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PERSPECTIVE

Visual Ecology in Challenging Environments

A call to integrate non-visual functions of pigments and their interactions with visual functions to understand global change impacts on visual systems

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Abstract

1. Animal coloration serves a variety of visually related functions in nature (e.g. mate choice, aposematism and camouflage) but the pigments in integumentary tissues such as skin, scales and feathers may also serve functions unrelated to the visual environment (e.g. temperature regulation, detoxification and pollutant protection). Our understanding of the significance of the non-visual functions of animal integumentary pigments, as well as how they interact with the visually related functions to shape animal visual systems, remains limited.
2. Furthermore, due to their important roles in shaping species interactions and mediating interactions in the environment, animal colour traits are likely to be impacted by global change (e.g. increased temperatures, altered habitat quality and quantity, increased environmental stochasticity, pollutants and novel species assemblages).
3. Considering the effects of global change on both visual and non-visual functions is important for understanding whether the selection is acting directly on the pigment or on coloration. Since changing the trait distributions can then lead to changes in visual systems, we advocate for studies to consider all potential functions of integumentary pigments, both visual and non-visual functions and their interaction.
4. Towards this goal, we first highlight common functions of pigments with a focus on non-visual functions across animal systems. Then we synthesize our current understanding of how global change can impact pigmentation and discuss factors that can modify the interactions between climate change and pigment function. Lastly, we discuss how changes in colour traits can impact visual systems and provide an example using amphibians and their responses to climate change as a model.

KEYWORDS
antioxidation, carotenoid, coloration, global change, melanin, pigment, selective pressure, thermoregulation

1 | INTRODUCTION

Vision plays a central role in the ecology of many organisms, shaping the outcomes of their interactions with each other and the environment (e.g. predator–prey; host–parasite). The evolution of visual systems is impacted by variation in visual traits (e.g. coloration; Endler et al., 2005), which can have signalling roles but which may also have *non-signalling functions* that have significant and synergistic effects (Koneru & Caro, 2022). Importantly, animal coloration, which derives from diverse pigments and structures and is shaped by numerous biotic and abiotic factors, occurs in both integumentary structures (i.e. skin, fur, feathers, beaks, scales and shells), and non-integumentary structures (i.e. inner organs and blood; Hill & McGraw, 2006). Because integumentary structures are the component that interacts directly with the environment, this is the tissue that is most likely to have an impact on the evolution of visual systems and is thus the focus of this perspective. To date, substantial progress has been made on our understanding of how organisms detect visual cues including the precise estimations of colour vision and visual capabilities (e.g. Maia et al., 2019; van den Berg et al., 2020; Vorobyev & Osorio, 1998) and how specific visual systems may be influenced by their environments (e.g. Endler, 1992; Härer et al., 2018; Leal & Fleishman, 2002). However, given the range of pigmented integumentary tissues that occur in nature (Figure 1), there is still much to learn about the non-visual functional significance of these pigments and how they may subsequently influence visual systems, particularly as global change alters selective landscapes (Koneru & Caro, 2022; Rojas, 2016).

As human impacts increase, natural ecosystems are expected to face a diversity of pressures associated with environmental change (i.e. pollutants and habitat alteration) that may influence pigmentation and coloration (Delhey & Peters, 2017; Koneru & Caro, 2022). Increased extreme temperature variability associated with global climate change may decouple coevolved pigment and pattern relationships leading to important functional and ecological consequences. For example, heat and cold shocks during butterfly development have been shown to uncouple pigments from pattern formation in adults, resulting in potentially maladaptive displays (Connahs et al., 2016). Similarly, artificial light at night can change amphibian coloration and, importantly, the ability for some amphibian species to match their backgrounds (Horn et al., 2023). An important limitation in our understanding of how environmental change influences visual ecology is that research tends to consider cases where colour is a trait that performs a known function, such as when it is used for communication, camouflage or thermoregulation (e.g. Delhey & Peters, 2017; Zimova et al., 2016). In these cases, selective pressures act directly on coloration (Figure 2). In contrast, while relevant to animal fitness and survival, the effects of the environmental change on pigments with functions such as antioxidation, support and physical protection have rarely been considered. The physiology, complex nature and functional obscurity of many pigments often prevent evolutionary ecologists from incorporating this information into studies of coloration. In this perspective piece, we argue for the need to consider the myriad functions of pigments themselves when making predictions about species' responses to global change, and the subsequent impacts on visual systems, because the functional significance of the pigment will determine which traits selection affects (Figure 2). Despite the past research bias towards visually adaptive signals, it is important to acknowledge that there are likely many unknown non-visual roles and synergistic effects of pigments involved in organismal responses to global change.

To address these gaps in our understanding of the functions of pigmentation and coloration, and their subsequent impacts on visual systems in the face of global change (defined as any human-induced environmental change), we will (1) summarize the main functions pigments can have in integument with a focus on non-visual roles, (2) provide an overview of how global change could impact coloration and pigmentation, (3) discuss some of the known modifiers between pigment functions and their interactions with global change and (4) connect these changes in colour traits to possible subsequent visual system evolution. Though both structural elements and pigments contribute to animal coloration (Figure 2), we focus here on pigments. Throughout this perspective, we highlight select examples that illustrate exciting directions in coloration research and where possible, we point the reader towards useful and insightful reviews.

2 | FUNCTIONS OF PIGMENTS IN INTEGUMENT

Pigments in animal integument have numerous roles with often diametrical selective pressures (Cuthill et al., 2017). Thus, sexually selected signals can experience trade-offs with colours used for camouflage, and signalling functions also can be constrained by non-signalling functions. For example, melanin is an important thermoregulator for lepidopterans that allows them to warm up faster and fly for longer distances and durations (Davis et al., 2005; Hegna et al., 2013). However, in species like the wood tiger moth (Figure 1b), pigments that create warning coloration trade-off with melanin used for thermoregulation, such that individuals with more melanin are more likely to be predated (Hegna et al., 2013). We briefly summarize below the known functions of pigments in animal integument, with an emphasis on the understudied non-visual functions.

2.1 | Communication and camouflage

A vast majority of the literature on animal coloration has been devoted to determining the information content and intended receiver of a particular display or ornament (Cuthill et al., 2017). Briefly, signals convey information about an individual to potential mates or conspecifics, or signals can be used to generate unique patterns that allow for individual recognition by conspecifics (Laidre & Johnstone, 2013; Price, 2006). Antipredatory signals may be formed by contrasting colours that indicate toxicity or noxious behaviour

FIGURE 1 Pigments are used to make the wide variety of animal coloration displayed here. Pigments used for signals have to date been given the most attention for the likely impacts of global change on their display. However, many of the pigments above actually have non-visual or unknown functions. (a) The function of the low and high melanin concentrations in the, respectively, light and dark polymorphs of these timber rattlesnakes (*Crotalus horridus*) are unknown. (b) The dark melanins of the wood tiger moth (*Parasemia plantaginis*) aid in thermoregulation but reduce the warning signal created by the contrast between melanins and the yellow colour. (c) The barred owl (*Strix varia*) feather has melanized (dark) and un-pigmented (white) sections. (d) The bright red skin of the northern red salamander (*Pseudotriton ruber*) advertises its toxicity as a part of a Müllerian mimicry group. (e) The blue colour created by biliverdin in these eastern blue bird (*Sialia sialis*) eggs is hypothesized to have a thermoregulatory function in some species because biliverdin reflects near infrared wavelengths. (f) The seemingly obvious orange morph of the brown anole (*Anolis sagrei*) is more cryptic than the brown morph to bird predators. (g) The orange belly of the harlequin toad (*Atelopus aff. franciscus*) has an unknown function. (h) The bright orange colours on the plastron of the painted turtle (*Chrysemys picta*) are attributed to stored carotenoids that may be moved into the bloodstream to counteract oxidative stress during recovery from overwintering stress. (i) The pigmented bib and mask of the common yellowthroat (*Geothlypis trichas*) are used as signals to advertise quality. Photo credits: Julian Avery (a, c, d, e, i), Beth Reinke (f, h), Bibiana Rojas (g), Wikimedia Commons (b: Charles J. Sharp).

