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## Review article

**Thermal effects of plumage coloration**SVANA ROGALLA,<sup>\*1,2</sup>  MATTHEW D. SHAWKEY<sup>1</sup>  & LILIANA D'ALBA<sup>1,3</sup> <sup>1</sup>*Evolution and Optics of Nanostructures Group, Department of Biology, University of Ghent, K. L. Ledeganckstraat 35, 9000, Ghent, Belgium*<sup>2</sup>*Instituto Biofisika (UPV/EHU, CSIC), Barrio Sarriena, 48940, Leioa, Spain*<sup>3</sup>*Naturalis Biodiversity Center, Darwinweg 2, Leiden, 2333 CR, The Netherlands*

Plumage coloration can have substantial effects on a bird's energy budget. This is because different colours reflect and absorb light differently, affecting the heat loads acquired from solar radiation. We examine the thermal effects of feather coloration on solar heat gain and flight performance and discuss the potential role of plumage colour on a bird's energy budget. Early investigations of the effects of plumage colour on thermoregulation revealed complex interactions between environmental conditions and physical properties of the plumage that may have led to diverse behavioural and physiological adaptations of birds to their thermal environment. While darker feather surfaces absorb more light, and heat more, than light-coloured surfaces under exposure to the sun, this relationship is not always straightforward when considering heat transfer to the skin. Heat transfer through plumage varies depending on multiple factors, such as feather density and transmission of light. For instance, higher transmissivity of light-coloured plumage can increase heat loads reaching skin level, while conduction and convection transfer heat from the surface of dark feathers to the skin. Solar heating can affect the metabolic costs of maintaining a constant body temperature, and depending on environmental conditions, colours can have either a positive or negative effect on a bird's energy budget. More specifically, solar heating can be advantageous in the cold but may increase the energetic costs associated with thermoregulation when ambient temperature is high. More recent studies have further suggested that the thermal properties of feather coloration might reduce the energetic costs of flight. This is because surface heating can affect the ratio between lift and drag on a wing. As concluding remarks, we provide future directions for new lines of research that will aid in improving our understanding of the thermal effects of feather coloration on a bird's energy budget, which can potentially explain factors driving colour evolution and distribution patterns in birds.

**Keywords:** feather coloration, flight, metabolic costs, solar heat loads.

**FUNCTIONS OF AVIAN PLUMAGE**

Feathers are remarkable structures that are found in diverse shapes, sizes and colours. Although often considered as unique features of birds, feathers originated in non-avian dinosaurs about 80 million years

before the origin of birds (Benton *et al.* 2019), and probably initially evolved through natural selection on communication (sexual selection and camouflage) and thermal insulation functions (Prum 1999). Plumage mediates the interactions between birds' external and internal environment (Wolf & Walsberg 2000). As such, the avian integument can provide physical protection against water, radiation and extreme temperatures. For example, elaborate feather structures at micro- and nano-

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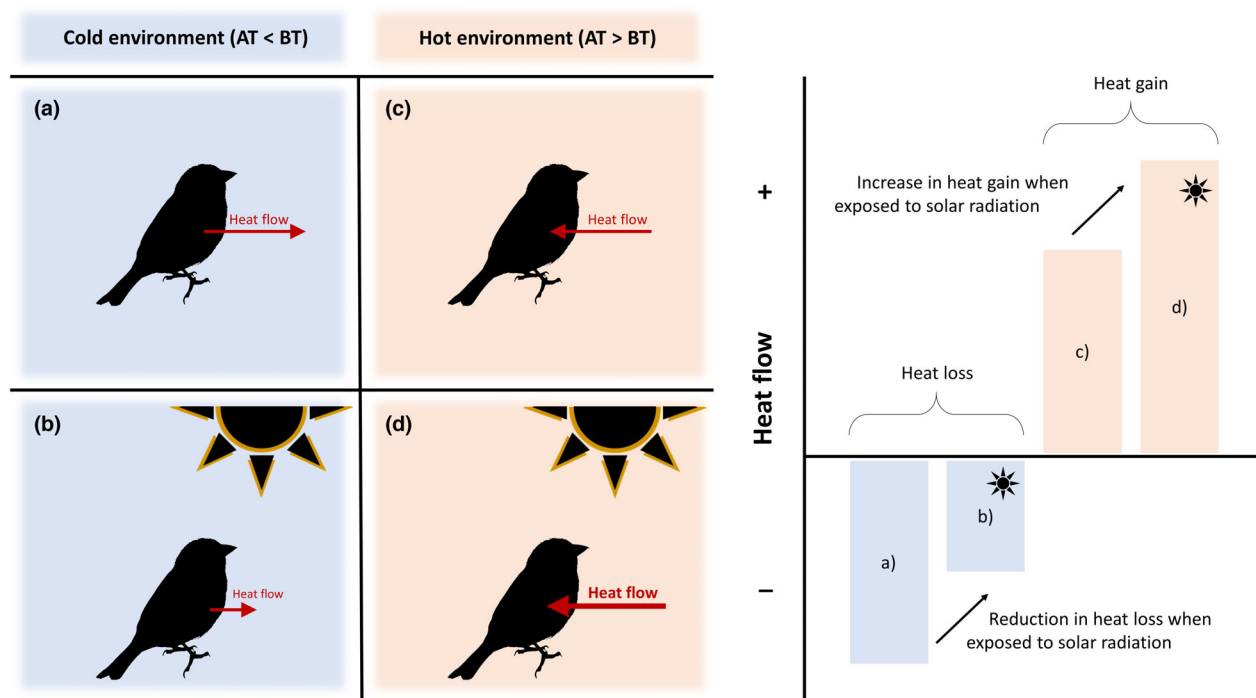
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scales and the use of preen oil increase hydrophobicity (Liu *et al.* 2008), while melanin pigmentation of feathers and skin guards against ultraviolet radiation (Burt 1979, Nicolai *et al.* 2020). Importantly, the thermal properties of plumage determine the heat flux between the feather surface and the skin (Wolf & Walsberg 2000). For instance, when ambient temperatures are low, heat flows from the warmer interior of the bird to the colder environment, whereas under ambient temperatures exceeding a bird's body temperature, this gradient is reversed (Fig. 1a and 1b) (Cowles *et al.* 1967, Heppner 1970, Prinzinger *et al.* 1991, Nord & Nilsson 2019, Szafranska *et al.* 2020). This relationship is mediated by the thermal properties of the plumage, which result from an interplay of multiple morphological features including feather macrostructure and microstructure, coloration, plumage depth, feather density, and the amount of trapped air (Cena & Monteith 1975a, Walsberg 1988, Osváth *et al.* 2018). Denser plumage is

known to have stronger insulative properties, restricting the heat transfer between the feather surface and skin (D'Alba *et al.* 2009, Osváth *et al.* 2018). For example, the highly derived and insulative plumage of penguins helps these birds maintain a body temperature of 38°C even when ambient temperatures are as low as -40°C in the Antarctic (Williams *et al.* 2015). Furthermore, birds can adjust their plumage thickness according to environmental conditions. For instance, by fluffing up in the cold they increase the amount of trapped air and, hence, their insulating efficiency, ultimately reducing heat loss to the surrounding environment (Stettenheim 2000). On the other hand, in a hot environment and under exposure to intense solar radiation, the erection of the scapular feathers can function as heat shields by retarding heat gain from solar radiation (Lustick 1984).

