

Infrared thermography is a useful tool in research on thermoregulation and evolution of heat tolerance

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Abstract

Non-invasive methods for measuring thermal tolerance and thermoregulation in large numbers of individuals under natural environmental conditions are useful to understand the capacity of species to adapt to future climate scenarios. Infrared thermography (IRT) is one such tool in research on thermal adaptation, but concerns have been raised about its reliability, specifically the correlation between surface temperature (T_s) and body temperature (T_b) (Monge et al., (2025). What does IRT tell us about the evolutionary potential of heat tolerance in endotherms? *Evolution Letters*, 9(2), 184–188). Here, we discuss the biological inferences that can be made from data on T_s and T_b , and whether T_s needs to be correlated with T_b to be informative in studies of thermoregulation in free-living organisms. We also present a framework illustrating biological insights that can be gained by integrating IRT with data on different phenotypic traits, fitness metrics, pedigree information and other physiological traits, including T_b . We illustrate the utility of this new framework by demonstrating how it has increased our understanding of the evolution of thermal tolerance in a large animal where T_b is not easily measured, the ostrich (*Struthio camelus*) (Svensson et al., (2024). Heritable variation in thermal profiles is associated with reproductive success in the world's largest bird. *Evolution Letters*, 8(2), 200–211). Integrating IRT with individual fitness data and pedigree information in field studies can aid our biological interpretation of T_s in future research on the ecology and evolution of thermal tolerance in both endotherms and ectotherms.

Keywords: heritability, ostrich, *Struthio camelus*, thermal imaging, thermoregulation, thermal adaptation

Non-invasive methods for measuring thermal tolerance in large numbers of individuals outside the laboratory will increase our understanding of the evolutionary responses of species to climate change. Measuring surface temperatures using infrared thermography (IRT) is a potentially useful approach, but it has been the subject to some recent methodological debate (Monge et al., 2025). The main criticism is that surface temperatures (T_s) might not accurately reflect internal body temperatures (T_b) (Eastick et al., 2019; McCafferty et al., 2021; Monge et al., 2025). Can this issue be overcome, or should we stop using IRT in studies of animal thermal tolerance? These questions have implications beyond research on thermal adaptation, including measurement theory, which is the research discipline that deals with the biological meaning of variables, their theoretical context, and how we interpret biological measurements (Houle et al., 2011).

A central tenet of the evolutionary theory on thermoregulation is that variation in T_s facilitates the stabilization of T_b under fluctuating temperatures (see Box 1 for definitions of T_s and T_b). Maintaining a stable T_b across different thermal environ-

ments should increase fitness and could lead to the evolution of homeothermy (Boyles et al., 2011). This is consistent with findings of strong phylogenetic niche conservatism and slow evolution of T_b (Moreira et al., 2021) that was noted already by the late evolutionary biologist George C. Williams (Williams, 1992). Behavioral, physiological, and morphological traits, such as wing flapping, panting, sweating, and emitting excess heat through bare skin parts, or organisms having body parts where plumage or pelage is not so dense (“thermal windows”), have evolved to stabilize internal T_b near some thermal fitness optimum in spite of external temperature changes (Huey et al. 2003; Muñoz 2022; Muñoz & Losos 2018; Eastick et al., 2019; Fuller et al., 2003; Périard et al., 2015; Weissenböck et al., 2010). T_s and T_b may become further decoupled during stressful conditions, such as when birds that are adapted to hot environments are exposed to cold stress (Szafranska et al., 2020). Mechanisms that maintain T_b by dissipating heat through surface areas will, therefore, likely reduce the correlation between T_s and T_b , especially under shifting environmental conditions.

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Recently, [Monge et al. \(2025\)](#) argued that there is no conclusive evidence that T_s reflects T_b in endotherms, questioning the use of IRT. They suggested that if IRT is to be used, then body parts involved in heat retention, dissipation, or gain must be identified, and checked to see if they provide a good proxy measure for T_b ([Monge et al., 2025](#)). [Monge et al. \(2025\)](#) cite several studies on birds and mammals and argue based on these studies that the relationship between T_b and T_s may be weak or even absent, reducing the utility of IRT.