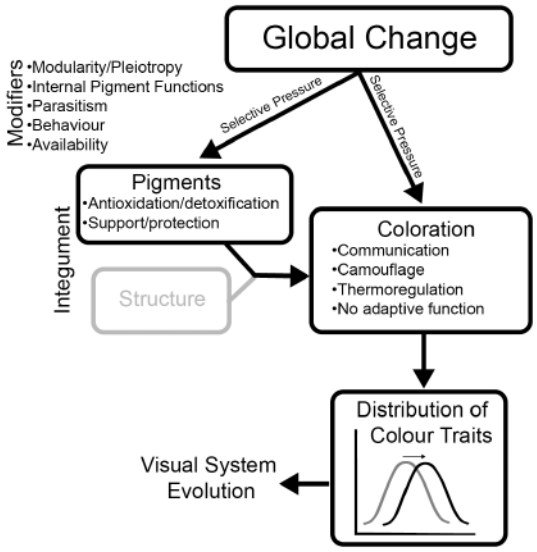

FIGURE 2 Theoretical framework illustrating how global change can impact colour and visual system evolution. Coloration can be made by pigments (specific biomolecules), structure (tissue that differentially reflect wavelengths of light) or a combination of the two. Selection will act on coloration in cases where the colour is used for communication, camouflage or thermoregulation and will act directly on pigments when the pigments are used for antioxidation, detoxification, structural support or protection. The strength and direction of the selective pressure on either or both traits may be altered by the modifiers. Changes to an organism's coloration will then impact the colour trait distribution of the ecosystem, which may also have impacts on visual systems of species within the ecosystem (intended receivers, predators, etc.).

(i.e. aposematism; Poulton, 1890), colours that mimic predators or aposematic organisms, or colours that are suddenly revealed in an attempt to startle predators and prey (i.e. deimatic or startle displays; Cuthill et al., 2017; Schlenoff, 1985).

Camouflage is another potential antipredatory mechanism; colours, colour gradients, and patterns allow for crypsis and masquerade to keep the animal from being detected by predators (Caro, 2011; Stevens & Merilaita, 2011) or parasites (Caro et al., 2014; Côte et al., 2018). Pigments can have a role in crypsis achieved by background matching, disruption or distraction (Caro, 2011; Stevens & Merilaita, 2011). Some organisms can change colours rapidly by changing the density of pigment granules within chromatophores, facilitating the use of colours and patterns to communicate with conspecifics or to camouflage within their environment (Stuart-Fox & Moussalli, 2009). In all of these cases, pigments alone or in combination with structurally created colours can have primary roles in generating the visual signal.

2.2 | Thermoregulation

Other functions of pigments can act independent of visual systems. For instance, though thermoregulation is complex and requires consideration of behaviour, physiology and the structure of the pigment-containing integument, pigments like melanins are well known to have a role in thermoregulation (Karell et al., 2011; Stuart-Fox et al., 2017; Zeuss et al., 2014). The structure of melanin allows for the absorption of many wavelengths of light, making it an ideal thermoregulatory agent in ectotherms and animals in cool regions (Dreiss et al., 2016; Goldenberg et al., 2021; Hegna et al., 2013). As such, many insects have seasonal polyphenisms that are more melanized during cooler seasons, allowing for individuals to maintain an optimal temperature for activity (e.g. Clusella-Trullas et al., 2007; Fields & McNeil, 1988; Kingsolver, 1995). Additionally, a comparative study found support for relationships between both mean annual solar radiation and mean annual temperature and the reflectance of multiple species of lizards (Clusella-Trullas et al., 2008). Darker species were more common in climates with less radiation and cooler temperatures, while lighter species were more common in climates with more radiation and hotter temperatures (Clusella-Trullas et al., 2008). Latitude and substrate type can also influence a range of other ectotherms in less obvious ways; for example, pigmentation on the undersides of snakes and turtles may facilitate heat reflectance or conduction (Goldenberg et al., 2021; Willemsen & Hailey, 1999).

Pheomelanin and eumelanin are the two types of melanin that make reddish-brown and brown-black hues, respectively, and feathers or other integument with these pigments may have different insulative properties, leading to differential winter survival in some polymorphic species (Karell et al., 2011; but see Galván & Solano, 2016). Melanins can be important thermoregulators for mammals as well. In the naked mole rat, melanin in the dermis functions as a thermoregulator to compensate for the lack of fur (Daly & Buffenstein, 1998) and the black skin of polar bears absorbs thermal radiation from scattered light reflected off unique guard hairs despite freezing temperatures (Khattab & Tributsch, 2015).

Pigments besides melanins can also have thermoregulatory functions. In fact, the thermal effect of pigmentation depends more on the absorption of near-infrared wavelengths than on wavelengths in the human visual spectrum (Stuart-Fox et al., 2017), and so pigments that may not appear dark to humans can still be thermoregulators. Protoporphyrins and biliverdins are common pigments in avian eggshells that can provide brown, blue, red and white speckles or shadings in combination with other pigments (Gosler et al., 2005; Kennedy & Vevers, 1953). They reflect in the near-infrared, making them ideal thermoregulatory pigments for ground-nesting bird eggs to avoid overheating from solar radiation (Bakken et al., 1978; though see Westmoreland et al., 2016). Though colour with a thermoregulatory function has to be balanced with pressures imposed by natural or sexual selection (e.g. Hegna et al., 2013), Bakken et al. (1978) proposed that protoporphyrin may be used in eggshells instead of melanin precisely because it can be both cryptic and high near-infrared reflecting. Another integumentary pigment that may have a thermoregulatory role is the haemoglobin in highly vascularized tissues, such as the un-feathered facial tissues of vultures (Negro et al., 2006). Many birds with this type of coloration are large-bodied,

dark-coloured and live in warm climates such that heat may be easily dissipated through the unadorned tissue (Bortolotti, 2006; Negro et al., 2006).

Dark colours allow an animal to absorb solar energy and so the ability to darken quickly allows animals to reach optimal temperatures through increased absorption of solar energy. Conversely, animals that can lighten quickly are able to escape potentially damaging effects of increased temperatures. This type of morphological colour change with temperature is called thermochromy and may be widespread across ectotherms, including animals such as lizards, fishes, crabs and caterpillars (Stuart-Fox & Moussalli, 2009; Umbers et al., 2014). Though several studies have shown differences in temperature obtained by individuals on either end of their intraspecific colour spectrum, it is unknown whether this thermoregulation actually contributes to a fitness advantage in most cases (Umbers et al., 2014). Thermoregulation is not likely to be the only function of pigments in animals with thermochromy (Stuart-Fox & Moussalli, 2009), but in some species, pigment distribution is necessarily temperature-dependent, setting up a potential cost to thermochromy if it is also used for camouflage or communication (Garcia et al., 2003; Walton & Bennett, 1993).

2.3 | Antioxidation/detoxification

All major classes of animal pigments have antioxidant potential as a result of the conjugated bond structure that allows them to absorb certain wavelengths of light (McGraw, 2005). The molecular structure of pigments can also give them the ability to quench free radicals (reviewed in McGraw, 2005). Antioxidants combat reactive oxygen species (ROS) by accepting or donating unpaired electrons to interrupt oxidation–reduction cycles. ROS are produced as a natural by-product of cellular metabolism and are increased in times of high energy demand such as development, reproduction and periods of physiological or environmental stress (Metcalfe & Alonso-Alvarez, 2010). ROS are valuable but highly unstable, and if the levels of ROS overwhelm available antioxidants, oxidative stress can lead to DNA and protein damage that have significant fitness consequences (Monaghan et al., 2009).

