Review

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Thermal consequences of colour and near-infrared reflectance

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The importance of colour for temperature regulation in animals remains controversial. Colour can affect an animal's temperature because all else being equal, dark surfaces absorb more solar energy than do light surfaces, and that energy is converted into heat. However, in reality, the relationship between colour and thermoregulation is complex and varied because it depends on environmental conditions and the physical properties, behaviour and physiology of the animal. Furthermore, the thermal effects of colour depend as much on absorptance of near-infrared ((NIR), 700–2500 nm) as visible (300–700 nm) wavelengths of direct sunlight; yet the NIR is very rarely considered or measured. The few available data on NIR reflectance in animals indicate that the visible reflectance is often a poor predictor of NIR reflectance. Adaptive variation in animal coloration (visible reflectance) reflects a compromise between multiple competing functions such as camouflage, signalling and thermoregulation. By contrast, adaptive variation in NIR reflectance should primarily reflect thermoregulatory requirements because animal visual systems are generally insensitive to NIR wavelengths. Here, we assess evidence and identify key research questions regarding the thermoregulatory function of animal coloration, and specifically consider evidence for adaptive variation in NIR reflectance.

This article is part of the themed issue 'Animal coloration: production, perception, function and application'.

1. Introduction

An important potential adaptive function of animal coloration is to help regulate body temperature. All else being equal, low reflectance (typically dark) surfaces absorb more incident solar radiation than do high reflectance (light-coloured) surfaces, and conversely, light surfaces reflect more solar radiation. However, whether solar energy absorbed at an animal's surface influences heat load depends on environmental conditions and the behaviour and physical properties of the animal, such as body size and the optical and structural properties of the fur, feathers, scales or cuticle that form the layer between the surface and the epidermis (i.e. the insulating layer). These physical properties clearly vary greatly between different animal groups, particularly ectotherms and endotherms. Counterintuitively, the amount of energy that is absorbed by the skin may be greater in individuals with light than dark fur or feathers if incident radiation penetrates more easily through light than dark coats [1]. Furthermore, colour may have a negligible influence on heat load relative to other thermoregulatory mechanisms (e.g. behavioural and physiological mechanisms). Given the complex relationship between colour and thermoregulation, it is not surprising that opinion and evidence for the role of colour in thermoregulation remains mixed, despite many decades of research.

Animal coloration reflects a compromise between multiple competing functions such as camouflage, signalling, physical protection (e.g. from physical wear and bacterial degradation [2,3]), physiological protection (oxidative damage and immune defence) and thermoregulation. Evolutionary 'solutions'
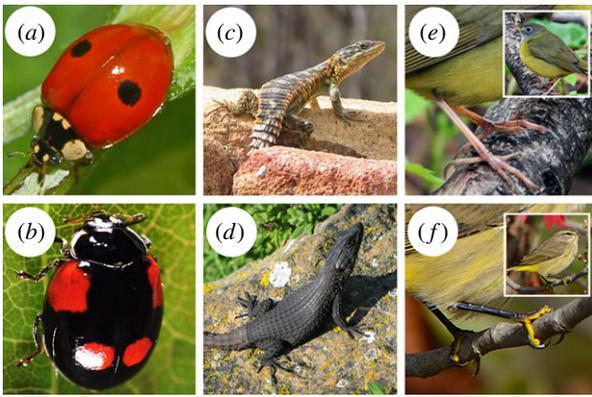
Figure 1. Examples of thermal melanism. The red form of the two-spot beetle (*Adalia bipunctata*) (*a*) cannot maintain as high body temperatures as the melanistic form (*b*), resulting in activity level differences [4]. Light-coloured species of girdled lizards (*Cordylus*) such as *C. cordylus* (*c*) occur in warmer and less overcast areas than darker species such as *C. niger* (*d*) which have smaller, usually cooler ranges [5]. North American warblers (Parulidae) with melanized legs, such as the palm warbler (*Setophaga palmarum*) (*f*) tend to remain at higher latitudes for longer and have more northerly distributed breeding ranges than warblers with pale legs, such as the Connecticut warbler (*Oporornis agilis*) (*e*) [6]. *Image credits: (a) Ettore Balocchi; (b) Pavel Kirillov; (c) and (d) Susana Clusella-Trullas; (e) Matt Stratmoen; (f) David Inman.*