Current research, however, shows that the correlation between T_b and T_s is often positive, although its strength seems to vary between different environmental settings and organisms. We note that in several studies on endotherms, T_s and T_b were surprisingly strongly correlated, including at least one study highlighted by [Monge et al. \(2025\)](#). In nestling blue tits (*Cyanistes caeruleus*) 78% and 93% of the variation in T_s was explained by variation in T_b before and after experimental cooling ([Andreasson et al., 2016](#)). In red-footed boobies (*Sula sula*) T_b explained between 76% and 83% of T_s , the latter measured in different facial body parts (eye, face and bill; [Gauchet et al., 2022](#)). In zebra finches (*Taeniopygia guttata*) T_s and T_b were strongly correlated under hot (35 °C; $R^2 = 0.41$; $P = 0.006$), but not under cold conditions (5 °C; $R^2 = 0.11$; $P = 0.25$) ([Szafrńska et al., 2020](#)). Also, in the study on mallard ducks (*Anas platyrhynchos*) that was highlighted by [Monge et al. \(2025\)](#), there was a strong and highly significant ($P < 0.001$) relationship between cloacal temperature (a proxy of T_b) and T_s , the latter estimated using IRT ([Bakken et al., 2005](#)). In contrast, in a field study on vervet monkeys (*Chlorocebus pygerythrus*), the relationship between T_b and T_s was weak, motivating the authors to question the utility of IRT ([McFarland et al., 2020](#)). In field studies of small-bodied ectotherms (insects), T_s and T_b were found to be strongly correlated ([Svensson et al., 2020](#); [Tsubaki et al., 2010](#)), likely because their small body size contribute to make T_s and T_b to converge and become similar below a certain size threshold ([Box 1](#)).

The different results from these previous studies using IRT therefore likely reflect variation in study design, whether T_s and T_b are compared across or within individuals, how much ambient temperatures vary, the area of the body measured, effects of body size, and other biological details of the focal study organism, including possible differences between endo- and ectotherms. The question remains, however, whether the complex relationship between T_b and T_s would therefore necessarily reduce the utility of IRT in studies of thermal tolerance?

[Monge et al. \(2025\)](#) advocate that employing “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.” While combining measures of T_s and T_b is of course interesting to better understand thermoregulation, we believe that the rationale for measuring T_s is richer than that described by [Monge et al. \(2025\)](#), something that we develop further in this article ([Figure 1](#)). Here, we describe a framework for how measures of T_s can be used in studies of endotherm thermoregulation, and what they tell us ([Box 1](#); [Figure 1](#)). We illustrate this new framework with our recent empirical study on thermal tolerance in ostriches (*Struthio camelus*) ([Svensson et al., 2024](#)), while we also acknowledge the limitations of IRT.

Box 1: Definitions of body temperature (T_b) and surface temperature (T_s) in this paper

Body temperature (T_b) and surface temperature (T_s) are two terms that are frequently used in discussions about animal thermoregulation and the utility of IRT ([Monge et al., 2025](#)). Although both T_b and T_s are seemingly straightforward concepts, they are in practice both difficult to measure empirically and define in an operational way. Here, we pragmatically define T_b as whole animal body temperature (internal and external), and T_s as external surface temperature only. It follows that T_s then becomes nested within T_b , although [Monge et al. \(2025\)](#) and many others seem to want to restrict the use of T_b to encompass only internal body temperature. As there will always be a temperature gradient from the surface temperature of an organism to its innermost temperature, some relevant question to ask are: where does T_s become T_b ? Could and should these two temperature measures be demarcated from each other and if so how? Therefore, while T_b and T_s are seemingly straightforward to define, operationally they are not that easy to separate in empirical field studies. The relationship between these two important temperature variables therefore should therefore naturally become a discussion within the field of measurement theory ([Houle et al., 2011](#)).

We emphasize that all empirical measures of both T_b and T_s are only components of whole animal body temperatures, as they are typically estimated from a limited region within the body of an animal or on a restricted area of its surface. Given that regional heterothermy is common and that animals show temperature variation across both internal and external body parts, it follows that any point estimates of temperature, measured either within the body of an animal or from parts of its surface will at most be a proxy for either T_b or T_s . Sometimes the term T_c is used, referring to “core body temperature,” but most studies using the term T_b do in practice estimate some thermal body component, not whole-animal body temperature across all body parts (which is extremely difficult, if not impossible to measure). For example, cloacal temperature is often used in avian studies as a proxy for T_b ([Bakken et al., 2005](#)), but just like single point estimates of T_s from a limited area of the body will not capture whole animal surface temperature, cloacal temperature is unlikely to be perfectly correlated with core body temperature, and is therefore at best a proxy for T_b .

