

**Current evidence of climate driven colour changes in insects and its impact
on sexual selection**

Md Tangigul Haque¹, Md Kawsar Khan^{1,2#}, Marie E. Herberstein^{1#}

[#] Md Kawsar Khan and Marie E. Herberstein are joint senior author

1. School of Natural Sciences, Macquarie University, NSW-2109, Australia

2. Department of Biology, Chemistry and Pharmacy, Free University Berlin, 14195
Berlin, Germany

Correspondence:

Md Tangigul Haque

School of Natural Sciences

Macquarie University,

NSW-2109, Australia

E-mail: mdtangigul.haque@students.mq.edu.au

23 **Abstract**

24 Insects exhibit diverse colours that play a crucial role in communication that directs inter- and
25 intra-species interactions such as predator-prey interactions and sexual selection.
26 Anthropogenic climate change may impact insects colour expression and consequently their
27 physiology and behaviour. Insects can respond to changing climatic through phenotypic
28 plasticity or genetic modification, however it is unclear how any of the resulting changes in
29 body and wing colour may impact interactions with conspecifics and heterospecific (e.g.,
30 predator, prey, and mate). The aim of this review is to synthesis the current knowledge of the
31 consequences of climate driven colour change on insects. Firstly, we discussed the
32 environmental factors that affect insect colours, and then we outlined the adaptive mechanisms
33 in terms of phenotypic plasticity and microevolutionary response. Secondly, we conducted a
34 systematic review and performed a qualitative analysis to understand how experimental rearing
35 temperature influences insect colouration. Finally, we gave an overview of the beneficial or
36 maladaptive impact of colour change on sexual selection. We concluded by identifying
37 research gaps and highlight potential future research areas.

Introduction

Insects belong to the largest class of invertebrates and play a crucial role in ecosystem (Badejo et al., 2020; Noriega et al., 2018; Folgarait, 1998). They exhibit diverse species specific, population specific and sex-specific body colours and patterns, which can also vary across life stages (Figure 1) (Khan, 2020; Khan & Herberstein, 2020b; Wittkopp & Beldade, 2009). Insects colour originates from the pigments that are deposited underneath the cuticle, or cuticular surface structures, or a combination of both (Chapman & Chapman, 1998). These colours may function in interspecific communication (e.g. aposematism, crypsis including mimicry and camouflage), intraspecific communication (e.g. signalling), thermoregulation and UV-protection (Futahashi, 2020; Figon & Casas, 2018; Caro, 2005; Cott, 1940). For example, a non-territorial damselfly (*Xanthagrion erythroneurum*) undergoes ontogenetic colour change from yellow to red colour after few days of their emergence, which signals sexual maturity but may also have an impact on predation risk (Khan & Herberstein, 2020a). On the other hand, the yellow abdominal stripes in hornets (*Vespa orientalis*) assist in thermoregulation (Plotkin et al., 2009). Appreciating the complexity of body colours and their function is of utmost important in understanding the species specific ecology and evolution (Endler & Mappes, 2017).

Anthropogenic climate change may impact insect in many ways such as phenotypic changes of individuals, genetic, and microevolutionary changes of populations and communities (Larson et al., 2019; Parmesan & Yohe, 2003; Root et al., 2003; Stenseth et al., 2002; Walther et al., 2002; McCarty, 2001; Davis & Shaw, 2001; Hughes, 2000). There are several lines of evidence (temporal, geographical, and experimental studies) that indicate that insect colours vary in response to climatic factors such as temperature and humidity (Lis et al., 2020; Wilts et al., 2019; MacLean et al., 2019; Xing et al., 2018). For example, Zvereva et al., (2019)

observed a declining pattern of dark colour in subarctic leaf beetle morphs (*Chrysomela lapponica*) by experimentally increasing minimum spring temperature. Though climate change may be related to insects colour, the relationship between climate and insect colour is complex as there are several biotic and abiotic factors associated with climate change (reviewed in Clusella-Trullas & Nielsen, 2020).

