential in researching associations between heat and water balance, T_b regulation, and fitness in wild endotherm populations with the aid of IRT. However, we want to emphasize the fact that the physiological response to warming in endotherms is much more complex than what IRT alone can reveal, and that, at least for now, this technique needs to be coupled with traditional methods to inform the response to extreme heat. Overall, the use of IRT opens new avenues for more studies of variation in thermal physiology traits, heritability, and adaptive potential, which hopefully will expand to include informative measures of heat tolerance to assess the physiological effects and evolutionary consequences of warming on endotherm populations.

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References

Bakken, G. S., Van Sant, M. J., Lynott, A. J., & Banta, M. R. (2005). Predicting small endotherm body temperatures from scalp temperatures. *Journal of Thermal Biology*, 30, 221–228. https://doi.org/10.1016/j.jtherbio.2004.11.005

Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar, A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., & Olalla-Tárraga, M. A. (2021). The evolution of critical thermal limits of life on Earth. *Nature Communications*, *12*(1), 1198. https://doi.org/10.1038/s41467-021-21263-8

Berteaux, D., Réale, D., McAdam, A. G., & Boutin, S. (2004). Keeping pace with fast climate change: Can arctic life count on evolution? *Integrative and Comparative Biology*, 44(2), 140–151. https://doi.org/10.1093/icb/44.2.140

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*, 51(5), 676–690. https://doi.org/10.1093/icb/icr053

Cabello-Vergel, J., González-Medina, E., Parejo, M., Abad-Gómez, J. M., Playà-Montmany, N., Patón, D., Sánchez-Guzmán, J. M., Masero, J. A., Gutiérrez, J. S., & Villegas, A. (2022). Heat tolerance limits of Mediterranean songbirds and their current and future vulnerabilities to temperature extremes. *Journal of Experimental Biology*, 225(23), jeb244848. https://doi.org/10.1242/jeb.244848

Crawford, E. C. Jr., & Schmidt-Nielsen, K. (1967). Temperature regulation and evaporative cooling in the ostrich. *The American Journal of Physiology*, *212*(2), 347–353. https://doi.org/10.1152/ajplegacy.1967.212.2.347

Freeman, M. T., Czenze, Z. J., Schoeman, K., & McKechnie, A. E. (2022). Adaptive variation in the upper limits of avian body temperature. *Proceedings of the National Academy of Sciences*, 119(26), e2116645119. https://doi.org/10.1073/pnas.2116645119

Fuller, A., Kamerman, P. R., Maloney, S. K., Mitchell, G., & Mitchell, D. (2003). Variability in brain and arterial blood temperatures in free-ranging ostriches in their natural habitat. *The Journal of Experimental Biology*, 206(Pt 7), 1171–1181. https://doi.org/10.1242/jeb.00230

Galván, I., Palacios, D., & Negro, J. J. (2017). The bare head of the Northern bald ibis (*Geronticus eremita*) fulfills a thermoregulatory function. *Frontiers in Zoology*, 14, 15. https://doi.org/10.1186/s12983-017-0201-5

Gamboa, M. P., Ghalambor, C. K., Sillett, T. S., Morrison, S. A., & Funk, W. C. (2022). Adaptive divergence in bill morphology and other thermoregulatory traits is facilitated by restricted gene flow in song sparrows on the California Channel Islands. *Molecular Ecology*, 31, 603–619. https://doi.org/10.1111/mec.16253

Gearhart, C., Adams, A. M., Pinshow, B., & Korine, C. (2020). Evaporative water loss in Kuhl's pipistrelles declines along an environmental gradient, from mesic to hyperarid. *Comparative Biochemistry and Physiology A*, 240, 110587. https://doi.org/10.1016/j.cbpa.2019.110587

Greenberg, R., Cadena, V., Danner, R. M., & Tattersall, G. (2012). Heat loss may explain bill size differences between birds occupying different habitats. *PLoS One*, *7*(7), e40933. https://doi.org/10.1371/journal.pone.0040933

Herrando-Pérez, S., Ferri-Yáñez, F., Monasterio, C., Beukema, W., Gomes, V., Belliure, J., Chown, S. L., Vieites, D. R., & Araújo, M. B. (2019). Intraspecific variation in lizard heat tolerance alters estimates of climate impact. *Journal of Animal Ecology*, 88(2), 247–257. https://doi.org/10.1111/1365-2656.12914