Figure 2. Sunlight reaching the Earth's surface (ASTM G173−03 standard irradiance spectrum for dry air) showing ultraviolet (UV), visible and near-infrared (NIR) components. NIR light contributes about 55% of the total energy in sunlight at sea level.

to these competing requirements will depend on the relative strength of selection for each function and the extent to which different functions are mutually exclusive. For example, increased melanism may enhance thermoregulation (figure 1) and physical protection, but compromise camouflage or warning signal efficacy [7]. To support the hypothesis that colour variation observed in nature reflects adaptation for thermoregulation requires three forms of evidence: (i) that colour differences between individuals influence their heat load; (ii) that the differences in heat load experienced by colour variants affect individual fitness; and (iii) that colour variation within or between individuals and populations is associated with the thermal conditions experienced. These three forms of evidence are available for very few species (but see [8–10] for *Colias* butterflies).

Animals absorb radiant energy from two regions of the electromagnetic spectrum: solar radiation (i.e. direct sunlight, 290–2600 nm at sea level) and thermal radiation (primarily, 8–13 μm [4]). Colour only affects the amount of solar radiation absorbed, whereas all biological tissues absorb thermal radiation from the air, ground and other objects, irrespective of colour. In terms of solar radiation, around 55% of the radiant energy in direct sunlight (figure 2) falls within the near-infrared ((NIR), 700–2500 nm), with 45% falling within the animal-visible spectrum (300–700 nm). Therefore, when examining the thermal consequences of colour variation, it is essential to consider how an animal's surface reflects the full solar spectrum, not just animal-visible wavelengths, because the thermal effects of 'colour' will depend as much on absorptance of NIR as visible wavelengths. Importantly, animal visual systems are largely insensitive to NIR wavelengths, presumably due to spontaneous activation of photopigments (i.e. photoreceptor noise) with λ_{max} beyond 700 nm [11]. Thus, in contrast with the animal-visible spectrum, variation in NIR reflectance will not be a direct consequence of selection for camouflage and signalling requirements, although
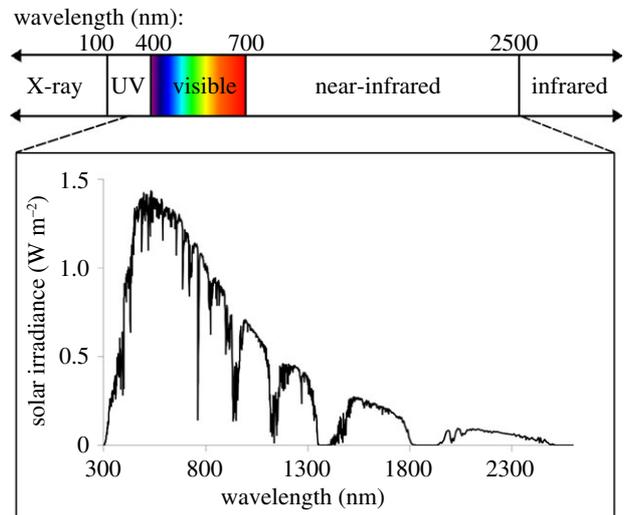
it may nevertheless be a correlated consequence of selection on visible colour.