Evolutionary adaptation to new climatic conditions can bring substantial individual fitness benefits in terms of survivability, but can carry fitness costs in terms of reduced reproductive output through sexual selection (Candolin & Heuschele, 2008). Colour polymorphisms, which refers to the occurrence of two or more discrete colour pattern variants within population, can enhance the adaptability of an individual to a novel environment, resulting in expansion of population geographical ranges and may mitigating population extinction risk (Y. Takahashi & Noriyuki, 2019; Forsman et al., 2016; Wennersten & Forsman, 2012; Forsman et al., 2008). Butterflies and moths, for example, are active flyers who can shift their geographic ranges in response to new environmental conditions (Pöyry et al., 2009; Parmesan et al., 1999). Understanding the selective mechanisms, including the genetic basis of colour polymorphisms, are important for estimating extinction risk under a changing climate (True, 2003).

The aim of this review is to examine the contemporary evidence of insect responses (colour change) against a rapidly changing climate and review the impact of climate driven colour change on sexual selection in insects. First, we provide the current evidence of insect colour change in response to environmental factors (Table 1). Second, we discuss the mechanisms of colour change in insects and finally, we review the impact of colour change on sexual selection in insects (Table 2). We highlighted the current gaps and proposed future directions where further research is required. We believe, our review will provide insights how insects colour

varies across climate and will highlight the ecological and evolutionary consequences of such variations under the rapidly changing climate.

Insect colour: production mechanism and link to environmental factors

Insects exhibit colours mainly in two ways: through pigmentation or structure. Pigments or their precursor can either be synthesised in epidermal cells or extracted from diet (e.g. carotenoids) (Dresp, 2014; Wittkopp & Beldade, 2009). There are eight classes of pigments, namely, melanins, ommochromes, pteridines, tetrapyrroles, carotenoids, flavonoids, papiliochromes, and quinones that are involved in insect colouration (Futahashi & Osanai-Futahashi, 2021). Of these, melanins, ommochromes, and pteridines are the dominant colour pigments in some insects i.e., dragonflies (Futahashi & Osanai-Futahashi, 2021). On the other hand, tetrapyrroles, carotenoids, flavonoids, papiliochromes, and quinones are the main contributors to colour in grasshoppers, aphids, butterflies and moths (Futahashi & Osanai-Futahashi, 2021; Burghardt et al., 2000; Tsuchida, 2016; Stavenga et al., 2014b). Finally, pigments can also contribute to insects structural colours (Yoshioka & Kinoshita, 2006).

Structural colours in insects are the result of light refraction, interference or diffraction caused by photonic structures in the insect integument (Sun et al., 2013; Kemp et al., 2006; Vukusic & Sambles, 2003). Several insect groups such as butterflies, moths and beetles exhibit structural colours (Burg & Parnell, 2018; Stavenga et al., 2018, 2014a; Mason, 2002; Vukusic et al., 2000; Ghiradella et al., 1972). For example, metallic structural colours are common in beetles and are generated by epicuticular multilayer reflectors (McNamara et al., 2012). In addition to pigmentation and structural colour, some insects such as fireflies, beetles, and springtails also produces colour by luciferases, an enzyme capable of producing light in bioluminescence (Viviani, 2002).

The expression of insect colours in terms of quantity and quality can be impacted by environmental factors including temperature, rainfall, and solar radiation (Elith et al., 2010; Cott, 1940). Temperature directly affects insects physiology and pigment production (Hassall & Thompson, 2012). For example, insects in colder environments tend to be darker, as melanin production is greater in colder temperatures (De Souza et al., 2017). The selective advantage of this response to environmental temperature is the conversion of solar radiation to heat allowing greater activity for reproduction and foraging (Clusella Trullas et al., 2007; De Souza et al., 2017). Not surprisingly, solar radiation is an important predictor for colour lightness in insects - geometrid moths become increasingly lighter with increasing solar radiation (Heidrich et al., 2018). However, this pattern is not universal – in pierid butterflies, colour lightness usually decreases with high levels of solar radiation (Stelbrink et al., 2019).