Hoffmann, A., & Sgrò, C. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479–485. https://doi.org/10.1038/nature09670

Humanes, A., Lachs, L., Beauchamp, E. A., Bythell, J. C., Edwards, A. J., Golbuu, Y., Martinez, H. M., Palmowski, P., Treumann, A., van der Steeg, E., van Hooidonk, R., & Guest, J. R. (2022). Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proceedings Biological Sciences*, 289(1981), 20220872. https://doi.org/10.1098/rspb.2022.0872

Husby, A., Visser, M. E., & Kruuk, L. E. B. (2011). Speeding up microevolution: The effects of increasing temperature on selection and genetic variance in a wild bird population. *PLoS Biology*, *9*(2), e1000585. https://doi.org/10.1371/journal.pbio.1000585

IPCC. (2023). Climate change 2023: Synthesis report. In Core Writing Team, H. Lee, & J. Romero (Eds.), *Contribution of working groups I, II and III to the sixth assessment report of the intergovernmental panel on climate change* (pp. 1–34). IPCC. https://doi.org/10.59327/IPCC/AR6-9789291691647.001

Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sinauer Associates, Inc.

McCafferty, D. J. (2012). Applications of thermal imaging in avian science. *Ibis*, 155(1), 4–15. https://doi.org/10.1111/ibi.12010

McCafferty, D. J., Gilbert, C., Paterson, W., Pomeroy, P. P., Thompson, D., Currie, J. I., & Ancel, A. (2011). Estimating metabolic heat loss in birds and mammals by combining infrared thermography with biophysical modelling. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, 158(3), 337–345. https://doi.org/10.1016/j.cbpa.2010.09.012

McFarland, R., Barrett, L., Fuller, A., Hetem, R. S., Porter, W. P., Young, C., & Henzi, S. P. (2020). Infrared thermography cannot be used to approximate core body temperature in wild primates. *American Journal of Primatology*, 82(12), e23204. https://doi.org/10.1002/ajp.23204

McKechnie, A. E., & Wolf, B. O. (2019). The physiology of heat tolerance in small endotherms. *Physiology (Bethesda, Md.)*, 34(5), 302–313. https://doi.org/10.1152/physiol.00011.2019

McQueen, A., Barnaby, R., Symonds, M. R. E., & Tattersall, G. J. (2023). Birds are better at regulating heat loss through their legs than their bills: Implications for body shape evolution in response to climate. *Biology Letters*, 19(11), 0373. https://doi.org/10.1098/rsbl.2023.0373

Mitchell, D., Maloney, S. K., Snelling, E. P., de França Carvalho Fonsêca, V., & Fuller, A. (2024). Measurement of microclimates in a warming world: Problems and solutions. *Journal of Experimental Biology*, 227, jeb246481. https://doi.org/10.1242/jeb.246481

Palacio, R. D., & Clark, J. S. (2023). Incorporating intraspecific variation into species responses reveals both their resilience and vulnerability to future climate change. *Ecography*, 2023(11), e06769. https://doi.org/10.1111/ecog.06769

Phillips, P. K., & Sanborn, A. F. (1994). An infrared, thermographic study of surface temperature in three ratites: Ostrich, emu and double-wattled cassowary. *Journal of Thermal Biology*, 19(6), 423–430. https://doi.org/10.1016/0306-4565(94)90042-6

Playà-Montmany, N., & Tattersall, G. J. (2021). Spot size, distance and emissivity errors in field applications of infrared thermography. *Methods in Ecology and Evolution*, 12, 828–840. https://doi.org/10.1111/2041-210X.13563

Postma, E. (2014). Four decades of estimating heritabilities in wild vertebrate populations: Improved methods, more data, better estimates? In: A. Charmantier, D. Garant, & L. E. B. Kruuk (Eds.), *Quantitative genetics in the wild* (pp. 16–33). Oxford University Press.