Here, we discuss factors that may influence the relationship between 'colour' and heat load in ectotherms and endotherms and the interaction between 'colour' and other mechanisms of thermoregulation, particularly behavioural mechanisms. Colour is a perceived property and therefore necessarily concerns only animal-visible wavelengths; however, for brevity, when we refer to the effect of 'colour' on thermoregulation, we take 'colour' to mean the spectrum of direct sunlight reflected from an animal's surface (i.e. 300–2500 nm); unless we specifically refer to animal-visible (300–700 nm) or NIR (700–2500 nm) wavelengths. We review available data on variation in NIR reflectance in animals and critically evaluate evidence for adaptive variation in NIR reflectance associated with thermal requirements. Lastly, we suggest research required to gain a more complete understanding of the complex relationship between colour and thermoregulation in animals.

2. Colour and thermoregulation in ectotherms

Support for an effect of skin reflectance on body temperature and heating rates derives from both theoretical (biophysical) modelling [5,12] and experimental approaches in a variety of ectotherms (e.g. insects [13], reptiles [14] and amphibians [15]). The role of colour in thermoregulation seems equally important for species inhabiting hot/dry habitats or highly variable habitats where high reflectance can reduce heat load during periods of heat stress [16,17]. Under the same experimental conditions, differences in body temperature of similar sized individuals with dissimilar reflectance are generally less than 3°C (reviewed in [18,19]), although relatively small absolute temperature differences can be biologically important, particularly near critical thermal limits. Some of the strongest evidence for the importance of colour for thermoregulation derives from species that exhibit rapid (physiological) colour change in response to temperature, being darker when cold and lighter when hot [15,17,20–23]. This has demonstrated effects on heating rates and equilibrium

body temperature, reducing the basking time needed to reach active body temperatures [20].

Other effects such as convective and evaporative heat loss, body size and shape, and thermoregulatory strategies (posture, shuttling) can very quickly mask or surpass the effect of body colour [24]. These relations may explain the lack of support for the thermal melanism hypothesis in some studies, particularly those examining field body temperatures [18]. Often, a suite of characteristics in addition to reflectance contribute to the thermal benefit of colour (discussed below). For example, in pierid butterflies, it is the themoregulatory posture, the reflective white colour in the medial and distal areas of the wing and the melanization at the base of the wing that jointly affect thermoregulatory performance [25]. Disentangling the relative contributions of these individual factors empirically is particularly challenging but reasonable estimates can be obtained using biophysical models [26,27].

To infer that colour variation is an adaptive response for thermoregulation ultimately requires that thermal benefits of differing skin reflectance translate to fitness benefits. For example, darker individuals in cold habitats should experience longer activity periods, higher growth rates, increased fecundity and/or survival than lighter individuals. In general, there is reasonable support for these relationships [18] although most studies use behavioural and performance traits as proxies for fitness. An important consideration is that given the small magnitude of the effect of colour on body temperature relative to, for example, postural adjustments or body size, only detailed examinations of time and energy budgets generally uncover fitness benefits. These benefits can be substantial when accumulated across an organism's lifespan. For example, at low temperatures but variable levels of radiation, ladybird beetles with increased melanization take significantly less time to become active [12] (figure 1). Biophysical models have also shown that increased melanization in lizards can reduce the amount of time basking and the probability to encounter critical temperature limits [5,21]. Indeed the consequence of colour may be crucial at particular times or events that only become apparent with a good knowledge of the study system.

A relationship between skin coloration within or among closely related species and microclimate, ideally incorporating genetic information (e.g. [28]), provides additional evidence of an adaptive response (including plasticity) of colour for thermal benefits. Geographical clines of melanization are evident in a range of ectotherms including butterflies [8], flies [29], ladybird beetles [30], reptiles [31] and amphibians [15], across both latitudes and altitudes (figure 1). Patterns of thermal melanization have also been found at larger scales, both regional and global. Dark-coloured butterfly and dragonfly species are favoured in cooler climates of Europe [32] and lizard species with low skin reflectance generally inhabit areas with reduced mean annual solar radiation across latitudes [33]. Changes in coloration in response to temperature variation can result from phenotypic plasticity, for example due to developmental exposure to varying thermal regimes, but can also reflect a combination of environmental and genetic aspects, including maternal effects. In ladybird beetles and butterflies, there is abundant evidence that cold temperature can induce melanism in larvae and adults (e.g. [34,35]) with more melanin in individuals reared at cold temperatures and/or shorter photoperiods. The functional significance of thermally