Humidity can also trigger body colour changes in insects, even within the same individual, such as in *Adscita statice*, a green forester moth that changes its colour at dusk and dawn with humidity changes (Wilts et al., 2019). The ambient humidity changes the multilayer refractive index which changes the moth's colour from red to green (Wilts et al., 2019). Moreover, male Hercules beetles, *Dynastes hercules*, change the colour of the elytra from black (at night) to yellowish (in the morning) associated with a humidity shift from high to low (Hinton & Jarman, 1973). There is also evidence that insect melanization increases with decreasing humidity which helps them to reduce cuticular water loss and makes them more resistant to desiccation than less melanized individuals (Parkash et al., 2008). However, results from a selection experiment that selected for darker and lighter phenotypes of *Drosophila melanogaster* over generations found no relationship between desiccation tolerance and colour (Rajpurohit et al., 2016). It is possible that there are other physiological mechanisms that are responsible desiccation tolerance in insects. As might be expected, the response of organisms to

environmental change is complex, highly context-dependent and is shaped by both their physical and biological environments.

Insect colour functions

Insects colour may provide immunological protection, facilitate mimicry, camouflage, thermoregulation and communication (Khan & Herberstein, 2021; Cott, 1940). In terms of immunological protection, darker insect cuticles can increase resistance against pathogens and parasites (Armitage & Siva-Jothy, 2005) because melanin pigment deposited in the insect cuticle plays a significant role in immune reactions, because melanin is a rate limiting molecule of the phenoloxidase cascade (Sugumaran & Barek, 2016; José de Souza et al., 2011; Armitage & Siva-Jothy, 2005; Sugumaran, 2002; Söderhäll & Cerenius, 1998; Neville, 1975).

Colour can be a significant element of camouflage, that includes specific mechanism such as crypsis, disruptive patterning, counter illumination and countershading (Stevens & Merilaita, 2009; Cott, 1940). A common form of animal camouflage is background matching, for example, Morpho dragonfly (*Zenithoptera lanei*) camouflage against the water background through counter-brightness strategies to avoid predators (Cezário et al., 2022). In addition, green lacewings, *Chrysopa* match the green colour of leaves thereby avoiding predation (Edmunds, 2005). Countershading is another form of camouflage. Caterpillars and green grasshoppers improve crypsis by reducing ventral shadow through a paler green colour creating a uniformly green appearance when viewed from the side (Stevens & Ruxton, 2019; Rowland et al., 2008; Evans & Schmidt, 1990). In addition, insects such as eyed hawkmoth (*Smerinthus ocellata*) caterpillar uses reverse countershading strategies (Cott, 1940). Finally, disruptive colouration can also improve camouflage, as is seen in many green grasshoppers, shield bugs

and caterpillars whose disruptive patterns draw the attention of predators away from the overall shape of the insects (Khramov & Chemakos, 2022; Kang et al., 2015; Edmunds, 2005).

Insects also use colours for signalling in the context of individual recognition, warning colouration (aposematism), mate choice and assessment of rivals (Khan & Herberstein, 2021, 2020a; Khan, 2020; Khan & Herberstein, 2020b; Skaldina, 2017; Injaian & Tibbetts, 2014; Tibbetts, 2010; Tibbetts & Dale, 2004; Cott, 1940). For example, some species of *Polistes* wasps and *Pachycondyla villosa* ants recognise individuals by facial colour patterns (Sheehan et al., 2014; Sheehan & Tibbetts, 2009; D'Ettorre & Heinze, 2005). Warning colours typically combine a dark background colour with bright red, orange, yellow or white stripes and spots (Ruxton et al., 2004; Mappes et al., 2005; Cott, 1940). These are often coupled with a secondary defense, such as a toxin, sending an unpalatability signals to predators (Lindström et al., 2004; Cott, 1940). For example, ladybird beetle (*Harmonia axyridis*) pupae signal their unpalatability to predators through their conspicuous black dots against red cuticle warning colouration (Lindstedt et al., 2019). Besides predator-prey interactions, bright colouration can also functions as a warning signal to avoid unwanted mating. For example, pre-reproductive female *Agriocnemis femina* damselflies reduce male mating harassment by the exhibiting a conspicuous red colouration (Khan, 2020).

Colour is an important component in mimicry, where the resemblance to another species carries a selective advantage. In Mullerian mimicry, several toxic and unpalatable species converge in their warning colours deterring a shared predator. Iconic Mullerian mimics include the Amazonian butterfly, *Heliconius numata*, which exhibited different patterns of tiger mimicry (Llaurens et al., 2014; Joron, 2009), Batesian mimics on the other hand, are not toxic but mimic an unpalatable species, gaining protection without the cost of producing a toxin. Species such

as viceroy butterflies, hoverflies, striped beetles, diurnal moths and crane flies are perfectly palatable Batesian mimics of monarch butterfly, wasps and bees, respectively (Thompson & Jiggins, 2014; Kunte, 2009; Joron, 2009).