Coloration also affects the thermal properties of plumage. Variation in reflectance and absorption of light affect the heating of the feather surface (Wolf



**Figure 1.** (a) Under cold conditions, when ambient temperatures (AT) are below a bird's body temperature (BT), heat flows from the warmer interior of the bird to the colder environment. (b) When the plumage surface is heated by the sun under cold conditions, the temperature gradient between the body and the surrounding air is reduced, reducing heat loss to the environment. (c) When ambient temperatures exceed body temperature, the temperature gradient is reversed and heat flows into the bird's body. (d) Under high ambient temperatures, additional solar radiation increases heat flow into the body. Larger font/symbol sizes are used to visualize increasing intensities.

& Walsberg 2000, Rogalla *et al.* 2021a). When the plumage surface is heated by the sun under cold conditions, the temperature gradient between the skin and the feathers is reduced, which in return decreases heat loss to the environment (Fig. 1c) (Cowles *et al.* 1967, Lustick 1969, Lustick *et al.* 1970, Heppner 1970). However, when ambient temperatures are high and feather surface temperature exceeds skin and body temperature because of solar heating, birds gain excessive heat (Fig. 1d) (Cowles *et al.* 1967, Lustick 1969, Lustick *et al.* 1970, Heppner 1970). In endothermic species, maintaining a relatively high body temperature within a narrow range by means of metabolic heat production is crucial to avoid reduced performance (Boyles *et al.* 2011). Particularly during flight, which is energetically very costly (Guigueno *et al.* 2019), birds generate a large amount of body heat that must be dissipated to avoid overheating (Powers *et al.* 2015). Interestingly, solar heat loads can affect the metabolic costs of maintaining a constant body temperature, and this effect is stronger in birds with darker, less-reflective plumage (Hamilton & Heppner 1967, Lustick 1969, De Jong 1976, Ellis 1980, Angelier 2020). On the other hand, solar heating of feather surfaces might affect the energetic costs of birds during flight. Recent studies have suggested that colour-induced thermal effects on wing surfaces could alter the flight efficiency of birds (Hassanalian *et al.* 2017, 2018a, 2018b, 2019, Rogalla *et al.* 2019, 2021b). This is because increasing wing surface temperatures improve the ratio between lift and drag forces on the wing (Hassanalian *et al.* 2017, Rogalla *et al.* 2021b). Despite the diversity of integumentary coloration in birds, most studies have focused on thermal properties by performing binary comparisons of dark and light colours (Ellis 1980, Hochscheid *et al.* 2002, Margalida *et al.* 2008, Rogalla *et al.* 2019), and only recently have the thermal properties of different plumage colours, including those of iridescent feathers, been described (Shawkey *et al.* 2017, Rogalla *et al.* 2021a).

In this review, we discuss the effects of thermal properties of feather coloration on solar heat loads and flight performance and the potential role of plumage colour on a bird's energy budget. To present a thorough overview of the relevant literature, we searched Web of Science (<https://www.webofknowledge.com>) and Google Scholar (<https://scholar.google.com/>) using different combinations of the following keywords: feather

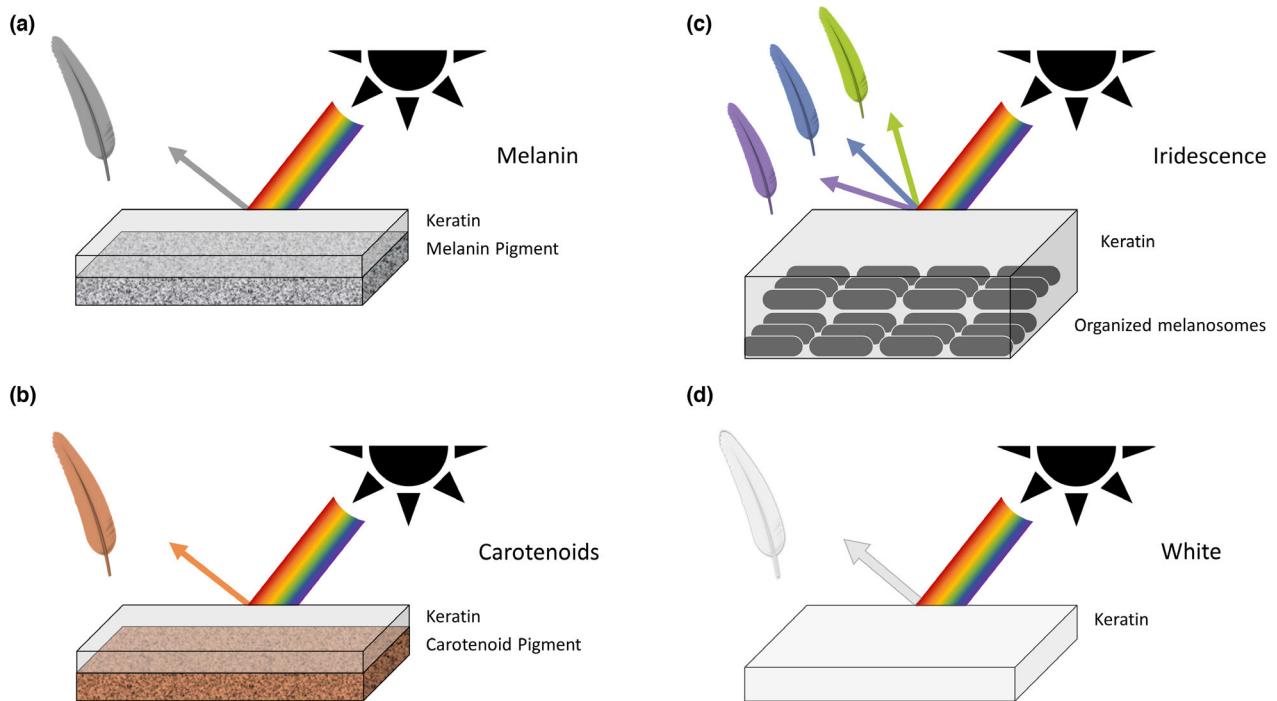
coloration/plumage coloration (or colour) and solar heat loads/solar heating/radiative heating/thermal properties. Based on this literature research, we (1) describe the most common determinants of plumage coloration and their thermal properties, (2) review the effects of integument coloration on heat gain and metabolism, (3) discuss the thermal effects of wing coloration on flight performance and (4) consider whether thermal effects play a role in the evolution of plumage coloration. Finally, we provide directions and new perspectives for future research.