induced melanism can, however, be related to other factors such as disease and desiccation resistance, protection from ultraviolet radiation and crypsis or a combination of these [36]. In some cases, these factors may relate to climate gradients as much as the thermal benefit of melanization [37] and this is further complicated by known pleiotropic effects of genes implicated in the production of melanin pigments [38].

3. Colour and thermoregulation in endotherms

The relationship between 'colour' and thermoregulation is more complex in endotherms than ectotherms because of the presence of an insulating layer over most of the body. Two properties of that insulating layer, in addition to surface reflectance, influence heat load at the skin: the structure of the coat (fur, feathers) and the optical properties of individual hairs or feathers [1]. Structural properties determine the probability per unit area of penetrating radiation being intercepted by the coat. For fur, structural properties include the density, length and diameter of the hairs while for feathers they include the density and arrangement, as well as the proportion of the lattice of barbs and barbules comprising open space. Importantly, these structural properties can be modified behaviourally, for example by ptilo- or piloerection (fluffing up), and are often not uniform through the depth of the coat (e.g. presence of down or short and dense fur close to the skin).

Optical properties of individual hairs or feathers determine whether intercepted radiation is absorbed, transmitted or scattered towards the skin (generating heat), or reflected or scattered away from the skin. Together, these properties determine overall surface reflectance and penetration of radiation into the fur or feathers. Heat load at the skin can differ markedly for species with different optical properties of hairs or feathers (e.g. very transparent versus opaque hairs), irrespective of colour (for mathematical formulations of these relationships see [1,39]). For example, the increased surface reflectance of white winter coats compared with darker summer coats in several subarctic mammals is counteracted by increased penetration of radiation into the coat [40]. Furthermore, increased insulation of the winter coat means that thermal effects of colour on heat gain are negligible [40] and this is also true of species with highly insulated coats occurring in hot environments [41].

Given the great variation between species in both structural and optical properties of the coat, irrespective of colour, Walsberg [1] concluded that 'it is apparent that no general answer is possible to the common question of whether animals with dark or light coats acquire greater solar heat loads'. Nevertheless, as insulation decreases, the effect of colour on heat load will generally increase [41]. For example, rare but naturally occurring black and white female colour morphs of Springbok (*Antidorcas marsupialis*) have higher and lower mean core body temperature, respectively, than the normal brown colour morph [42]. Higher body temperatures of the black morph are costly in summer but advantageous in winter and vice versa for lower body temperatures of the white morph [42]. This thermal effect of colour in ungulates with low-insulation coats is corroborated in other species [43].

Although the presence of an insulating layer in most endotherms complicates the relationship between colour and thermoregulation, most birds and mammals also have some parts of the body in which an insulating layer is

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minimal or absent (e.g. legs and beaks of birds). These body parts may be particularly important for thermoregulation [44] and colour may play a role. For example, across 115 species of warblers (Parulidae, pictured in figure 1), dark-legged species experience a significant thermal advantage in colder climates, with dark leg coloration correlated to more northern winter distributions, earlier arrival in Spring and later departure in Autumn [6]. Despite such cases, macro-ecological patterns of colour variation in birds and mammals are more often explained by a range of other selective pressures than thermoregulation [3,45]. In particular, increased melanization in more humid environments (Golger's rule) or the apparent prevalence of black in deserts [46] is generally attributed to the role of melanin in physiological processes (e.g. hydroregulation) and physical protection, especially from ultraviolet radiation and/or resistance to bacterial degradation [2,47].