In integument, some pigments can prevent/screen solar ultraviolet (UV) radiation when electron transfer is triggered by UV light, shifting the absorbance spectrum, and some pigments can reduce damage from solar UV radiation by quenching dangerous free radicals that are produced by UV (reviewed in Cockell & Knowland, 1999; Krinsky, 1989). Melanin is thought to have a screening role in integument for a taxonomically wide variety of species (Cockell & Knowland, 1999; Galván et al., 2018), and carotenoids have been hypothesized to do the same in some species (Bortolotti, 2006; Cockell & Knowland, 1999), though the relevance of the free radical quenching power of carotenoids has also been demonstrated in animal tissue (Weaver et al., 2018). Melanin is produced in response to UV radiation in humans and some aquatic and marine organisms (Garcia et al., 2003, 2004; Häder et al., 2007; Lowe & Goodman-Lowe, 1996) though it has not yet been determined whether this pigmentation provides a fitness benefit in most cases (Rowland, 2011), and it likely occurs in many other animal groups. Importantly, much is still untested about pigment deposition in animal integuments as an adaptation for UV protection and the biological relevance of pigments as antioxidants other than as UV screens or mitigators in integument is largely unknown, despite McGraw's (2005) review that identified the potential for most pigments to function as antioxidants.

UV light is not the only type of radiation that may be combated by the antioxidation power of pigments. Tree frogs within the Chernobyl Exclusion Zone (10–15 generations after the famous nuclear power plant disaster) were significantly darker than those outside the zone, suggesting selection against light morphs at the time of the explosion (Burraco & Orizaola, 2022). This may be because melanin can protect against ionizing radiation (Burraco & Orizaola, 2022), though this has mostly been investigated in fungi (e.g. Pacelli et al., 2017).

An additional potential role of pigments is to facilitate the removal of endogenous pollutants. Goiran et al. (2017) found that some sea snakes are more likely to be melanistic in polluted aquatic habitats where UV protection or thermoregulation are unlikely to be a driving factor in coloration. They hypothesized that melanized snake skin would contain more trace elements of pollutants from the environment because of melanin's ability to bind internally circulating heavy metals. They were able to demonstrate that dark body portions do hold more pollutants than the light portions on individual animals (Goiran et al., 2017).

2.4 | Structural support and protection from physical damage

Another function of pigments that is especially relevant to the integument is the stabilization of structure and protection from injury or damage. Because of the use of *Drosophila* as a model system in genetics, the development, metabolism and distribution of pigments in insects are relatively well understood (Wittkopp & Beldade, 2009). In insect integument, melanins may be used to strengthen cuticles by cross-linking proteins (Bai et al., 2022; Riley, 1997) and to improve wound healing (Sugumaran, 2002). Gosler et al. (2005) found that protoporphyrins were deposited in calcium-poor portions of avian eggshells and that the amount of protoporphyrin increased as environmental calcium decreased, suggesting that protoporphyrin can have a structural strengthening function as well. The aforementioned infrared reflectance of protoporphyrins and biliverdins may also help prevent water loss in eggshells (Gosler et al., 2005).

Gloger's rule, which states that darker individuals are more common in wet, humid environments and light individuals in dry, arid environments, has been recently supported by a large macroecological study of Passerines (Delhey et al., 2019). Much has

been hypothesized about the mechanism behind Gloger's rule (Delhey, 2017). One of the hypotheses is that animals in wetter environments are more prone to bacterial and microbial degradation and so darker colours (often pigment based) may be an adaptation to deal with these challenges (Burtt & Ichida, 1999), but experiments that have tested the effects of melanin, carotenoids, blue structural colours and psittacofulvins, on bacterial degradation have found conflicting results, and it remains debated in the literature (Cristol et al., 2005; Delhey, 2017; Grande et al., 2004; Gunderson et al., 2016).

2.5 | Non-adaptive

Not all integumentary pigments are necessarily adaptive, but could instead be the result of selection acting on another aspect of phenotype (i.e. see pleiotropy discussion below), intralocus sexual conflict, an evolutionarily neutral mutation or the result of a recent transition where adaptive coloration no longer has relevance (Assis et al., 2022; Wicksten, 1989). However, if the pigment absorption, metabolism, transport or expression likely incurs an energy cost, this is evidence that the pigment may have a functional significance. In some cases, genetic models allow for the direct comparison of pigmented and non-pigmented individuals in order to definitively identify whether and by what mechanism pigments provide fitness benefits (as in Koch et al., 2018). When these types of models are not available, clever experimental designs that make predictions and explicitly test them can be used (as in Smith et al., 2016).

3 | IMPACT OF GLOBAL CHANGE ON COLOUR TRAITS

3.1 | Global change and communication/camouflage

Potential impacts of global change on coloration used for visual signalling associated with communication and camouflage has been reviewed elsewhere (e.g. Delhey & Peters, 2017; Koneru & Caro, 2022) and so will be discussed only in brief here. The light environment affects the efficacy of visual signal transmission, and so the environment in which the organism is displaying plays an important role in the evolution of the signal (Endler, 1992). Both communication and camouflage can be impacted by global change if the background, transmission or irradiance spectra of the environment changes (Delhey & Peters, 2017; Gomez & Théry, 2004). This can have significant effects on species that use colour for mate identification or choice, such as the cichlids of Lake Victoria, where increased turbidity caused by anthropogenic eutrophication resulted in low species diversity and duller colours because of hybridization (Seehausen et al., 1997). Varied environments, such as increased or decreased canopy cover, changes in habitat quality or quantity, or altered turbidity can therefore impact the evolution of colour signals (Cosentino et al., 2017; Goiran et al., 2017; Koneru & Caro, 2022). In some cases, environmental factors such as background albedo or food availability, are strong drivers of coloration (Barzaghi et al., 2022; Sanchez et al., 2019). Furthermore, among species that are chemically defended, coloration can depend on other traits including body size and whether species are nocturnal or diurnal (Roberts et al., 2022).

At broad ecological scales, climate change specifically will result in novel species assemblages through range expansions, local extinctions, phenological shifts and biotic homogenization. These anthropogenic novel species assemblages will lead to new interspecific interactions, all of which have potential to impact animal communication (Williams & Jackson, 2007). In areas where species can adapt to novel competitors without changing habitat use, and in species in which integumentary coloration has a signalling role, character displacement that impacts phenotype may occur when the novel competitor occupies a similar niche. Alternatively, character displacement may facilitate the use of new habitats which could select for differences in the population's signal (Pfennig & Pfennig, 2012). Support for this idea comes from research by Martin et al. (2015) that shows sympatric sets of avian species are more divergent in plumage than allopatric populations, possibly through competition for signalling space. Collectively, these examples underscore the importance of considering the role of global change on colour, as these factors can alter other traits (i.e. size and diel pattern) in a diversity of ways.

3.2 | Global change and thermoregulation

Impacts of global change on the thermoregulation of species with melanin-based pigmentation have been reviewed by Roulin (2014). Specifically, Roulin (2014) highlighted several mechanisms in which climate change could result in shifts in thermoregulation including altered survival of the polymorphs, differential dispersal, varied genetic adaptations and an evolutionary trend towards monomorphism (Roulin, 2014). For species in which thermal energy drives distributional patterns (e.g. dragonflies and butterflies), global change may lead to range contractions of darker species that occupy cooler habitats, and at smaller scales, shifts to covered habitat may occur (Zeuss et al., 2014). The continuous variation in melanin coloration present in many species may act as an agent of evolutionary rescue, allowing for potential adaptation to changing temperatures. In contrast, global change factors may lead to conflict between multiple functions of colour. For instance, while coloration is associated with both thermoregulation and camouflage functions, colour is more commonly adjusted for camouflage functions, suggesting that compromising camouflage may entail a greater potential immediate survival cost (Park et al., 2023; Smith et al., 2016). However, with temperatures expected to rise with climate change, investigating potential shifts in priority between thermoregulation and camouflage functions can shed light on the evolutionary factors shaping colour.