## DETERMINANTS OF PLUMAGE COLORATION AND THEIR THERMAL PROPERTIES

The optical properties of avian plumage, including coloration, result from close interactions between different mechanisms including variation in feather microstructure, deposition of pigments, and nanostructural arrangements within the feather barb and barbules (Fig. 2) (Hill *et al.* 2006). For example, spacing between barbules and barb shape predict feather reflectance, particularly in the near-infrared range (Stuart-Fox *et al.* 2018).

Feather coloration depends strongly on the concentration of pigments deposited in the feathers. Pigments selectively absorb particular wavelengths of visible light. The most abundant and widespread pigment in avian integument is melanin, which produces grey, brown or black colours (McGraw 2006a) (see Box 1). The second most prevalent pigments are carotenoids, which produce either yellow, orange or red colours (McGraw 2006b). Less common are porphyrins that produce a range of colours, including the greens and reds in turacos as well as psittacofulvins that give parrots their bright colours (McGraw 2006c). Nanostructured tissues produce non-iridescent structural colours, for example blue, as well as iridescent colours through coherent light scattering (Prum 2006). Nanostructured iridescent feather colours are produced by combinations of air, keratin and melanosomes (organelles that contain melanin pigment) that differ in size, shape and spatial distribution (Prum 2006). White, on the other hand, is produced by wavelength-independent, diffuse scattering of light and the absence of pigment (Ilgic *et al.* 2018).

Radiative heating of feathers is strongly linked to the type and amount of pigment, and the



**Figure 2.** Colour-producing mechanisms. (a) Melanin pigment granules within the keratin of the feather barbule and an overlying keratin cortex produce grey, brown or black colours. (b) Carotenoid pigments produce either yellow, orange or red colours. (c) Nanostructured iridescent colours are produced by the organized arrangement of melanosomes that results in coherent light scattering. Iridescent feathers change their colours with a change in viewing angle. (d) White is produced by the absence of pigment and diffuse scattering of light.

spectral emission of the light source (Monteith & Unsworth 2013). For example, melanin absorbs over a broad spectrum that extends from the ultraviolet to the near infrared (from 300 to >1300 nm) (Piletic *et al.* 2010, Mendenhall *et al.* 2015, Stavenga *et al.* 2015), whereas carotenoids absorb within a narrow range (400–600 nm) (Bauernfeind 1981), meaning that melanin absorbs more radiation overall (Fig. 3). Concurrently, melanin-based colours reflect less light than carotenoid-based colours (Rogalla *et al.* 2021a).

A recent study of the thermal properties of sunbird (Nectariniidae) feather coloration showed that nanostructured, melanin-based, iridescent feathers (green, purple, blue) reflected less light and heated more than unstructured melanin-based colours (grey, brown, black), carotenoid-based colours (yellow, orange, red) and non-pigmented whites (Rogalla *et al.* 2021a). The higher heating rates of iridescent feathers were linked to greater melanin content within feather barbules and, to a minor extent, to the shape of the melanosomes, with

higher aspect-ratio (i.e. longer) melanosomes absorbing more light and heating more (Rogalla *et al.* 2021a). Temperatures at skin level were closely linked to the temperatures at the feather surfaces and overall decreased with increasing reflectivity (Rogalla *et al.* 2021a).

Plumage reflectivity (calculated as a function of reflectance and irradiance of the light source) depends on wavelength and varies not only over the ultraviolet and visible spectrum, but also over the near infrared (Fig. 3) (Shawkey *et al.* 2017, Medina *et al.* 2018). While variation in feather coloration over the visible spectrum is probably a result of multiple selection pressures, including camouflage and signalling, variation in near-infrared reflectance probably fulfils a thermoregulatory function (Medina *et al.* 2018). As visible reflectance might be a poor predictor of near-infrared reflectance, it is important to consider both parts of the spectrum in studies of animal coloration and thermal properties (Stuart-Fox *et al.* 2017).



## Box 1

**Melanin**

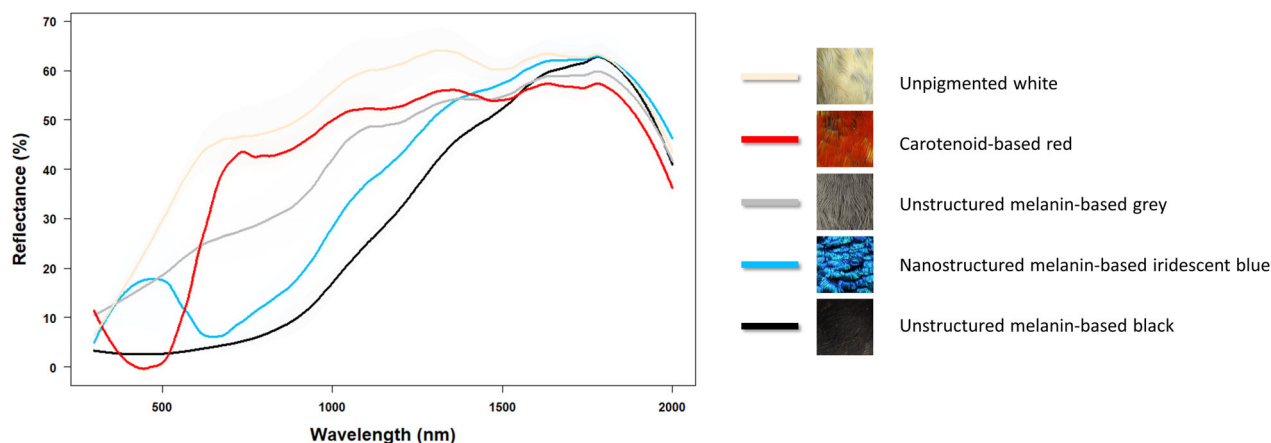
Melanins are a ubiquitous but still poorly understood group of pigments whose characteristic property is broad absorption across the visible and near-infrared (NIR) spectrum (Wolbarsht *et al.* 1981, Zonios *et al.* 2008) up to at least 1300 nm (Mendenhall *et al.* 2015). Solar energy absorbed by melanin is readily converted into heat (Riley 1997). The two chemical forms found in feathers are dark black eumelanin and red-brown pheomelanin. Eumelanin absorbs significantly more visible light than pheomelanin, but whether this is also true in the NIR part of the spectrum is not yet known. However, there are some disparities between the pigment types in the NIR (Piletic *et al.* 2010). Pure forms of both pigments are rarely found in feathers, but are instead mixed (McGraw 2006a) within pigment-bearing organelles called melanosomes. When deposited in an unorganized manner in feathers, these melanosomes produce dark black, brown, red and grey colours. By contrast, when arranged at a nanometre scale, they can produce bright iridescent colours across the visible spectrum by coherent light scattering (Prum 2006). More importantly, both visible and NIR reflectance of feathers can be affected not only by melanin chemistry in feathers, but also by its morphology and spatial arrangement (Eliason *et al.* 2013), while melanin content can determine radiative heat gain (Rogalla *et al.* 2021a). Although in some species melanin pigmentation can be associated with aspects of individual quality (e.g. Roulin 2007), there is no apparent general pattern of selection on melanin-based coloration (Meunier *et al.* 2011). Hence, selection can favour either dark or pale colour traits depending on ecological factors (Meunier *et al.* 2011), and further studies on the effects of melanin-based colouration in a broader ecological context are needed.