4. Interaction between colour and behaviour

Arguably one of the most important ways that animals regulate body temperature is through behavioural adjustments, such as postural changes, moving into or out of shade or areas sheltered from wind, or ruffling fur or feathers. Such behavioural mechanisms may either counteract or augment the influence of 'colour' on body temperature. Behavioural differences (e.g. thermoregulatory behaviour or microhabitat choice) between colour variants may compensate for any differences in heat load due to 'colour', such that there are no differences in body temperatures experienced by different colour variants (e.g. [48,49]). Thus, even when a difference between the heat load of colour variants can be demonstrated in the laboratory, effects in the wild may be negligible (e.g. [50]). Alternatively, colour and behaviour may also act in concert; for example, individuals may maximize the effect of colour on heating rates through postural adjustments that provide maximum exposure to solar radiation during basking. Some desert-dwelling birds (e.g. Chilean grey gull (*Larus modestus*) and greater roadrunner (*Geococcyx californianus*)) sleek their dark feathers in the cold, early morning and ruffle their feathers later in the hottest part of the day, thereby, respectively, increasing or decreasing penetration of solar radiation to the skin [46,51]. During basking, many animals increase total surface area or expose dark-coloured body regions, which otherwise remain partially or entirely hidden. Dunnarts (*Sminthopsis crassicaudata*), for example, expose the darker band of fur proximal to the skin during basking and torpor, which increases heating rate and subcutaneous temperature [52]. By contrast, the lighter distal band of fur does not affect thermal properties but varies according to camouflage requirements [52]. Similarly, in lepidopterans, basking behaviour (especially wing angle) and melanization pattern interact to influence thermoregulation. In *Pieris* butterflies, melanization at the wing base increases absorption of solar radiation whereas, depending on wing angle, more distal white parts of the wing can reflect solar radiation to the body (reflectance basking; [25]). These examples all highlight that the effects of colour (dark or light) on thermoregulation vary depending on behaviour.

Colour may be particularly important for thermoregulation when behavioural mechanisms are insufficient or unavailable, particularly when mobility is limited, although trade-offs with mortality risks may constrain this relationship. For ectotherms, mobility is often limited at low body temperatures and dark coloration may substantially reduce the basking time required to reach active body temperatures [21]. However, once an individual reaches an active body temperature, it may rely more on behavioural mechanisms of thermoregulation than colour [20]. Even for more mobile animals, colour may mediate trade-offs between behavioural thermoregulation and other requirements such as foraging or signalling. For example, in environments with high insolation, light coloration may enable individuals to remain exposed for longer, thereby increasing time for foraging or territory defence [17].

5. The neglected role of the near-infrared

The great majority of research on colour and thermoregulation has focused on animal-visible wavelengths, which are influenced by multiple interacting selection pressures. By contrast, variation in NIR reflectance may be less constrained by selection for signalling or camouflage because animal eyes (and other sensory organs) are largely insensitive to NIR wavelengths [11]. Some snakes have heat-sensing organs, which enable them to literally see infrared radiation: information from heat-sensing pits is integrated by the central nervous system with information from the eyes to produce a single image of the environment [53]. However, these infrared organs have maximum sensitivity to thermal radiation in the wavelength range 8000–12 000 nm. The surface morphology of the pits is designed to dissipate or minimize signal from other wavelengths including the NIR (reviewed in [53]). Thus, snakes with infrared organs are unlikely to be sensitive to variation in NIR reflectance. Several behavioural studies suggest sensitivity to NIR wavelengths based on photoreception rather than thermoreception [54], but these studies are conducted in the absence of visible light (300–700 nm) and it is unclear whether the animals show ecologically significant NIR sensitivity under normal viewing conditions. Furthermore, visual pigments with maximum sensitivities (λ_{max}) beyond 700 nm have not yet been identified and may not exist in nature because higher λ_{max} results in excessive spontaneous activation, that is, signal noise. Consequently, it remains unclear whether the apparent match of some animals (e.g. some frogs [55,56]) to the vegetation background in part of the NIR (700–900 nm) improves camouflage.