3.3 | Global change and antioxidation/detoxification

Because extreme environments (Storey, 1996), urbanization (Isaksson, 2015) and pollutants (Lushchak, 2011) cause oxidative stress in many species, global change is likely to increase the need for antioxidants. Unfortunately, the long-term impacts of oxidative stress on populations in the wild have yet to be studied thoroughly (Selman et al., 2012) so it is not well understood how species can respond or whether integumentary pigments will have a role in species responses. One anticipated effect of global change is an increase in UV radiation in regions with depleted ozone coverage and minimal cloud coverage (Caldwell et al., 1998; Roulin, 2014). This may increase the selective pressure for UV screening pigments, but again, there has been little to no work addressing this. Similarly, increased pollution may lead to darker phenotypes better suited to sequester contaminants in the integument (Goiran et al., 2017; Martin et al., 2022). While wild populations are well known to exhibit changes in coloration in response to pollution and environmental change (Pacyna et al., 2018; Pérez et al., 2010), the mechanisms leading to these changes and the synergistic role pigments have with circulating antioxidants is an area that warrants further study.

3.4 | Global change and structural support/protection

It is largely unknown how global change may impact pigments used for structure or physical protection. Increasing temperatures could potentially increase selective pressure for pigments in eggs to mitigate water loss but that remains to be tested. Other tissues could be similarly affected by global change, potentially interfering or interacting with Gloger's rule, but these need to be investigated further in order to make meaningful predictions. Because many pigments do have structural roles in the integument, protecting against UV and mechanical damage (Hill & McGraw, 2006), in addition to varied signalling properties, the effects of global change on pigments and their structural roles warrant increased research.

4 | GLOBAL CHANGE MODIFIERS OF PIGMENT FUNCTIONS

For all of the above functions, we considered how global change may impact each pigment function separately. However, pigments are likely to serve multiple functions within integument, which may result in these adaptations counter-acting, enhancing or trading-off with each other. Thus, the many possible functions of a pigment need to be considered when making predictions about how species' visual systems will respond to global change. Because coloration can be impacted by multiple selective pressures, interactions and pleiotropic effects, global change is likely to affect other aspects of organismal biology that then impact pigments or colour and eventually visual system evolution. We briefly summarize some of the factors that can modify the way global change interacts with coloration below. These factors are not meant to be comprehensive, but do present some examples of indirect ways global change may affect colour traits.

4.1 | Modularity and pleiotropy

Global change may impact pigmentation through changes to selective pressures on non-coloration-related traits, either because of modular evolution that links pigmentation tightly with another trait, or through pleiotropic effects. Temperature differences and increased environmental stochasticity induced by global change may specifically affect the genetic modularity of pigments and patterns. For example, heat and cold shock during the development of butterflies has been shown to result in the decoupling of certain pigments and colour patterns, leading to maladaptive phenotypes (Connahs et al., 2016). Other pigments are physiologically modular; for instance, in crustaceans, carotenoids form protein complexes that result in a change in the wavelengths of light that are absorbed (Cheesman et al., 2008; Zagalsky et al., 1990). Any environmental change that impacts proteins may also impact the wavelengths of light that are absorbed, which could have subsequent impacts on colour traits. Another way that global change may impact pigment-based phenotypes is by introducing selective forces that act on another trait or suite of traits, and cause pleiotropic effects that impact pigmentation in indirect or unexpected ways. For instance, mutations in *Rps19* and *Rps20*, which encode ribosomal proteins and cause a suite of trait changes such as reduced body size and erythrocyte count, result in more melanocyte accumulation in the epidermis of mice (McGowan et al., 2008). Changes in environment that alter selective pressures on phenotypes such as these may lead to colour changes. Additionally, pleiotropic effects are one of the possible explanation for selection regimes on colour polymorphisms in the tawny owls that change under different climate conditions, and so will likely also be impacted by global change (Karell et al., 2011). Thus, modularity and pleiotropic effects frequently impact pigment and coloration, and so global change has an even greater chance of having evolutionary consequences for integumentary coloration, and potentially visual systems.

4.2 | Internal pigment functions

Pigments are not confined to integument in many animals and are present in nervous systems, bloodstreams and various organs (Hill, 1992; McGraw, 2005; McGraw et al., 2003). In some cases, pigments are stored in the integument until they are needed elsewhere (Rajasingh et al., 2007). If global change impacts the metabolism, absorption, expression, synthesis or use of pigments and there is a correlation between the internal and integumentary functions, we can expect that pigment-based phenotypes

may be indirectly altered. For example, Reinke et al. (2017) found no signalling function for the carotenoid-based ventral coloration of painted turtles (*Chrysemys picta*). They propose that the pigment may instead be stored ventrally in the integument until it can be mobilized as a circulating antioxidant after periods of freezing and anoxia (Reinke et al., 2017); global change that may affect the length of strength of freezing and anoxic periods could thus impact the selection regime. Similarly, the pink coloration of some salmonids is created by carotenoids that are bound to muscle in the integument and stored until sexual maturity, when they are released into the bloodstream by muscle degradation during spawning to produce Vitamin A (Rajasingh et al., 2007). Global change could affect the physiology and subsequent antioxidant or nutrient demand of either species, which may then have an effect on the coloration in the integument, and subsequently the evolution of the coloration in either system.

4.3 | Parasitism

Climate change is likely to directly impact host–parasite interactions, both for endo- and ecto-parasites (Côte et al., 2018; Hoberg & Brooks, 2007; Møller et al., 2010); this can have a downstream effect on coloration. Endoparasites have been found to inhibit carotenoid expression in birds and fish either directly by inhibiting carotenoid absorption, or indirectly by redirecting carotenoids from integument for antioxidant functions (Blount & McGraw, 2008). This may impact fitness both directly through reduced antioxidant capacity and indirectly by impairing signalling mechanisms that affect mating success. Parasitism can also impact melanin coloration (Jacquin et al., 2011). Due to the known immunoprotective effects of other pigments like pterins (McGraw, 2005), parasitism may also impact their expression in integument, though this has not been well-studied. Coloration can also affect parasitism (e.g. Barber et al., 2001; Côte et al., 2018), such that any of the effects of the environment on coloration described above may also have effects on parasitism and, subsequently, fitness. Global trends indicate that diseases are emerging at unprecedented rates which can induce shifts in integument coloration. Therefore, considering coloration changes with shifting parasitism patterns in response to global change has important evolutionary implications for integumentary coloration, and potentially for visual systems.

4.4 | Behaviour

Many colour signals rely critically on behaviour. For instance, elaborate courtship dances that display colours or ornaments, the unken reflex of amphibians with red ventral sides (Brodie, 1977), or the startle display of praying mantises that reveals bright colours (Maldonado, 1970) all rely on behaviour that could be disrupted or impacted by habitat changes, environmental heterogeneity or novel species interactions (discussed in Boughman et al., 2024). There is also compelling evidence that aquatic species will undergo bathymetric shifts in response to pollution, turbidity or temperature and nutrient degradation, which has implications for the perception of their signals and their ability to find prey and mates in conditions where signal transmission is no longer as effective (i.e. water depth influences wavelength attenuation and the ability of pigments to reflect visible light Caves & Johnsen, 2021).

4.5 | Availability

Pigments that are exogenously obtained through diet or maternal reserves may be impacted by global change that alters their availability or accessibility (reviewed in Koneru & Caro, 2022). For example, McGraw et al. (2001) show how dietary supplementation can influence bird plumage coloration, and they describe new ways in which invasive plant species can bring novel or higher concentrations of pigment, generating individuals and populations that exhibit different coloration.

5 | COLOUR TRAIT DISTRIBUTION IMPACTS ON VISUAL SYSTEMS

The evolution of sensory systems is driven in part by the environment and is the basis for the sensory drive hypothesis of speciation (Price, 2017). Though much of the classic work on visual system evolution has been done in the context of signal processing (e.g. Endler, 1992; Endler et al., 2005), non-signal visual traits are likely to also impact visual systems. For example, if the distribution of the colour of a prey species is affected by pollution, or thermoregulation, or any of the interactions with global change described above, the visual system of predators may also be impacted through time (Caves & Johnsen, 2021). Species that rely upon visual contrast for prey acquisition may undergo selection as light environments or backgrounds shift in response to pollution, rendering their preferred prey or sensory modalities less effective (Caves & Johnsen, 2021; Kelley et al., 2018). Given that the visual system can thus be impacted by the distribution of colour traits, and that how these traits are impacted by global change may be both directly and indirectly impacted by the visual and non-visual functions of the pigments behind them, it is necessary to integrate all functions of pigments in order to understand the impacts on visual system evolution (Figure 2).