It is debatable whether producing iridescent plumage coloration is a costly trade-off for sexual selection in the context of reduced thermal tolerance. However, many sunbirds live in areas with high temperature fluctuations, specifically extremely cold nights and hot afternoons. Higher heat loads on iridescent male sunbirds in the cold early morning hours could be energetically advantageous, whereas an additional heat load during a

hot afternoon would increase the costs of thermoregulation (Rogalla *et al.* 2021a). Although it is not known whether iridescence is linked to a thermoregulatory cost, displaying strongly iridescent (i.e. more melanized) plumage might further be linked to a cost of greater melanin production (Galván & Solano 2016, Roulin 2016). To fully understand whether plumage iridescence could result in a thermal cost, thus representing a costly trade-off for sexual selection, more studies on a range of taxa are needed. These studies should pay specific attention to species occurring in hot climates and where the males display their vivid iridescent colours in open, sunny habitats. Furthermore, while incorporating variation in structure and density of the plumage (Cena & Monteith 1975a, Walsberg 1988, Osváth *et al.* 2018), these studies should consider more broadly how colour-induced differences in feather surface heating affect heat transfer to the skin level and hence the overall heat gain.

### Thermal effects of integument coloration on heat gain

Generally, heat transfer through plumage occurs through radiation (heat transfer through the emission of electromagnetic waves), convection (heat transfer through the movement of a liquid or gas) and conduction (heat transfer through the direct contact of particles) (Walsberg 1988). Interestingly, approximately 95% of the total heat flow through a bird's plumage is evenly divided between convection through air and conduction, both along the solid elements of the feathers and through the air contained within the plumage (Walsberg 1988, Wolf & Walsberg 2000). Radiative heat transfer, on the other hand, accounts for only about 5% of the total heat flow because radiation penetration into the plumage is intercepted by the feathers before reaching the skin level (Walsberg 1988, Wolf & Walsberg 2000). Radiation penetration into avian plumage varies with feather density, positioning and coloration, as a result of differential radiation absorption by pigments (Wolf & Walsberg 2000, Sedghi *et al.* 2020). Darker tissues reflect less and absorb more light than light-coloured tissues (Cena & Monteith 1975b). This correlation, which is wavelength- ( $\lambda$ ) dependent, can be described by applying the Kubelka–Munk equation as follows:



**Figure 3.** Comparison of reflectance spectra of differently coloured plumage patches over the ultraviolet and visible spectrum (300–700 nm) and the near infrared (701–2000 nm). Data were retrieved from Rogalla *et al.* (2021a).

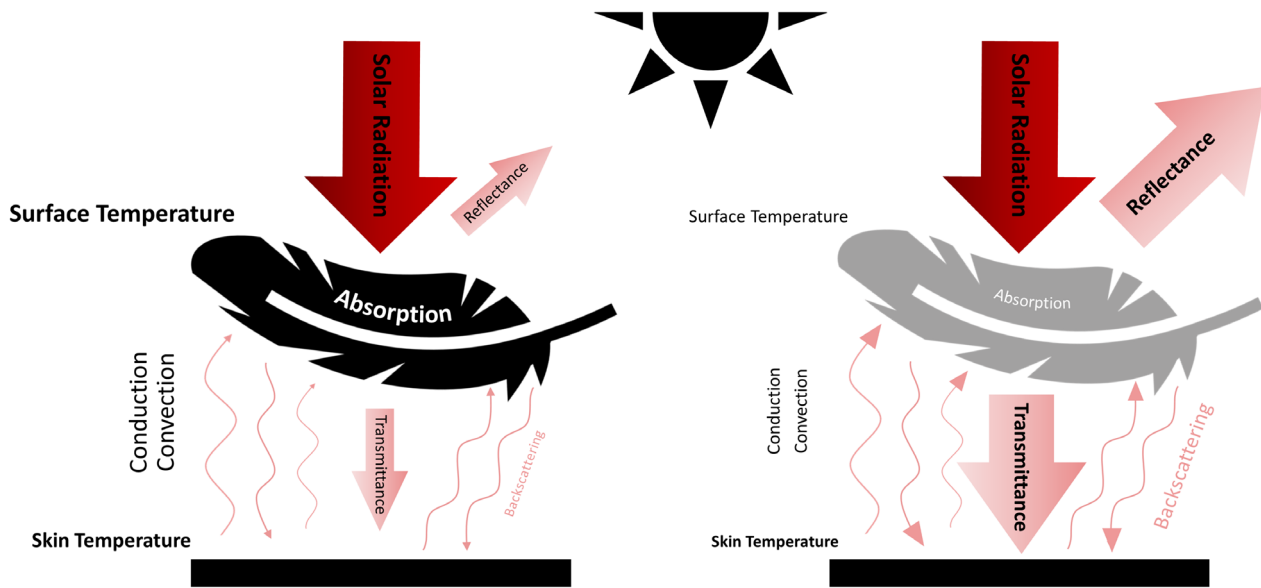
$$\alpha(\lambda) + \rho(\lambda) + \tau(\lambda) = 1,$$

where  $\alpha(\lambda)$  is the fraction of incident energy absorbed,  $\rho(\lambda)$  is the reflected fraction, which is scattered away from the skin, and  $\tau(\lambda)$  is the transmitted fraction, which is scattered towards the skin (Cena & Monteith 1975b). In darker plumage most radiation is absorbed in the upper feather layers, whereas in light-coloured plumage the radiation penetrates much deeper into the plumage (Walsberg 1983a, Wolf & Walsberg 2000). Heating at the skin level beneath light-coloured plumage is mostly caused by the greater transmittance of light (Burt 1979) and backscattering effects (Cui *et al.* 2018) (Fig. 4). The skin beneath darker feathers, on the other hand, heats up mostly through conduction and convection (Wolf & Walsberg 2000) (Fig. 4).