Thus, although we pragmatically adopt the general terminology used by [Monge et al. \(2025\)](#), we emphasize that none of the empirical studies they cite have measured whole-animal body temperature. All studies in this field—to our knowledge—use various proxies of T_b that could be appropriate to a lesser or greater extent. Below a certain body size, T_s and T_b will become increasingly similar to each other and might approach whole-animal T_b . Consistent with this, T_s in small ectotherms is strongly correlated with internal body temperatures, as shown in some IRT-studies on insects ([Tsubaki et al., 2010](#); [Svensson et al., 2020](#)).

Phenotypic and genetic variances and covariances of surface temperatures

Understanding the evolution of thermal tolerance requires that we quantify phenotypic and ideally also additive genetic variation from many individuals with a known pedigree within and

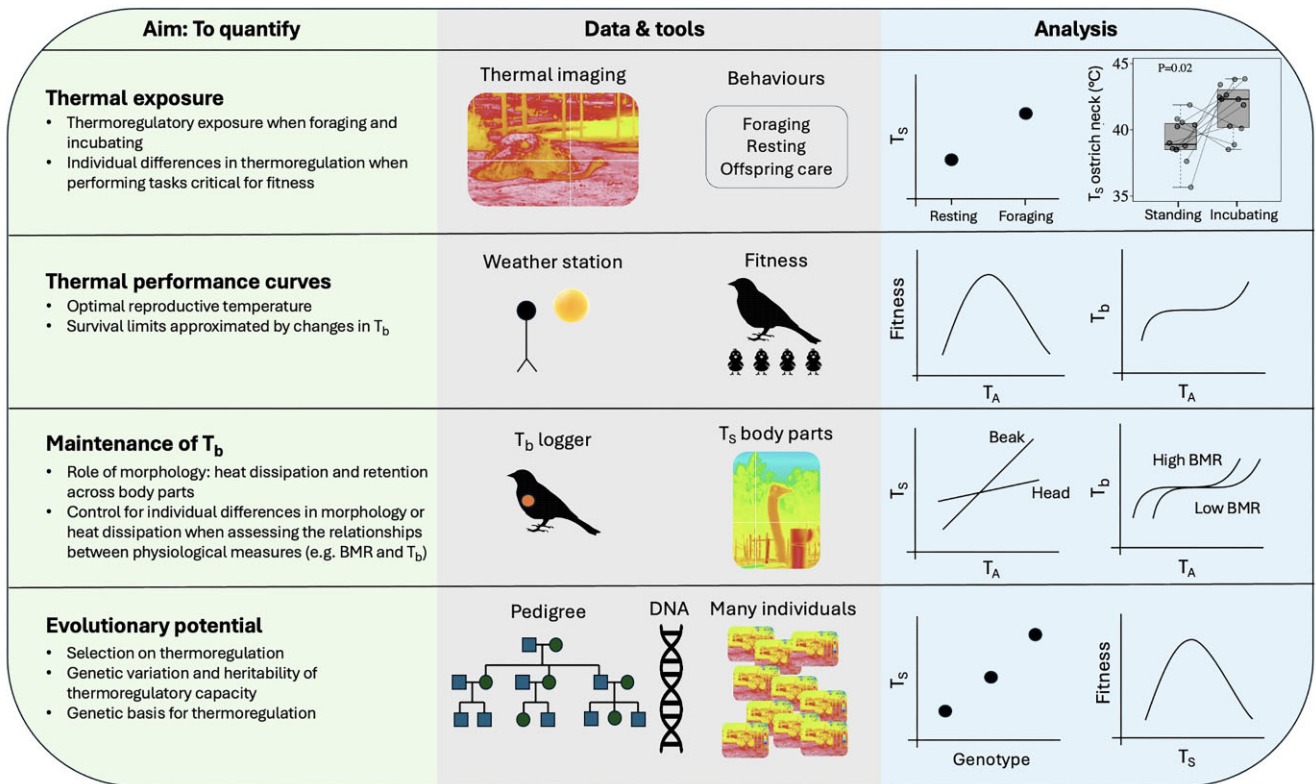


Figure 1. Four areas where our understanding of thermal biology can be improved by combining surface (T_s) and/or body (T_b) temperatures with other types of data, such as BMR (“basal metabolic rate”) and ambient temperatures (T_A). The suggested tools and analyses are not exhaustive but illustrate the types of questions that can be addressed by integrating different approaches. For example, cloacal temperatures may be suited to monitoring large numbers of individuals of some species, while IRT techniques may be useful for species that are difficult to handle, such as ostriches. The figures shown under “Analysis” are conceptual and illustrative, except the plot of ostrich neck T_s measurements (top right) where we present new IRT data. We measured T_s on incubating female ostriches and compared them to non-incubating females, thereby getting an estimate of thermal exposure during incubation (top right; see text for further statistics). These new data illustrate how combining T_s measurements with behavioral observations can help us understand how activities, such as incubation, can increase thermal exposure and heat stress and the need for efficient thermoregulation.