6 | FRAMEWORK FOR EVALUATING THE INTERACTIVE FUNCTIONS OF PIGMENTATION IN THE FACE OF GLOBAL CHANGE

In this section, we offer an example framework using amphibians and amphibian responses to climate change as a model for how

to evaluate the diverse and interactive functions of pigmentation while also incorporating a global change perspective (Figure 3). This framework to investigate the impacts of global change on non-visual functions of pigments, and ultimately, the evolution of visual systems can be applied to any system by (1) investigating the impact of global change on coloration in that system, (2) assessing how the colour impacts the species ecology or physiology, (3) determining how the environment used by the organism may change based on the colour-related ecology or physiology and (4) hypothesizing how the change in environment use may subsequently impact visual system evolution. This framework inherently considers the diversity of functions of pigments, cohesively evaluates how these diverse functions may be influenced by global change factors and how they may impact visual system evolution, and advocates for the testing of trade-offs between functions of colour under global change conditions. Collectively, as humans modify natural ecosystems, understanding how environmental change influences animal coloration, their associated functions, the evolution of visual systems, and how they interact has important implications to visual ecology and conservation.

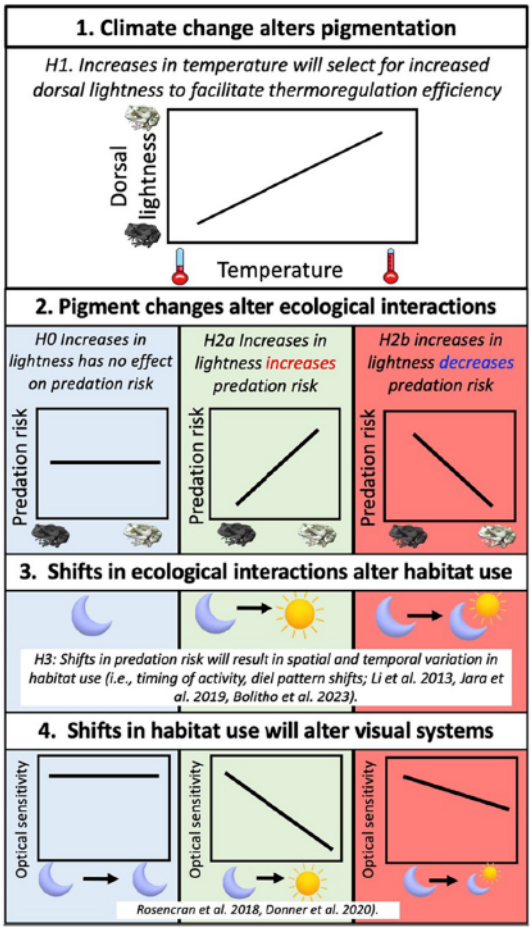

FIGURE 3 Example framework for investigating how climate change induced changes in pigmentation (1) can result in shifts in ecological interactions (2) that alter amphibian habitat use (3), which can ultimately lead to selection for alternative visual systems (4).

7 | CONCLUSION

Most studies of global change and phenotype focus on how environmental changes will impact coloration when colour has a primary visual signalling function, but much remains to be understood about the non-visual functions of pigment and how they may interact with colour and the visual functions. Pigments function in visual communication, camouflage, thermoregulation, antioxidation/detoxification, structural support and protection from damage, and these functions act synergistically to produce the diverse range of phenotypes we observe in animals. This perspective emphasizes that a species' response to global change will be affected by the functions and interactions of colour and pigment that are relevant to that organism, as that will determine which trait selection will impact, and that this has a collective potential effect on the evolution of the visual system (Figure 2). Modularity, pleiotropy, the internally relevant pigment functions, parasitism, behaviour and availability will also contribute to the evolution of phenotypes with global change.

Determining how a visual system may be impacted by global change can require first identifying which of the aforementioned functions are biologically relevant for the integumentary pigments of species who have an evolutionary influence on the visual system. Currently, no studies have been conducted on the impact of global change on the selective pressures affecting pigments that are used for antioxidation, structure or support despite their likely interactions with colour and visual signals. Understanding variation in pigment and coloration with respect to environmental variables will allow us to predict coloration changes, which will ultimately improve our ability to predict and forecast species range distributions, determine best management practices and design the most effective conservation targets.

AUTHOR CONTRIBUTIONS

Beth A. Reinke and Julian D. Avery conceived of the ideas and wrote the first draft. Jessica Hua wrote and designed the framework section and significantly revised the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

There are no data in this perspectives piece.

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REFERENCES

Assis, B. A., Avery, J. D., Earley, R. L., & Langkilde, T. (2022). Fitness costs of maternal ornaments and prenatal corticosterone manifest as reduced offspring survival and sexual ornament expression. *Frontiers in Endocrinology*, *13*, 801834. https://doi.org/10.3389/fendo.2022.801834

Bai, T.-T., Pei, X.-J., Liu, T.-X., Fan, Y.-L., & Zhang, S.-Z. (2022). Melanin synthesis genes BgTH and BgDdc affect body color and cuticle permeability in *Blattella germanica*. *Insect Science*, *29*(6), 1552–1568. https://doi.org/10.1111/1744-7917.13024

Bakken, G. S., Vanderbilt, V. C., Buttemer, W. A., & Dawson, W. R. (1978). Avian eggs: Thermoregulatory value of very high near-infrared reflectance. *Science*, *200*(4339), 321–323. https://doi.org/10.1126/science.200.4339.321

Barber, I., Arnott, S. A., Braithwaite, V. A., Andrew, J., & Huntingford, F. A. (2001). Indirect fitness consequences of mate choice in sticklebacks: Offspring of brighter males grow slowly but resist parasitic infections. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1462), 71–76. https://doi.org/10.1098/rspb.2000.1331

Barzaghi, B., Melotto, A., Cogliati, P., Manenti, R., & Ficetola, G. F. (2022). Factors determining the dorsal coloration pattern of aposematic salamanders. *Scientific Reports*, *12*(1), 17090. https://doi.org/10.1038/s41598-022-19466-0

Blount, J. D., & McGraw, K. J. (2008). Signal functions of carotenoid colouration. *Carotenoids*, *4*, 213–236. https://doi.org/10.1007/978-3-7643-7499-0

Bortolotti, G. R. (2006). Natural selection and coloration: Protection, concealment, advertisement, or deception? In G. E. Hill & K. J. Mcgraw (Eds.), *Bird coloration. Volume 2: Function and evolution* (pp. 3–35). Harvard University Press.

Boughman, J. W., Brand, J. A., Brooks, R. C., Bonduriansky, R., & Wong, B. B. M. (2024). Sexual selection and speciation in the Anthropocene. *Trends in Ecology & Evolution*, *39*, 654–665. https://doi.org/10.1016/j.tree.2024.02.005

Brodie, E. D. (1977). Salamander antipredator postures. *Copeia*, *1977*(3), 523–535.

Burraco, P., & Orizaola, G. (2022). Ionizing radiation and melanism in Chornobyl tree frogs. *Evolutionary Applications*, *15*(9), 1469–1479. https://doi.org/10.1111/eva.13476

Burtt, E. H., & Ichida, J. (1999). Occurrence of feather-degrading bacilli in the plumage of birds. *The Auk*, *116*(2), 364–372. https://doi.org/10.2307/4089371

Caldwell, M. M., Bjorn, L. O., Bornman, J. F., Flint, S. D., Kulandaivelu, G., Teramura, A. H., & Tevini, M. (1998). Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology B: Biology*, *46*, 40–52. https://doi.org/10.1016/S1011-1344(98)00184-5

Caro, T. (2011). The functions of black-and-white colouration in mammals. In M. Stevens & S. Merilaita (Eds.), *Animal camouflage: Mechanisms and function* (pp. 298–329). Cambridge University Press.