Only a few studies have quantitatively compared heating at skin level under dark- and light-coloured plumage. In black Brown-necked Ravens *Corvus ruficollis* exposed to the sun, surface temperatures were 5.5°C higher than those of brown ravens (black Ravens whose feathers were bleached with H<sub>2</sub>O<sub>2</sub>) (Marder 1973). Temperatures reached at skin level, however, were only 0.3–0.5°C higher under the black compared with the brown plumage (Marder 1973). In Rock Doves *Columba livia* exposed to the sun, plumage temperatures were 3.1°C higher in dark compared with light morphs, leading to a difference of 0.5°C in body temperature (Angelier 2020). These

colour-induced temperature differences are sensitive to changes in wind speed (forced convection) and changes in plumage thickness, which can be modified by feather fluffing (Marder 1973, Walsberg *et al.* 1978, Wolf & Walsberg 2000). Plumage thickness determines the probability that a ray propagating to the skin will be intercepted by a feather element, and so affects the mode of heat transfer from the feather surface to the skin (Walsberg 1988). Indeed, in some species, such as the Emu *Dromaius novaehollandiae*, the dense plumage provides almost complete protection from solar radiation by preventing heat transmission to the skin (Maloney & Dawson 1995, Dawson & Maloney 2004). Sunbirds (Nectariniidae) have less dense plumage and the differential temperatures between feather surface and skin decrease with plumage reflectivity (Rogalla *et al.* 2021a). Interestingly, the skin beneath darker, more melanized plumage heats up less than at the feather surface, whereas the skin beneath light plumage heats up more than at the surface. This suggests deeper light penetration, and thus higher rates of heat transfer into lighter coloured plumage (Rogalla *et al.* 2021a).

However, skin coloration can have an additional effect on solar heat gain (see section below). Darker skin increases heat gain at skin level either when beneath lighter coloured, more light-transmitting tissues (e.g. Polar Bears *Ursus maritimus*; Grojean *et al.* 1980) or when directly exposed to the sun (Ohmart & Lasiewski 1971). Differences in the optical properties of avian



**Figure 4.** Thermal effects of solar radiation illustrated for a dark- (left) and a light- (right) coloured feather. The darker feather absorbs more light at the surface, which leads to a higher increase in surface temperature. Although less light is transmitted through the feather, the skin heats up as a result of conduction and convection. The lighter feather reflects more and absorbs less sunlight and its surface heats up less. The skin surface beneath light plumage heats up as the result of deeper light penetration, higher transmittance and backscattering of the light. Heat transfer mechanisms are illustrated based on the studies of Cena and Monteith (1975a, 1975b), Burt (1979), Walsberg (1983a), and Wolf and Walsberg (2000). Larger font/symbol sizes are used to visualize increasing intensities. This figure was originally published in Rogalla *et al.* (2021a).

integument can strongly affect plumage surface heating and heat transfer to skin level (Fig. 4), where it can directly affect a bird's body temperature and thereby the costs of maintaining thermal balance (Irving & Krog 1955, Angelier 2020).

## METABOLIC EFFECTS OF PLUMAGE COLORATION

The range of ambient temperatures over which a bird uses the minimum amount of energy and water expenditure needed to maintain its body temperature is called the thermal neutral zone. Beyond this range, metabolic costs increase sharply to maintain thermal balance (Boyles *et al.* 2011, McKechnie & Wolf 2019, Cunningham *et al.* 2021; for further details on avian thermophysiology, see Box 2). Under exposure to solar radiation, the thermal effects of feather coloration can play a significant role in a bird's energy budget, strongly affecting the metabolic costs of maintaining a constant body temperature (Hamilton & Heppner 1967, Lustick 1969, De Jong 1976, Ellis 1980, Angelier 2020). Plumage surface temperatures in live birds have been reported to reach

values of up to 83.9°C (79.6–92.3°C) under direct exposure to the sun (Marder 1973). In a cool environment, when ambient temperature is below a bird's thermal neutral zone, solar radiation can significantly reduce the energetic costs of thermoregulation (Morton 1967, Hamilton & Heppner 1967, Heppner 1970, De Jong 1976). For example, Morton (1967) observed that White-crowned Sparrows *Zonotrichia leucophrys* feed less when exposed to thermal radiation relative to non-irradiated birds under the same conditions. A few studies have also examined the effects of solar radiation on avian metabolic rates (Hamilton & Heppner 1967, Lustick 1969, De Jong 1976, Ellis 1980). De Jong (1976) measured oxygen consumption by White-crowned Sparrows under different ambient temperatures and simulated exposure to solar radiation. When ambient temperatures were below the thermoneutral range, irradiance caused substantial reductions in thermoregulatory energy expenditure with rates of oxygen consumption reduced to up to 44% at 1°C compared with the rates of non-irradiated birds.

Hamilton and Heppner (1967) experimentally tested the effect of plumage coloration on



## Box 2

**Avian thermophysiology**

Birds are distributed worldwide, spanning all climatic zones from the poles to the equator. On their breeding grounds they commonly face daily and seasonal temperature fluctuations, and migratory birds (20% of all species; Kirby *et al.* 2008) might be exposed to thermal extremes when crossing atypical climate zones. As endotherms, birds need to regulate their body temperature within a narrow range over a wide span of thermal conditions, so they must balance metabolic heat production with heat exchanged with the environment (Dawson & Whittow 2000). The temperature range in which a bird uses the minimum amount of energy needed to maintain its body temperature is called the thermal neutral zone. Outside this zone, metabolic costs rise rapidly to maintain core body temperature (Boyles *et al.* 2011, McKechnie & Wolf 2019, Cunningham *et al.* 2021). This means that on top of the basal metabolic costs required for maintenance in endotherms, there are additional thermoregulatory costs applying at either extreme hot or extreme cold ambient conditions (Kendeigh 1944, Dawson & O'Connor 1996). Taken together, basal and thermoregulatory costs account for 40–60% of the total daily energy expenditure (Walsberg 1983b). Returning metabolic rate to neutrality when ambient temperatures reach values beyond the limits of the thermal neutral zone can result in significant fitness consequences that can affect survival (McKechnie & Wolf 2010) and reproductive success (Bolger *et al.* 2005, Cunningham *et al.* 2013, Bourne *et al.* 2020). To reduce the costs of thermoregulation, some birds have adjusted their metabolic rates to extreme environments or thermal fluctuation throughout the year (Tieleman & Williams 2000, Smit & McKechnie 2010). Furthermore, birds have evolved some adaptive strategies of heterothermy to reduce metabolic costs when ambient temperatures reach values beyond the thermal neutral zone (McKechnie & Lovegrove 2002, Angilletta *et al.* 2010, Ruf & Geiser 2015). Interestingly, heterothermic responses in birds occur throughout the avian phylogeny and are not restricted to birds with a specific body mass nor to species occupying specific climate zones (McKechnie & Lovegrove 2002). Other means of heat dissipation include the use of thermal windows: body parts that are uninsulated and highly vascularized, and through which heat can be dissipated by increased blood flow (Tattersall *et al.* 2009, 2017, van de Ven *et al.* 2016).