Schmidt-Nielsen, K., Kanwisher, J., Lasiewski, R. C., Cohn, J. E., & Bretz, W. L. (1969). Temperature regulation and respiration in the Ostrich. *The Condor*, 71(4), 341–352. https://doi.org/10.2307/1365733

Soravia, C., Ashton, B. J., & Ridley, A. R. (2022). Periorbital temperature responses to natural air temperature variation in wild birds. *Journal of Thermal Biology*, 109, 103323. https://doi.org/10.1016/j.jtherbio.2022.103323

Stager, M., Senner, N. R., Swanson, D. L., Carling, M. D., Eddy, D. K., Greives, T. J., & Cheviron, Z. A. (2021). Temperature heterogeneity correlates with intraspecific variation in physiological flexibility in a small endotherm. *Nature Communications*, 12(1), 4401. https://doi.org/10.1038/s41467-021-24588-6

Svensson, E. I., Schou, M. F., Melgar, J., Waller, J., Engelbrecht, A., Brand, Z., Cloete, S., & Cornwallis, C. K. (2024). Heritable variation in thermal profiles is associated with reproductive success in the world's largest bird. *Evolution Letters*, 8(2), 200–211. https://doi.org/10.1093/evlett/qrad049

Szafrańska, P. A., Andreasson, F., Nord, A., & Nilsson, J. A. (2020). Deep body and surface temperature responses to hot and cold environments in the zebra finch. *Journal of Thermal Biology*, 94, 102776. https://doi.org/10.1016/j.jtherbio.2020.102776

Tabh, J. K. R., Burness, G., Wearing, O. H., Tattersall, G. J., & Mastromonaco, G. F. (2021). Infrared thermography as a technique to measure physiological stress in birds: Body region and image angle matter. *Physiological Reports*, 9(11), e14865. https://doi.org/10.14814/phy2.14865

Tapper, S., Nocera, J. J., & Burness, G. (2021). Body temperature is a repeatable trait in a free-ranging passerine bird. *Journal of Experimental Biology*, 224(20), jeb243057. https://doi.org/10.1242/jeb.243057

Tattersall, G. J., Chaves, J. A., & Danner, R. M. (2018). Thermoregulatory windows in Darwin's finches. *Functional Ecology*, 32(2), 358–368. https://doi.org/10.1111/1365-2435.12990

Teplitsky, C., & Charmantier, A. (2019). Evolutionary consequences of climate change in birds. In: P. O. Dunn, & A. P. Møller (Eds.), *Effects of climate change on birds* (pp. 134). Oxford University Press

Tieleman, B. I., Williams, J. B., Buschur, M. E., & Brown, C. R. (2003). Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology*, 84(7), 1800–1815. https://doi.org/10.1890/0012-9658(2003)084[1800:pvolaa]2.0.co;2

van de Ven, T. M. F. N., Martin, R. O., Vink, T. J. F., McKechnie, A. E., & Cunningham, S. J. (2016). Regulation of heat exchange across the Hornbill Beak: Functional similarities with Toucans? *PLoS One*, 11(5), e0154768. https://doi.org/10.1371/journal.pone.0154768

van der Vinne, V., Pothecary, C. A., Wilcox, S. L., McKillop, L. E., Benson, L. A., Kolpakova, J., Tam, S. K. E., Krone, L. B., Fisk, A, S., Wilson, T. S., Yamagata, T., Cantley, J., Vyazovskiy, V. V., & Peirson, S. N. (2020). Continuous and non-invasive thermography of mouse skin accurately describes core body temperature patterns, but not absolute core temperature. *Scientific Reports*, 10, 20680. https://doi.org/10.1038/s41598-020-77786-5

Ward, J., McCafferty, D., Houston, D., & Ruxton, G. D. (2008). Why do vultures have bald heads? The role of postural adjustment and bare skin areas in thermoregulation. *Journal of Thermal Biology*, 33, 168–173. https://doi.org/10.1016/j.jtherbio.2008.01.002

Wu, N. C., Alton, L., Bovo, R. P., Carey, N., Currie, S. E., Lighton, J. R. B., McKechnie, A. E., Pottier, P., Rossi, G., White, C. R., & Levesque, D. (2024). Reporting guidelines for terrestrial respirometry: Building openness, transparency of metabolic rate and evaporative water loss data. *Comparative Biochemistry and Physiology Part A*, 111688, https://doi.org/10.1016/j.cbpa.2024.111688

Young, E. A., & Postma, E. (2023). Low interspecific variation and no phylogenetic signal in additive genetic variance in wild bird and mammal populations. *Ecology and Evolution*, 13(11), e10693. https://doi.org/10.1002/ece3.10693