Caro, T., Izzo, A., Reiner, R. C., Walker, H., & Stankowich, T. (2014). The function of zebra stripes. *Nature Communications*, *5*, 3535. https://doi.org/10.1038/ncomms4535

Caves, E. M., & Johnsen, S. (2021). The sensory impacts of climate change: Bathymetric shifts and visually mediated interactions in aquatic species. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1949), 20210396. https://doi.org/10.1098/rspb.2021.0396

Cheesman, D. F., Lee, W. L., & Zagalsky, P. F. (2008). Carotenoproteins in invertebrates. *Biological Reviews*, *42*(1), 131–160. https://doi.org/10.1111/j.1469-185x.1967.tb01343.x

Clusella-Trullas, S., Terblanche, J. S., Blackburn, T. M., & Chown, S. L. (2008). Testing the thermal melanism hypothesis: A macrophysiological approach. *Functional Ecology*, *22*(2), 232–238. https://doi.org/10.1111/j.1365-2435.2007.01377.x

Clusella-Trullas, S., van Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, *32*(5), 235–245. https://doi.org/10.1016/j.jtherbio.2007.01.013

Cockell, C. S., & Knowland, J. (1999). Ultraviolet radiation screening compounds. *Biological Reviews*, *74*(3), 311–345. https://doi.org/10.1111/j.1469-185X.1999.tb00189.x

Connahs, H., Rhen, T., & Simmons, R. B. (2016). Physiological perturbation reveals modularity of eyespot development in the painted lady butterfly, *Vanessa cardui*. *PLoS One*, *11*(8), e0161745. https://doi.org/10.1371/journal.pone.0161745

Cosentino, B. J., Moore, J.-D., Karraker, N. E., Ouellet, M., & Gibbs, J. P. (2017). Evolutionary response to global change: Climate and land use interact to shape color polymorphism in a woodland salamander. *Ecology and Evolution*, *7*(14), 5426–5434. https://doi.org/10.1002/ece3.3118

Côte, J., Boniface, A., Blanchet, S., Hendry, A. P., Gasparini, J., & Jacquin, L. (2018). Melanin-based coloration and host–parasite interactions under global change. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1879), 20180285. https://doi.org/10.1098/rspb.2018.0285

Cristol, D. A., Armstrong, J. L., Whitaker, J. M., & Forsyth, M. H. (2005). Feather-degrading bacteria do not affect feathers on captive birds. *The Auk*, *122*(1), 222–230.

Cuthill, I. C., Caspers, B., Mappes, J., Rowland, H. M., Cuthill, I. C., Allen, W. L., Arbuckle, K., & Caspers, B. (2017). The biology of color. *Science*, *357*, eaan0221. https://doi.org/10.1126/science.aan0221

Daly, T. J. M., & Buffenstein, R. (1998). Skin morphology and its role in thermoregulation in mole-rats, *Heterocephalus glaber* and *Cryptomys hottentotus*. *Journal of Anatomy*, *193*(4), 495–502. https://doi.org/10.1046/j.1469-7580.1998.19340495.x

Davis, A. K., Farrey, B. D., & Altizer, S. (2005). Variation in thermally induced melanism in monarch butterflies (Lepidoptera: Nymphalidae) from three North American populations. *Journal of Thermal Biology*, *30*(5), 410–421. https://doi.org/10.1016/j.jtherbio.2005.04.003

Delhey, K. (2017). Quick guide: Gloger's rule. *Current Biology*, *27*(14), R689–R691. https://doi.org/10.1016/j.cub.2017.04.031

Delhey, K., Dale, J., Valcu, M., & Kempenaers, B. (2019). Reconciling ecogeographical rules: Rainfall and temperature predict global colour variation in the largest bird radiation. *Ecology Letters*, *22*, 726–736.

Delhey, K., & Peters, A. (2017). Conservation implications of anthropogenic impacts on visual communication and camouflage. *Conservation Biology*, *31*(1), 30–39. https://doi.org/10.1111/cobi.12834

Dreiss, A. N., Séchaud, R., Béziers, P., Villain, N., Genoud, M., Almasi, B., Jenni, L., & Roulin, A. (2016). Social huddling and physiological thermoregulation are related to melanism in the nocturnal barn owl. *Oecologia*, *180*(2), 371–381. https://doi.org/10.1007/s00442-015-3491-3

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, *139*, S125–S153.

Endler, J. A., Westcott, D. A., Madden, J. R., & Robson, T. (2005). Animal visual systems and the evolution of color patterns: Sensory processing illuminates signal evolution. *Evolution*, *59*(8), 1795–1818. https://doi.org/10.1554/04-669.1

Fields, P. G., & McNeil, J. N. (1988). The importance of seasonal variation in hair coloration for thermoregulation of *Ctenucha virginica* larvae (Lepidoptera: Arctiidae). *Physiological Entomology*, *13*(2), 165–175. https://doi.org/10.1111/j.1365-3032.1988.tb00920.x

Galván, I., Rodríguez-Martínez, S., & Carrascal, L. M. (2018). Dark pigmentation limits thermal niche position in birds. *Functional Ecology*, *32*(6), 1531–1540. https://doi.org/10.1111/1365-2435.13094

Galván, I., & Solano, F. (2016). Bird integumentary melanins: Biosynthesis, forms, function and evolution. *International Journal of Molecular Sciences*, *17*(4), 520. https://doi.org/10.3390/ijms17040520

Garcia, T. S., Stacy, J., & Sih, A. (2004). Larval salamander response to UV radiation and predation risk: Color change and microhabitat use. *Ecological Applications*, *14*(4), 1055–1064. https://doi.org/10.1890/02-5288

Garcia, T. S., Straus, R., & Sih, A. (2003). Temperature and ontogenetic effects on color change in the larval salamander species *Ambystoma barbouri* and *Ambystoma texanum*. *Canadian Journal of Zoology*, *81*(4), 710–715. https://doi.org/10.1139/z03-036

Goiran, C., Bustamante, P., & Shine, R. (2017). Industrial melanism in the seasnake *Emydocephalus annulatus*. *Current Biology*, *27*(16), 2510–2513.e2. https://doi.org/10.1016/j.cub.2017.06.073

Goldenberg, J., D'Alba, L., Bisschop, K., Vanthournout, B., & Shawkey, M. D. (2021). Substrate thermal properties influence ventral brightness evolution in ectotherms. *Communications Biology*, *4*(1), 1–10. https://doi.org/10.1038/s42003-020-01524-w

Gomez, D., & Théry, M. (2004). Influence of ambient light on the evolution of colour signals: Comparative analysis of a neotropical rainforest bird community. *Ecology Letters*, *7*(4), 279–284. https://doi.org/10.1111/j.1461-0248.2004.00584.x

Gosler, A. G., Higham, J. P., & Reynolds, S. J. (2005). Why are birds' eggs speckled? *Ecology Letters*, *8*(10), 1105–1113. https://doi.org/10.1111/j.1461-0248.2005.00816.x

Grande, J. M., Negro, J. J., & Torres, M. J. (2004). The evolution of bird plumage colouration: A role for feather-degrading barcteria? *Ardeola*, *51*(2), 375–383.

Gunderson, A. R., Frame, A. M., Swaddle, J. P., Forsyth, M. H., Gunderson, A. R., Frame, A. M., Swaddle, P., Forsyth, M. H., & Behavior, B. (2016). Resistance of melanized feathers to bacterial degradation: Is it really so black and white? *Journal of Avian Biology*, *39*(5), 539–545. https://doi.org/10.1111/j.0908-8857.2008.04413.x

Häder, D. P., Kumar, H. D., Smith, R. C., & Worrest, R. C. (2007). Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. *Photochemical and Photobiological Sciences*, *6*(3), 267–285. https://doi.org/10.1039/b700020k

Härer, A., Meyer, A., & Torres-Dowdall, J. (2018). Convergent phenotypic evolution of the visual system via different molecular routes: How neotropical cichlid fishes adapt to novel light environments. *Evolution Letters*, *2*(4), 341–354. https://doi.org/10.1002/evl3.71

Hegna, R. H., Nokelainen, O., Hegna, J. R., & Mappes, J. (2013). To quiver or to shiver: Increased melanization benefits thermoregulation, but reduces warning signal efficacy in the wood tiger moth. *Proceedings. Biological Sciences/The Royal Society*, *280*(1755), 20122812. https://doi.org/10.1098/rspb.2012.2812

Hill, G. E., & McGraw, K. J. (2006). *Bird coloration* (Vol. *1*). Harvard University Press.