across populations. In most cases, it is easier to measure surface temperatures on a large numbers of individuals using IRT than it is to measure various aspects of T_b (Barham et al., 2025). One challenge of using IRT is that extensive efforts are required to make sure that IRT measurements are accurate (e.g., setting the emissivity properly, calibrating the camera to field conditions, ensuring that image angle and distance is accounted for etc.; see Svensson et al., 2024). Nevertheless, with these methodological limitations in mind, researchers can get repeated measures from the same individuals using IRT with minimal disturbance to normal behavior. Such data can then be used to calculate thermoregulatory indices or statistical surface temperature distributions across many individuals.

The value of IRT data will increase if such information can be connected to relatedness via a pedigree, enabling researchers to evaluate the potential of thermoregulation to evolve, by estimating quantitative genetic parameters (heritabilities, evolvabilities, genetic variances, and covariances; see Svensson et al., 2024). Estimating individual differences in T_s can also enabled us to estimate genetic covariances between thermal profiles and other phenotypic traits, such as body size, other fitness components, or T_b (Schou et al., 2022; Svensson et al., 2024). Estimates of both genetic variances and covariances between traits are crucial to predict direct and correlated evolutionary responses to selection on

thermoregulatory traits, like all other phenotypic traits (Lande & Arnold, 1983; Svensson, 2023).

The value of fitness data

Examining the relationships between T_b , T_s , and fitness has the potential to differentiate between adaptive thermoregulatory processes and non-adaptive or maladaptive effects. For example, an increase in T_b can be due to facultative hyperthermia or a failure of the thermoregulatory system. Investigating how survival and reproductive rates vary in relation to temperature changes can help distinguish between these two scenarios. Similarly, increased T_s can indicate increased heat dissipation as an adaptive response, or it can simply result from an inability to stabilize body temperature. This can potentially be resolved by relating T_s and T_b to fitness. In some cases, researchers can also estimate individual thermal reaction norms of how traits like T_s and T_b change with different ambient temperatures (Kellermann et al., 2019). Furthermore, in other systems researchers can estimate the strength of natural or sexual selection on such individual thermal reaction norms (Svensson et al., 2020). Estimating thermal reaction norms requires repeatedly measuring many individuals, which is feasible using non-invasive methods such as IRT, although in the future it might be possible with new data logger technology (Schou & Cornwallis, 2024).

Comparing surface temperatures across body parts

Surface temperatures change with ambient temperatures. Quantifying the magnitude of change for different body parts can provide information on the extent to which they are involved in thermoregulation. This has been particularly important in identifying peripheral body parts, such as bird beaks, that act as thermal radiators (Tattersall et al., 2009), or investigating how testicles or the brain, need to be regulated at temperatures that differ from internal body temperature (Fuller et al., 2003). Accurately quantifying operative environmental temperatures for freely moving animals in non-laboratory settings remains a major challenge in research on animal thermoregulation. One advantage of using IRT is that T_s comparisons between body parts can be made within the same thermal image, minimizing the effects of variation in operative environmental temperature on temperature measurements.

Thermal exposure and behavior

The thermal exposure of most animals is often extremely variable due to spatial and temporal differences in temperature caused by, e.g., habitat differences or cooler or warmer periods of the day. Most animals will be forced to perform tasks that are critical for aspects of fitness under sub-optimal temperatures. For example, some African mammals need to forage during the day due to the risk of predation at night, potentially exposing them to elevated thermal stress (Veldhuis et al., 2020). Combining IRT-measured estimates of T_s and behavioral observations could provide insights into the thermal costs of performing such costly behaviors, especially if combined with measures of fitness to estimate selection.