Variation in NIR reflectance is generated by both pigmentary and structural mechanisms. For example, the protoporphyrin and biliverdin pigments in avian eggshells produce very high NIR reflectance (more than 90%); whereas NIR reflectance of melanin often used to colour animal integuments is substantially lower [57]. Bakken *et al.* [57] showed that the high NIR reflectance of eggs pigmented by protoporphyrin (responsible for brown speckling) would reduce heat load by 31–38% compared with hypothetical melanin-pigmented eggs, potentially almost doubling the time that eggs of ground-nesting birds could remain unattended before the embryo experiences heat injury. In other species, high NIR reflectance is achieved by structural mechanisms. For example, Saharan silver ants are covered with tiny hairs, whose structure enhances both visible and NIR reflectance. This gives the ants a highly reflective silver appearance and reduces body temperature [58]. Similarly, chameleons have a layer of iridophore pigment cells, containing reflective
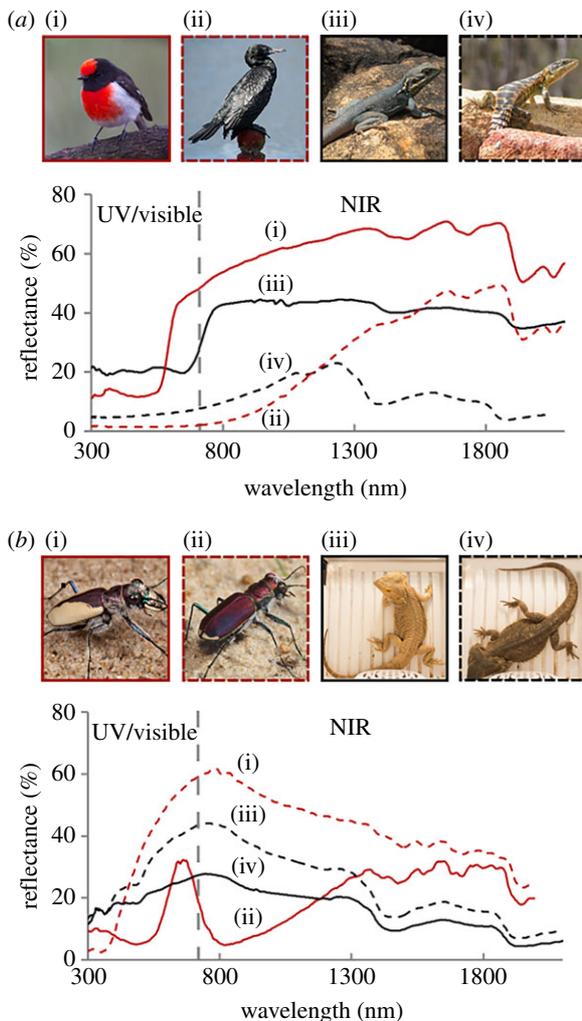
Figure 3. (a) Comparison of reflectance spectra in two bird and two lizard species, showing the variable relationship between visible and NIR reflectance. (i) Male red-capped robin (*Petroica goodenovii*) red breast feathers; (ii) little black cormorant (*Phalacrocorax sulcirostris*) black breast feathers; (iii) tawny dragon lizard (*Ctenophorus decresii*) blue-grey dorsal surface; (iv) Cape girdled lizard (*Cordylus cordylus*) dorsal area. *C. cordylus*: S Clusella-Trullas 2012, unpublished data; all other spectra: E Newton 2016, unpublished data. *Image credits: (i) Julie Burgher; (ii) Jon Sullivan; (iii) Claire McLean, (iv) S.C.-T.* (b) Examples of intra-specific variation in full-spectrum reflectance with demonstrated effect on body temperatures. The higher reflectance of (i) white elytra in a subspecies of tiger beetle (*Cicindela formosa gibsoni*) compared with (ii) the structural red elytra in a second subspecies (*C. f. pigmentosignata*) results in a mean equilibrium temperature difference of 2.2°C [60]. Spectra (iii) and (iv) show temperature-dependent reflectance change from (iii) 40°C to (iv) 15°C in the central bearded dragon (*Pogona vitticeps*). Biophysical models suggest that this 15% change on overall reflectance could reduce the time taken to reach active body temperature by an average of 22 min per active day, saving 85 h of basking time throughout the activity season [21]. Tiger Beetle spectral data reproduced with permission from Schultz & Hadley [60]. Bearded dragon spectral data reproduced with permission from Smith *et al.* [21]. Image credits: (i) Ted MacRae; (ii) David Rogers; (iii) and (iv) Kathleen Smith.