Hill, H. Z. (1992). The function of melanin or six blind people examine an elephant. *BioEssays*, *14*(1), 49–56. https://doi.org/10.1002/bies.950140111

Hoberg, E. P., & Brooks, D. R. (2007). How will global climate change affect parasite-host assemblages? *Trends in Parasitology*, *23*(12). https://doi.org/10.1016/j.pt.2007.08.016

Horn, K., Shidemantle, G., Velasquez, I., Ronan, E., Blackwood, J., Reinke, B. A., & Hua, J. (2023). Evaluating the interactive effects of artificial light at night and background color on tadpole crypsis, background adaptation efficacy, and growth. *Environmental Pollution*, *333*, 122056. https://doi.org/10.1016/j.envpol.2023.122056

Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: A question of evolving, acclimatizing or coping with urban environmental stress. *Functional Ecology*, *29*(7), 913–923. https://doi.org/10.1111/1365-2435.12477

Jacquin, L., Lenouvel, P., Haussy, C., Ducatez, S., & Gasparini, J. (2011). Melanin-based coloration is related to parasite intensity and cellular immune response in an urban free living bird: The feral pigeon *Columba livia*. *Journal of Avian Biology*, *42*(1), 11–15. https://doi.org/10.1111/j.1600-048X.2010.05120.x

Karell, P., Ahola, K., Karstinen, T., Valkama, J., & Brommer, J. E. (2011). Climate change drives microevolution in a wild bird. *Nature Communications*, *2*(1), 207–208. https://doi.org/10.1038/ncomms1213

Kelley, J. L., Chapuis, L., Davies, W. I. L., & Collin, S. P. (2018). Sensory system responses to human-induced environmental change. *Frontiers in Ecology and Evolution*, *6*. https://doi.org/10.3389/fevo.2018.00095

Kennedy, G. Y., & Vevers, H. G. (1953). The biology of *Asterias rubens* L.V. A porphyrin pigment in the integument. *J. Marine Biol. Assoc. United Kingdom*, *32*(1), 235–249. https://doi.org/10.1017/S002531540001153X

Khattab, M. Q., & Tributsch, H. (2015). Fibre-optical light scattering technology in polar bear hair: A re-evaluation and new results. *Journal of Advanced Biotechnology and Bioengineering*, *3*(2), 38–51. https://doi.org/10.12970/2311-1755.2015.03.02.2

Kingsolver, J. G. (1995). Fitness consequences of seasonal polyphenism in western white butterflies. *Evolution*, *49*(5), 942–954. https://doi.org/10.2307/2410416

Koch, R. E., Kavazis, A. N., Hasselquist, D., Hood, W. R., Zhang, Y., Toomey, M. B., & Hill, G. E. (2018). No evidence that carotenoid pigments boost either immune or antioxidant defenses in a songbird. *Nature Communications*, *9*(1), 1–7. https://doi.org/10.1038/s41467-018-02974-x

Koneru, M., & Caro, T. (2022). Animal coloration in the Anthropocene. *Frontiers in Ecology and Evolution*, *10*, 857317. https://doi.org/10.3389/fevo.2022.857317

Krinsky, N. I. (1989). Antioxidant functions of carotenoids. *Free Radical Biology and Medicine*, *7*(6), 617–635. https://doi.org/10.1016/0891-5849(89)90143-3

Laidre, M. E., & Johnstone, R. A. (2013). Animal signals. *Current Biology*, *23*(18), 829–833. https://doi.org/10.1016/j.cub.2013.07.070

Leal, M., & Fleishman, L. J. (2002). Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proceedings of the Royal Society of London B*, *269*, 351–359. https://doi.org/10.1098/rspb.2001.1904

Lowe, C., & Goodman-Lowe, G. (1996). Suntanning in hammerhead sharks. *Nature*, *383*(6602), 677.

Lushchak, V. I. (2011). Environmentally induced oxidative stress in aquatic animals. *Aquatic Toxicology*, *101*(1), 13–30. https://doi.org/10.1016/j.aquatox.2010.10.006

Maia, R., Gruson, H., Endler, J. A., & White, T. E. (2019). pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods in Ecology and Evolution*, *10*(7), 1097–1107. https://doi.org/10.1111/2041-210X.13174

Maldonado, H. (1970). The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Zeitschrift für Vergleichende Physiologie*, *68*(1), 60–71. https://doi.org/10.1007/BF00297812

Martin, J., Recio, P., Rodríguez-Ruiz, G., Barja, I., Gutiérrez, E., & García, L. (2022). Relationships between soil pollution by heavy metals and melanin-dependent coloration of a fossorial amphisbaenian reptile. *Integrative Zoology*, *17*, 596–607. https://doi.org/10.1111/1749-4877.12562

Martin, P. R., Montgomerie, R., & Lougheed, S. C. (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *The American Naturalist*, *185*(4), 443–451. https://doi.org/10.1086/680206

McGowan, K. A., Li, J. Z., Park, C. Y., Beaudry, V., Tabor, H. K., Sabnis, A. J., Zhang, W., Fuchs, H., de Angelis, M. H., Myers, R. M., Attardi, L. D., & Barsh, G. S. (2008). Ribosomal mutations cause p53-mediated dark skin and pleiotropic effects. *Nature Genetics*, *40*(8), 963–970. https://doi.org/10.1038/ng.188

McGraw, K. J. (2005). The antioxidant function of many animal pigments: Are there consistent health benefits of sexually selected colourants? *Animal Behaviour*, *69*(4), 757–764. https://doi.org/10.1016/j.anbehav.2004.06.022

McGraw, K. J., Gregory, A. J., Parker, R. S., & Adkins-Regan, E. (2003). Diet, plasma carotenoids, and sexual coloration in the zebra finch (*Taeniopygia guttata*). *Auk*, *120*(2), 400–410. https://doi.org/10.1642/0004-8038(2003)120[1212:DPCASC]2.0.CO;2

McGraw, K. J., Hill, G. E., Stradi, R., & Parker, R. S. (2001). The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American goldfinches (*Carduelis tristis*) and northern cardinals (*Cardinalis cardinalis*). *Physiological and Biochemical Zoology*, *74*(6), 843–852.

Metcalfe, N. B., & Alonso-Alvarez, C. (2010). Oxidative stress as a life-history constraint: The role of reactive oxygen species in shaping phenotypes from conception to death. *Functional Ecology*, *24*(5), 984–996. https://doi.org/10.1111/j.1365-2435.2010.01750.x

Møller, A. P., Fiedler, W., & Berthold, P. (2010). *Effects of climate change on birds*. Oxford University Press.

Monaghan, P., Metcalfe, N. B., & Torres, R. (2009). Oxidative stress as a mediator of life history trade-offs: Mechanisms, measurements and interpretation. *Ecology Letters*, *12*(1), 75–92. https://doi.org/10.1111/j.1461-0248.2008.01258.x

Negro, J. J., Sarasola, J. H., Fariñas, F., & Zorrilla, I. (2006). Function and occurrence of facial flushing in birds. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *143*(1), 78–84. https://doi.org/10.1016/j.cbpa.2005.10.028

Pacelli, C., Bryan, R. A., Onofri, S., Selbmann, L., Shuryak, I., & Dadachova, E. (2017). Melanin is effective in protecting fast and slow growing fungi from various types of ionizing radiation. *Environmental Microbiology*, *19*(4), 1612–1624. https://doi.org/10.1111/1462-2920.13681

Pacyna, A. D., Ruman, M., Mazerski, J., & Polkowska, Ż. (2018). Biological responses to environmental contamination. How can metal pollution impact signal honesty in avian species? *Ecology and Evolution*, *8*(15), 7733–7739. https://doi.org/10.1002/ece3.4192

Park, C., No, S., Yoo, S., Oh, D., Hwang, Y., Kim, Y., & Kang, C. (2023). Testing multiple hypotheses on the colour change of treefrogs in response to various external conditions. *Scientific Reports*, *13*(1), 4203. https://doi.org/10.1038/s41598-023-31262-y

Pérez, C., Lores, M., & Velando, A. (2010). Oil pollution increases plasma antioxidants but reduces coloration in a seabird. *Oecologia*, *163*(4), 875–884. https://doi.org/10.1007/s00442-010-1677-2

Pfennig, D. W., & Pfennig, K. S. (2012). *Evolution's wedge: Competition and the origins of diversity*. University of California Press.