The ostrich as a case study

In our field study of the ostrich, our primary aim was to quantify the potential for thermal tolerance to evolve (Svensson et al., 2024). As our general approach was recently questioned by Monge et al. (2025) who raised several critical questions, we hereby explain the logic of our approach and develop our general framework illustrated in Figure 1 further. The evolutionary potential of thermal tolerance depends on both the presence of additive genetic variation in thermal tolerance and the relationship between thermal tolerance and fitness. Estimating these two factors requires repeated measurements of large numbers of individuals, which ruled out measuring T_b . We used IRT to repeatedly measure T_s on 423 individuals to quantify individual variation, genetic variation, and selection on thermoregulation (Figure 1). Ostriches experience extreme temperature fluctuations, and their heads are always very exposed as they are vigilant for predators. Thermoregulation of the brain is generally critical for physiological functioning in animals (Beltrán et al., 2021; Kilgore et al., 1976). In the ostrich, however, thermoregulation of the brain appears to be decoupled from T_b (Fuller et al., 2003). This raises the question of whether temperature regulation of the head is under selection and heritable.

Another body part of the ostrich—the neck—is known to be involved in dry heat exchange over the range of ambient temperatures that are frequent at our study site [Crawford & Schmidt-Nielsen, 1967; Figure 2A in Svensson et al. (2024)]. Since the head

and the neck are consistently exposed to the same abiotic conditions, the neck provides a measure of the thermal stress that the brain is exposed to. Other body parts such as the legs are more problematic to measure because they are not consistently visible, as they are often covered by feathers or vegetation, and hidden when an ostrich is sitting down or incubating.

Measuring T_s of large numbers of individuals using IRT enabled us to estimate quantitative genetic parameters on the thermal reaction norms of different body parts: the head and neck. One of our findings was that egg laying rates of female ostriches increased with the difference between head and neck temperature under hot conditions (Svensson et al., 2024). This finding is important as it indicates strong and ongoing selection to stabilize head temperatures in female ostriches during heat stress, compared to weak selection on other body parts, such as the neck. Here, we present new results from these female ostriches, where we combined T_s measures of the head and neck with behavioral observations, namely if the ostrich was standing or incubating (Figure 1). We found that ostriches incubating during hot afternoons had higher neck temperatures compared to standing individuals, which was not the case during cooler mornings (paired t-tests: hot afternoons $t = 2.9$; $df = 11$; $P = 0.02$; cool mornings $t = 0.3$; $df = 7$; $P = 0.76$). Head T_s also increased, but less so than the neck T_s (paired t-tests: hot afternoons $t = 2.3$; $df = 11$; $P = 0.04$; cool mornings $t = -0.3$; $df = 7$; $P = 0.77$). Thus, incubation in the ostrich is consistent with a thermoregulatory cost (Figure 1).

This empirical field study on the ostrich was certainly not without challenges. We investigated and quantified the role of various confounding factors and their impact on IRT measures and our results (Svensson et al., 2024). These confounding factors included photographic angles, distance, feathered vs. bare surfaces, and body mass (see details of SI in Svensson et al., 2024). Each study system will without doubt have its own unique logistical challenges. It is therefore important to be aware of the limitations of IRT before embarking on new studies. It is crucial to regularly calibrate the thermal imaging camera, justify the choice of body parts, and standardize the extraction of data from thermal images. Despite these methodological challenges and limitations, our T_s measurements provided valuable information on the evolutionary potential of thermoregulation in the ostrich.

Conclusion

In summary, T_s is a biologically important thermal trait and should, therefore, not be viewed only as a proxy for T_b . IRT remains a useful technique for measuring T_s , but complementary techniques exist and will likely become more frequently used as sensor technology develops. A key challenge in future field studies of thermal tolerance and thermoregulation is how to interpret T_s across different contexts. One way to achieve this is to combine IRT with other information, such as T_b , physiological data, pedigree data, and fitness data (Figure 1). This will reveal how and why T_s changes within individuals (i.e., plasticity), between individuals (i.e., genetic variation in plasticity) and across generations (i.e., evolutionary change). Such data will advance our understanding of the evolution of thermal physiology under different ecological conditions. While we acknowledge the limitations of IRT, it nevertheless remains a highly useful tool in field studies of thermal adaptation, including both thermoregulation and thermal tolerance. After all, even partial solutions to

the empirical challenge of quantifying thermal tolerance, thermal reaction norms, and the efficiency and fitness consequences of thermoregulation are better than no solutions.

Data and code availability

Data and R-code associated with Figure 1 in this paper has been uploaded to Zenodo digital repository: DOI: <https://doi.org/10.5281/zenodo.15189106>

Author contributions

Conceptualization and writing of first draft: E.I.S., C.K.C., and M.F.S. Writing – reviewing and editing of later drafts: A.E., C.K.C., E.I.S., J.M., J.W., M.F.S., S.C., and Z.B.

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Conflict of interest

The authors declare no conflict of interest.

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