guanine crystals, whose size, shape and spacing produce high NIR reflectance [59]. Structural colours can vary dramatically within and between species, whereas pigments used tend to be more phylogenetically conserved. Owing to variation in structural properties, the relationship between visible and NIR reflectance varies greatly (figure 3). For example, the structurally produced metallic red and white

colour morphs of the tiger beetle *Cicindela formosa* differ in visible and NIR reflectance (unweighted for solar irradiance) by 21% and 35%, respectively; whereas metallic blue and white morphs of *C. horni* differ by 6.9% and −3.2%, respectively [60] (figure 3b). Thus, visible reflectance tends to be a poor predictor of NIR reflectance [61] (figure 3a).

The assumption that the NIR reflectance matches visible reflectance can give erroneous estimates of energy gain, especially when the difference between visible and NIR reflectance is substantial. As an indication, the net radiation absorbed by an animal exposed to sunlight can be calculated as: $[(1 - \text{visible reflectance}) \times \text{visible radiation}] + [(1 - \text{NIR reflectance}) \times \text{NIR radiation}]$. Here, we deliberately omit skylight and reflected sunlight absorptance as well as thermal (long-wave) radiation from the energy gain equation, and use a constant value of solar intensity of $1103\,\text{W m}^{-2}$. If we take the reflectance spectrum for the white colour morph of the tiger beetle (figure 3b(i)), the assumption that the reflectance in the visible equals the NIR reflectance adds approximately 78 W to the actual (correct) energy intake (685 W), or 11.3% error. For the red breast feathers of the red-capped robin (figure 3a(i)), this assumption also overestimates the energy gain by 40.2%. Moreover, using the average reflectance value across visible and NIR wavelengths and multiplying by the solar intensity rather than using the equation above underestimates the true energy intake by 4% and 16.5% for the tiger beetle and the robin examples, respectively.

Given that variation in NIR reflectance is not directly constrained by selection for signalling or camouflage, it is conceivable that NIR and visible reflectance spectra could vary in different ways to accommodate requirements of thermoregulation and camouflage or signalling, respectively [17]. For example, Bakken *et al.* [57] suggest that the use of protoporphyrin rather than melanin in bird eggs to produce brown speckling enables them to be camouflaged in the animal-visible spectrum but prevent overheating due to high NIR reflectance. The extent to which variation in animal-visible and NIR reflectance can provide adaptive solutions to competing requirements of thermoregulation and camouflage or signalling depends on the extent to which reflectance properties in these two parts of the spectrum vary.

Compared with data on reflectance in animal-visible wavelengths, there are very few data on NIR reflectance in animals, and its effects on thermoregulation. Often, studies that report animal skin reflectance across solar wavelengths provide only a single integrated value and do not provide the original spectral curves. The most extensive data on variation in NIR reflectance were collected by Ken Norris in 1967 on 20 species of desert reptiles [17]. Small species with high surface-mass ratio (more than 3.5) were consistently absorptive in the NIR, despite variable visible colour, which resembled that of the background. By contrast, large species (surface-mass ratio less than 3.5) were much more reflective in the NIR. Norris suggested that higher absorptivity of small species, combined with behaviour, allows rapid temperature adjustments, whereas larger species benefit most by reducing thermal load to prolong activity due to greater thermal lag [17]. Based on the few available data, it is clear that understanding the relationship between colour and thermoregulation requires consideration of NIR reflectance. However, it remains unclear whether variation in NIR reflectance in animals results from selection for thermoregulatory benefits or is largely a secondary consequence of selection on visible colour and structural

properties of integument for other reasons (communication, signalling, physical protection).