Poulton, E. B. (1890). *The colours of animals: Their meaning and use, especially considered in the case of insects*. D. Appleton.

Price, T. D. (2006). Phenotypic plasticity, sexual selection and the evolution of colour patterns. *Journal of Experimental Biology*, *209*(12), 2368–2376. https://doi.org/10.1242/jeb.02183

Price, T. D. (2017). Sensory drive, color, and color vision. *The American Naturalist*, *190*(2), 157–170. https://doi.org/10.1086/692535

Rajasingh, H., Våge, D. I., Pavey, S. A., & Omholt, S. W. (2007). Why are salmonids pink? *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(11), 1614–1627. https://doi.org/10.1139/f07-119

Reinke, B. A., Calsbeek, R., & Stuart-Fox, D. (2017). A test of an anti-predatory function of conspicuous plastron coloration in hatchling turtles. *Evolutionary Ecology*, *31*(4), 463–476. https://doi.org/10.1007/s10682-017-9892-5

Riley, P. A. (1997). Melanin. *The International Journal of Biochemistry & Cell Biology*, *29*(11), 1235–1239. https://doi.org/10.1016/S1357-2725(97)00013-7

Roberts, S. M., Stuart-Fox, D., & Medina, I. (2022). The evolution of conspicuousness in frogs: When to signal toxicity? *Journal of Evolutionary Biology*, *35*(11), 1455–1464. https://doi.org/10.1111/jeb.14092

Rojas, B. (2016). Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biological Reviews*, *92*, 1059–1080. https://doi.org/10.1111/brv.12269

Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change. *Global Change Biology*, *20*(11), 3344–3350. https://doi.org/10.1111/gcb.12594

Rowland, H. M. (2011). The history, theory and evidence for cryptic function of countershading. In M. Stevens & S. Merilaita (Eds.), *Animal camouflage: Mechanisms and function* (pp. 53–72). Cambridge University Press.

Sanchez, E., Pröhl, H., Lüddecke, T., Schulz, S., Steinfartz, S., & Vences, M. (2019). The conspicuous postmetamorphic coloration of fire salamanders, but not their toxicity, is affected by larval background albedo. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, *332*(1–2), 26–35. https://doi.org/10.1002/jez.b.22845

Schlenoff, D. H. (1985). The startle responses of blue jays to Catocala (Lepidoptera: Noctuidae) prey models. *Animal Behaviour*, *33*(4), 1057–1067. https://doi.org/10.1016/S0003-3472(85)80164-0

Seehausen, O., van Alphen, J. J., & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, *277*(5333), 1808–1811. https://doi.org/10.1126/science.277.5333.1808

Selman, C., Blount, J. D., Nussey, D. H., & Speakman, J. R. (2012). Oxidative damage, ageing, and life-history evolution: Where now? *Trends in Ecology & Evolution*, *27*(10), 570–577. https://doi.org/10.1016/j.tree.2012.06.006

Smith, K. R., Cadena, V., Endler, J. A., Porter, W. P., Kearney, M. R., & Stuart-Fox, D. (2016). Colour change on different body regions provides thermal and signalling advantages in bearded dragon lizards. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1832), 1–9. https://doi.org/10.1098/rspb.2016.0626

Stevens, M., & Merilaita, S. (2011). Animal camouflage: An introduction. In M. Stevens & S. Merilaita (Eds.), *Animal camouflage* (pp. 1–17). Cambridge University Press.

Storey, K. B. (1996). Oxidative stress: Animal adaptations in nature. *Brazilian Journal of Medical and Biological Research*, *29*, 1715–1733. https://pubmed.ncbi.nlm.nih.gov/9222437/

Stuart-Fox, D., & Moussalli, A. (2009). Camouflage, communication and thermoregulation: Lessons from colour changing organisms. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *364*(1516), 463–470. https://doi.org/10.1098/rstb.2008.0254

Stuart-Fox, D., Newton, E., & Clusella-Trullas, S. (2017). Thermal consequences of colour and near-infrared reflectance. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *372*, 20160345.

Sugumaran, M. (2002). Comparative biochemistry of eumelanogenesis and the protective roles of phenoloxidase and melanin in insects. *Pigment Cell Research/Sponsored by the European Society for Pigment Cell Research and the International Pigment Cell Society*, *15*(1), 2–9. https://doi.org/10.1034/j.1600-0749.2002.00056.x

Umbers, K. D. L., Fabricant, S. A., Gawryszewski, F. M., Seago, A. E., & Herberstein, M. E. (2014). Reversible colour change in Arthropoda. *Biological Reviews*, *89*(4), 820–848. https://doi.org/10.1111/brv.12079

van den Berg, C. P., Troscianko, J., Endler, J. A., Marshall, N. J., & Cheney, K. L. (2020). Quantitative colour pattern analysis (QCPA): A comprehensive framework for the analysis of colour patterns in nature. *Methods in Ecology and Evolution*, *11*(2), 316–332. https://doi.org/10.1111/2041-210X.13328

Vorobyev, M., & Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings. Biological Sciences/The Royal Society*, *265*(1394), 351–358. https://doi.org/10.1098/rspb.1998.0302

Walton, B. M., & Bennett, A. F. (1993). Temperature-dependent color change in Kenyan chameleons. *Physiological Zoology*, *66*(2), 270–287.

Weaver, R. J., Wang, P., Hill, G. E., & Cobine, P. A. (2018). An *in vivo* test of the biologically relevant roles of carotenoids as antioxidants in animals. *Journal of Experimental Biology*, *221*, jeb.183665. https://doi.org/10.1242/jeb.183665

Westmoreland, D., Schmitz, M., & Burns, K. E. (2016). Egg color as an adaptation for thermoregulation. *Journal of Field Ornithology*, *78*(2), 176–183.

Wicksten, M. K. (1989). Why are there bright colors in sessile marine invertebrates? *Bulletin of Marine Science*, *45*(2), 519–530.

Willemsen, R. E., & Hailey, A. (1999). A latitudinal cline of dark plastral pigmentation in the tortoise Testudo hermanni in Greece. *Herpetological Journal*, *9*(3), 125–132.

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475–482. https://doi.org/10.1890/070037

Wittkopp, P. J., & Beldade, P. (2009). Development and evolution of insect pigmentation: Genetic mechanisms and the potential consequences of pleiotropy. *Seminars in Cell and Developmental Biology*, *20*(1), 65–71. https://doi.org/10.1016/j.semcdb.2008.10.002

Zagalsky, P. F., Eliopoulos, E. E., & Findlay, J. B. C. (1990). The architecture of invertebrate carotenoproteins. *Comparative Biochemistry and Physiology—Part B: Biochemistry and Molecular*, *97*(1), 1–18. https://doi.org/10.1016/0305-0491(90)90171-O

Zeuss, D., Brandl, R., Brändle, M., Rahbek, C., & Brunzel, S. (2014). Global warming favours light-coloured insects in Europe. *Nature Communications*, *5*(1), 1–9. https://doi.org/10.1038/ncomms4874

Zimova, M., Mills, L. S., & Nowak, J. J. (2016). High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters*, *19*(3), 299–307. https://doi.org/10.1111/ele.12568

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