thermoregulation-associated metabolic costs by exposing (naturally) white- and black-dyed Australian Zebra Finches *Taeniopygia guttata* to artificial sunlight at an ambient temperature of 10°C. They confirmed that plumage colour can have a substantial effect on a bird's energy savings, in that black Zebra Finches used an average of 22.9% less energy than white Zebra Finches while being irradiated. They suggested that the energy savings can be linked to the temperature gradient between the bird and the surrounding air. Under cold conditions, and in the absence of solar radiation, heat flows from the warmer interior of the bird to the colder environment (Fig. 1a). When the plumage surface is heated by the sun, the temperature gradient between the skin and the feathers is reduced, which in return decreases the heat loss to the environment (Fig. 1b) (Cowles *et al.* 1967, Heppner 1970). A similar experiment performed by Lustick (1969) showed that Brown-headed Cowbirds *Molothrus ater obscurus* and wild-type, dark-grey Zebra Finches showed a decrease in oxygen consumption of about 26% when exposed to radiative heating. However, in

albino Zebra Finches, no effect of radiative heating on oxygen consumption was found. Interestingly, black, brown and dark-grey plumages were very similar in overall reflectance, but all colours differed strongly from the highly reflective white plumage of albino Zebra Finches. Hence, Lustick (1969) suggested that most birds other than those with white plumage can gain energetic benefits from exposure to solar radiation in cold environments (Lustick 1969).

At high ambient temperatures solar irradiance can increase heat loads, thereby adding a cost to thermoregulation (Lustick *et al.* 1970, De Jong 1976, Ellis 1980, Hochscheid *et al.* 2002). This is because the thermal gradient between a bird and its environment is reversed, so that the surrounding air is hotter than the bird and heat flows into the body (Fig. 1d) (Lustick *et al.* 1970, Szafrńska *et al.* 2020). This effect is magnified in birds with dark plumage. For example, black-plumaged juvenile Cape Gannets *Morus capensis* experience greater heat loads and are heat-stressed more easily than the white adults (Hochscheid *et al.* 2002). In herons, species

nesting in the direct sun (Little Blue Herons *Egretta caerulea*, Snowy Egrets *Egretta thula* and Cattle Egrets *Bubulcus ibis*) had lower basal metabolic rates than predicted from their body weight according to Lasiewski and Dawson (1967) (see Ellis 1980). This effect was stronger in darker species (Little Blue Herons), probably to counterbalance the external heat loads (Ellis 1980). For the polymorphic Rock Dove, higher plumage surface temperatures have been reported for darker individuals when exposed to solar radiation, resulting in slightly higher cloacal temperatures than paler individuals or birds that stayed in the shade (Angelier 2020). High solar irradiance when ambient temperatures are high can lead to a downwards shift of the upper critical temperature of the thermal neutral zone (Lustick 1969, De Jong 1976). When birds absorb more heat than they can dissipate, their body temperatures increase and they become hyperthermic (Lustick *et al.* 1970, Ellis 1980). Additionally, external solar heat loads substantially increase evaporative water loss at high ambient temperatures (Wunder 1979). In black male Lark Buntings *Calamospiza melanocorys*, evaporative water loss increased by 36% at 30°C and by 150% at 35°C when they were exposed to a heat lamp simulating the sun (Wunder 1979). Particularly in arid, highly irradiated and hot environments, such strong water loss can put a bird at the risk of dehydration.

Wind can also interact with solar radiation and affect energy expenditure. Although radiation absorption and penetration into the plumage depends strongly on microstructure and micro-optical properties of the plumage elements, solar heat gain can be extremely sensitive to changes in wind speed (Wolf & Walsberg 2000). At low wind speeds, birds with black plumages acquire much greater radiative heat loads than birds with white plumages. When exceeding wind speeds of 3 m/s, however, this relationship is reversed (Walsberg *et al.* 1978). Radiative heating of white plumages is affected less by convective cooling than is that of black plumages and this effect is strongest in erected feathers (Walsberg *et al.* 1978). Ptiloerection more strongly reduces heat gain through black plumages because most of the radiation is absorbed near the upper surface, where it is reduced by forced convection (wind). By contrast, radiation penetrates much deeper into white plumage, whereby the inside of

the plumage is mostly insulated from forced convection (Walsberg *et al.* 1978). As such, erected black plumages may acquire radiative heat loads lower than depressed white plumages when wind speeds are greater than 5 m/s (Walsberg *et al.* 1978). The thermal effects of feather coloration under solar radiation when taking the effects of wind into account can have significant biological implications. For example, the white coats of polar animals may be thermally highly advantageous; at the same time black desert birds may benefit from a decrease in radiative heat gain under windy conditions (Walsberg *et al.* 1978, Ward *et al.* 2002). Indeed, higher solar heat loads in dark rufous Red Grouse *Lagopus lagopus scotica* than in white Willow Ptarmigan *Lagopus lagopus lagopus* in still air are diminished under windy conditions despite similarities in feather density, plumage depth and plumage thermal resistance (Ward *et al.* 2007). The magnitude of the effect that wind can have on a bird's energy budget is clearly illustrated for Verdins *Auriparus flaviceps*. At wind speeds of 0.4 m/s, solar heat gain may reduce the metabolic rates of Verdins by 46%. At a wind speed of 3.0 m/s, however, solar heat gain only reduces the metabolic rate by 3% (Wolf & Walsberg 1996). These dimensions visualize the importance of microsite selection (e.g. sheltered or exposed to wind and/or sun) on the thermoregulatory costs of a bird (Wolf & Walsberg 1996, Cunningham *et al.* 2015, van de Ven *et al.* 2019). Under direct exposure to solar radiation and wind, birds can change their posture to actively modify the exposed surface area, or if bicoloured, expose different-coloured plumage according to their thermal needs (Lustick 1984).

The thermal effects of feather coloration on a bird's metabolism can directly affect its survival. Reduced metabolic costs in the darker, grey-phase Eastern Screech Owl *Megascops asio* at low ambient temperatures might explain the lower differential mortality compared with red-phased Owls (Mosher & Henny 1976). In Pied Flycatchers *Ficedula hypoleuca*, phenotypic colour variation can result in temperature-dependent effects on both breeding performance and offspring quality (Sirkiä *et al.* 2010, Järvisistö *et al.* 2015), whereby the stress experienced during reproduction might have carryover effects between breeding seasons that manifest as changes in the expression of melanin-based coloration (Järvisistö *et al.* 2016).