6. Conclusion and future directions

Just as apparently conspicuous colour patches (to humans) cannot be assumed to function as signals, dark or light colours cannot be assumed to play a role in thermoregulation. Nevertheless, for many species, colour has demonstrable effects on heat load and in some species this has been shown to affect individual fitness. Variable evidence for a relationship between colour and thermoregulation can be attributed to a number of factors including, but not limited to: (i) environmental conditions experienced by a species, such as thermal extremes and wind; (ii) the species' ecology, such as peak activity times, exposure to direct solar radiation and microhabitat choice; (iii) the interaction between colour and thermoregulatory behaviours such as basking, shuttling and ptilo- or piloerection; (iv) structural and optical properties of the integument, particularly the layer of insulating fur or feathers in endotherms; and (v) variation in NIR reflectance. Below we outline six outstanding questions in relation to the thermal consequences of colour variation in animals.

(1) *How does colour variation influence body temperatures and individual fitness?* Biophysical models of heat transfer [62,63] are often used to predict the thermal consequences of colour variation and such models are becoming increasingly sophisticated, incorporating information on microclimate and behaviour [64]. These models can be used to predict effects on fitness proxies such as activity time [20] and hold great promise in terms of predicting thermal consequences of colour and colour change in variable environments, including climate change scenarios [65]. Ultimately, such model predictions need to be empirically validated, preferably in the field.

(2) *How does the thermal influence of colour scale with body size?* According to biophysical principles, large animals are radiation coupled while small animals are convection coupled. Colour is, therefore, expected to have a greater influence on the thermal balance of large animals, whereas convection will be more likely to negate effects of colour in small animals [63]. However, this relationship depends greatly on microhabitat conditions and behaviour, and phylogenetic comparative studies are needed to qualify empirical relationships across diverse animal groups (e.g. [33]).

(3) *What is the relationship between visible and NIR reflectance—to what extent do they vary?* Data on NIR reflectance in animals are scarce but indicate substantial variation within and between species, largely independent of visible colour (figure 3). This raises the intriguing possibility that animals may accommodate requirements of thermoregulation and other functions of colour by variation in NIR and visible reflectance, respectively. However, the extent to which this occurs in nature remains unknown.

(4) *How do structural properties of animal integuments generate variation in NIR reflectance?* There is a need to link NIR reflectance variation to the structural properties of animal integuments. Not only is the NIR reflectance of proteins such as collagen, elastin and keratin unknown as far as we are aware, the nanophotonic structures that generate NIR reflectance variation in animals have rarely been characterized.

(5) *How does variation in NIR reflectance affect heating rates and equilibrium body temperatures of live animals?* Biophysical models indicate potentially significant effects of surface reflectance on activity times (e.g. [20]), but experimental tests that manipulate NIR reflectance through changes in skin properties or that simultaneously incorporate thermoregulatory adjustments (behavioural or physiological) to examine effects on heat load are non-existent, to our knowledge. Such experiments are needed to qualify thermal benefits of variation in NIR reflectance.

(6) *Is there evidence of adaptive variation in NIR reflectance?* To assess adaptive variation in NIR reflectance, we need empirical data on NIR reflectance across diverse animal groups, combined with phylogenetically controlled tests for correlations with thermal environment. Furthermore, we expect NIR reflectance to be associated with thermal environment in diurnal but not nocturnal animals. Evidence for adaptive variation in NIR reflectance would provide strong evidence that selection for thermoregulation has contributed to the extraordinary diversity of coloration (visible and NIR) in animals.

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