## EFFECTS OF SKIN COLORATION ON HEAT GAIN AND METABOLISM

The solar heat loads on a bird not only vary with the coloration of the plumage but also with the coloration of its skin. Indeed, some species expose their skin directly to the sun to increase solar heat gain when ambient conditions are cold (Ohmart & Lasiewski 1971). For example, the Greater Roadrunner *Geococcyx californianus*, a highly specialized desert species, opens its wings and scapular feathers to expose its dark dorsal skin, thereby increasing the direct absorption of sunlight in cold early morning hours and resulting in energy savings as high as 41% of standard metabolism (Ohmart & Lasiewski 1971). Below ambient temperatures of 10°C, roadrunners show hypothermic responses, yet when sunning, their body temperature can rise back to normothermic levels, although their oxygen consumption may remain at levels characteristic of hypothermic, non-irradiated birds (Ohmart & Lasiewski 1971). Similarly, some mousebirds (Coliidae) expose their black-pigmented skin on the belly to the sun while basking, a behaviour that can both aid in thermoregulation and improve the digestion of their herbivorous, fibre-rich diet (Downs *et al.* 2000, McKechnie *et al.* 2004). Interestingly, darker skin can also increase solar heat gain under light-coloured tissue, a phenomenon long discussed for Polar Bears (Grojean *et al.* 1980). Given that lighter coloured plumage increases the radiative heat transfer to the skin (Burt 1979, Walsberg 1983a, Wolf & Walsberg 2000), it might seem counterintuitive that black skin in birds has evolved more often towards the equator (Nicolai *et al.* 2020). However, the association of dark skin beneath white or bald patches could be explained by the photoprotective function of melanin pigments against ultraviolet (UV) radiation (Nicolai *et al.* 2020).

Although extremely dense plumage might in some cases prevent solar radiation from penetrating deeply enough to contribute to radiative heating of the skin (Maloney & Dawson 1995, Dawson & Maloney 2004), the direct exposure of dark skin to the sun that has been observed in other species suggests a thermoregulatory function of skin colour (Ohmart & Lasiewski 1971, Downs *et al.* 2000, McKechnie *et al.* 2004). However, more research is needed to fully understand the role of avian skin coloration in influencing solar heat loads and the

metabolic cost of maintaining a constant body temperature. Studies of the thermal effects of skin coloration should not only consider the darkness of the skin but also the density and colour of the overlying plumage.

## THERMAL EFFECTS OF WING COLORATION ON FLIGHT PERFORMANCE

The differential heating of feather surfaces under solar radiation may have further implications for flight efficiency. Flight is one of the most costly forms of animal locomotion (Guigueno *et al.* 2019). Costs, however, differ significantly with the flight mode applied. For instance, gliding flight is relatively cheap compared with active flapping flight (Norberg 1990). Surprisingly, the Andean Condor *Vultur gryphus*, which weighs up to 16 kg, has among the lowest movement costs among vertebrates because it relies mainly on soaring flight, only flapping for about 1% of its flight time (Williams *et al.* 2020). Despite flapping flight being the most expensive method of locomotion with regard to rate of energy expenditure, it allows speeds up to 10 times greater than on the ground (Alerstam 1991). Bearing this in mind, the costs of transport are reasonably low, enabling birds to cover extremely long distances during migration (Alerstam 1991). Indeed, the highest costs that a bird must overcome during flight are probably those during take-off and landing (Shepard *et al.* 2019, Williams *et al.* 2020).

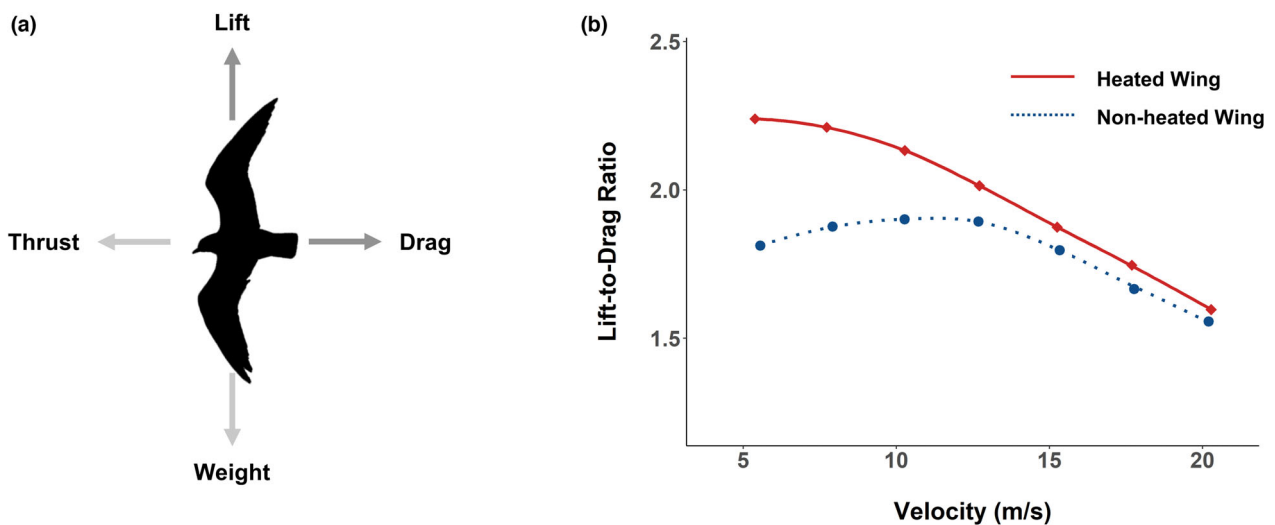
At least four forces apply to a flying bird: the bird's own body weight imposed by gravity, which it opposes by generating lift with its wings; and the drag opposite to the flight direction, which it overcomes by applying thrust (Fig. 5a; Pennycuik 2008). The ratio between lift and drag is also referred to as flight efficiency (Pennycuik 2008). Every reduction in drag or increase in lift can therefore improve the flight efficiency of a bird. Larger wing surfaces, for example, can increase lift (Tobalske 2007), while a streamlined body reduces drag (Pennycuik *et al.* 1988). Recent studies have suggested that wing surface heating under solar radiation could affect the lift-to-drag ratio of a flying bird and that this effect would be stronger in hotter, dark-winged birds (Hassanalian *et al.* 2017, 2018a, 2018b, 2019, Rogalla *et al.* 2019). Based on theoretical approaches, Hassanalian

*et al.* (2018a, 2018b) predicted a drag reduction correlated with surface temperature increases in bird wings. Heating experiments on different aerofoil shapes resulted in efficiency increases for some, but not all, shapes (Hassanalian *et al.* 2019). However, birds morph their wings to stabilize their flight, so wing shape not only differs between species but can be further adjusted to different flight conditions (Lentink *et al.* 2007, Harvey *et al.* 2019, Matloff *et al.* 2020). Temperature measurements on dried bird wings under simulated gliding flight conditions showed that darker wings consistently became hotter than pale wings, but that surface temperatures decreased with increasing flight velocity (Rogalla *et al.* 2019). Expanding on these findings, force measurements on bird wings revealed that surface heating of stuffed wings increases the ratio between lift and drag; in other words, this improves wing flight efficiency (Fig. 5b) (Rogalla *et al.* 2021b). However, this effect decreases with increasing flight velocities as wing surface temperatures drop (Fig. 5b) (Rogalla *et al.* 2021b).

Although only a few studies have explored the effects of feather surface heating on bird flight efficiency, in aeronautics thermal effects on flight efficiency are well studied. In multiple cases, heating of the upper surface of an aerofoil resulted in a decrease in friction drag, which was associated with a delay in the boundary layer transition

(Schmid & Selberg 1992, 1993, Kramer *et al.* 1999, Bushnell 2003) and might be caused by a decrease in air density and an increase in viscosity in the heated boundary layer (Kramer *et al.* 1999).

Interestingly, increases in flight efficiency in heated bird wings were larger at higher angles of attack (Rogalla *et al.* 2021b). During gliding flight, the angle of attack of the wings is relatively low (ca. 5–8 degrees) (Parrott 1970, Tucker & Parrott 1970), and, if the bird is flapping, its advance ratio (flight speed divided by wingtip speed) is high (Chin & Lentink 2016). It is reasonable to expect skin friction drag to be significant in such circumstances, and maintaining attached flow (i.e. avoiding boundary layer separation) could be particularly important, for example, to avoid stall during a manoeuvre or when encountering turbulence. In contrast, flow separation (i.e. stalling) is common during landing (Lee *et al.* 2015), and a potential key to avian flapping flight at low speeds may be dynamic stall (i.e. leading-edge vortices attached to the upper surface of the wing) (Pesavento & Wang 2009). In these cases, wings are used at a high angle of attack, the advance ratio is low, and drag about the wing is probably dominated by pressure due to the form of the wing rather than friction drag (Withers 1981, Usherwood 2010). Our present understanding of avian flight makes it relatively straightforward to predict



**Figure 5.** (a) Forces on a flying bird. Drag is directed opposite to the flight direction and is opposed by thrust, while lift is directed perpendicular to the flight direction and opposes the body weight imposed by gravity. (b) Lift-to-drag ratio increases for a heated wing (here shown for an angle of attack of 10°). Figure 5b was modified from Rogalla *et al.* (2021b).



drag reduction due to certain coloration if the bird is gliding (as shown in Rogalla *et al.* 2021b) or flapping at a relatively fast speed under high solar irradiance. In the case of flapping birds, where wings are not continuously exposed to the sun, the low thermal inertia of feathers (Tattersall *et al.* 2018) and instantaneous heating of feather surfaces with radiant heat exposure (Rogalla *et al.* 2019, 2021a) might still facilitate an increase in flight efficiency. In line with this hypothesis, a recent phylogenetic analysis showed that seabird wing coloration is associated with glide performance but found no effect of flight mode (Rogalla *et al.* 2021b). Another recent study on gulls, which rely mostly on powered flapping flight, has further shown that dark wing coloration was positively correlated with solar irradiance and that long-distance migrants had a greater proportion of black on their wingtips than short-distance migrants (Dufour *et al.* 2020), suggesting that these birds might benefit from the efficiency increase. However, the complex aerodynamics of slow-speed flapping, particularly during take-off and landing, mean that specific predictions are less clear. Indeed, it would be an interesting avenue for future research given the high energetic costs that are associated with take-off and landing. Additionally, research is needed to test the thermal effects of wing coloration on flight efficiency in a wider set of species, specifically focusing on the role of wing shape. Future work would further benefit from experimental tests using live birds flying under a heat source to perform flow characterizations and pressure distribution measurements.

### ECOLOGICAL RELEVANCE OF FUNCTIONAL PLUMAGE COLORATION

There is increasing evidence from comparative studies that colour-mediated thermal effects shape the evolution of plumage colour and that these effects can explain distribution patterns of colour variations both within and between species (Fargallo *et al.* 2018, Galván *et al.* 2018, Dufour *et al.* 2020). For example, birds with darker plumage in Spain are restricted to colder and less insolated environments than species with lighter plumage (Galván *et al.* 2018) and in Griffon Vultures *Gyps fulvus*, individuals fledged from nests that are more exposed to sunlight develop paler plumages (Fargallo *et al.* 2018). Future scenarios

predict that animals living in regions where the climate will become hotter and drier should evolve lighter coloration as a response to climate change (Delhey *et al.* 2020). Interestingly, in gulls a darker mantle coloration is positively correlated with solar irradiance and negatively with air temperature (Dufour *et al.* 2020), which may not only affect thermoregulation but might further improve flight performance (Rogalla *et al.* 2021b). Indeed, seabird wing coloration might have in part evolved to enhance flight under the extreme ocean conditions (Rogalla *et al.* 2021b). On the other hand, species that travel longer distances during migration have a lighter coloured body suggesting a thermoregulatory function of plumage colour during flight (Delhey *et al.* 2021). Future research may unveil the interaction between body colour and wing colour to test the hypothesis that dark-coloured wings have evolved to optimize flight performance, while light-coloured bodies might have evolved to compensate for additional thermoregulatory costs when flying under the sun.

### CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Colour-induced temperature differences in feather surfaces can have a significant impact on a bird's energy budget. In the cold, higher heat loads can reduce the metabolic costs of maintaining a constant body temperature, whereas under high ambient temperatures they may result in an additional cost to thermoregulation. Furthermore, wing surface heating might reduce the energetic costs of flight by improving the lift-to-drag ratio on the wing. However, many questions remain unanswered, and so we present some perspectives and directions for future research. First, we need a more fundamental understanding of the thermal properties of different colour-producing mechanisms and an integration of the contribution of plumage structural elements and integument on heat dynamics. The thermal properties of iridescent sunbird feathers have recently been described, but these properties remain unknown for nanostructured iridescent colours in other taxa, as well as for non-iridescent structural colours, such as blue. Further, the effects of colour-induced temperature differences on metabolic rates are commonly studied by comparing dark with light colours, in many cases by comparing black with white. To improve our understanding of the effects of a wider colour spectrum on metabolic



rates, specifically at the thermal extremes, more tests should be run on live birds of different colours using metabolic chambers. Additionally, colour- and temperature-dependent effects on flight efficiency so far have only been demonstrated on stuffed bird wings and aerofoils. Whether the higher heating rates of darker wings can improve flight efficiency in live birds remains elusive. The effects of feather surface heating on the flight performance of live birds can be tested both on birds in the wild, using biologging data, and under controlled conditions by using wind tunnel experiments. Exploring the colour- and temperature-dependent effects on flight efficiency in live birds will not only improve our understanding of the importance of colour for a bird's energy budget but will further provide new insights into the factors driving colour evolution in birds.

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## AUTHOR CONTRIBUTIONS

**Svana Rogalla:** Writing – original draft (lead); writing – review and editing (lead). **Matthew D. Shawkey:** Supervision (equal); writing – review and editing (equal). **Liliana D'Alba:** Supervision (equal); writing – review and editing (equal).

## Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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