Evidence of climate change impact on insect colour

Temporal studies

Insects have been shown to change their colour over time in response to climate change. A long-term study between 1953-2012 on *Colias meadii* butterflies in the USA showed that the wing melanization decreased with increasing temperature during this time period (MacLean et al., 2016). This pattern, however, is not true across space; melanism was studied in the same species, *Colias meadii*, over the same time period at different locations with melanism decreasing with increasing temperature in the Northern Canada but increasing with increasing temperature in southern USA (MacLean et al., 2019).

Another study provided evidence that European butterflies and dragonflies were becoming lighter, less melanized in warmer regions darker species shifted their distribution towards cooler region (Zeuss et al., 2014). A similar survey of the two-spot ladybird beetle, *Adalia bipunctata*, over 25 years showed a decreased frequency of the melanic morph concomitant with an increase of spring temperatures (Brakefield & de Jong, 2011). Similarly, darker morphs of leaf beetles (*Chrysomela lapponica*) were strongly declining with increased minimum spring daily temperatures between 1992 and 2018 (Zvereva et al., 2019). Conversely, the frequency of melanic stick insects (*Timea cristine*) morphs increased in warmer years (Nosil et al., 2018).

Geographic variation

Phenotypic differences across altitude and/or elevation are often used to anticipate how organisms might react to climate change (Fielding et al., 1999). Altitudinal (or elevational) variation is related to colour pattern polymorphism in several insect species (Hodkinson, 2005) whereby, the frequency of melanic morphs increases with altitude (Berry & Willmer, 1986; Hodkinson, 2005). Species, such as spittle bugs *Philaenus spumarius*, dung beetles *Onthophagus proteus*, *Eupteryx* leafhoppers and grasshoppers show increased melanization with altitude (Stanbrook et al., 2021; Guerrucci & Voisin, 1988; Stewart, 1986; Berry & Willmer, 1986; Brakefield & Willmer, 1985). However, in some ladybird beetles (*Adalia bipunctata*) the melanic frequencies decreased with altitude (Scali & Creed, 1975). Similarly, in geometrid moths in China the observation of darker colour moths at higher elevations was not consistent across different study sites (Xing et al., 2018). In addition to melanisms, structural colours that cause a metallic appearance also change with elevation. For example, the metallic colouration in *Oreina sulcata* beetle varies with elevation: green-colour morphs are more frequent at lower elevations, and darker and more reflective metallic morphs at higher elevations (Mikhailov, 2001).

Distributions across different latitudes can also relate to phenotypic variation in insects (Zheng et al., 2015). Variation in colour along latitudinal gradients is still a matter of debate (Gosden et al., 2011; Williams, 2007). Research suggests a bimodal effect of latitude: individuals tend to be darker both at higher latitude (i.e. in colder climates) and lower latitude (in warmer climate), with lighter morph at intermediate latitudes (Stewart, 1986; Watt, 1968; Williams, 2007). For example, *Colias* butterflies possess darker hindwing (undersides) at higher latitude and colder climates as well as lower latitudes and hotter climates (Watt, 1968).

By contrast, some insects are generally darker in colder climates and lighter in warmer climates. For example, *Tectocoris diophthalmus* bugs at temperate and lower latitude sites showed larger patches of blue against a lighter red background compared to subtropical and tropical bugs (Fabricant et al., 2018). On the other hand, in adult swallowtail butterflies (*Sericanus montelus*), males at lower latitudes were more likely to express darker colour than males at higher latitudes (Zheng et al., 2015). Similar result was also found in bumblebees (Williams, 2007).

Experimental evidence of temperature impact on insect colour

Various experimental studies provide support that temperature affects insect colour. For example, in Indian *Drosophila melanogaster*, pigmentation on the thorax and abdomen decreased with increasing temperature (Gibert et al., 1998). Contrary to this result, planthoppers *Saccharosydne procerus* produced darker colours at higher temperatures (Yin et al., 2015). Similarly, male territorial dragonflies, *Pachydiplax longipennis*, produced more dark coloured wing ornamentation when larvae were reared at higher temperature than when larvae were reared at lower temperature (Lis et al., 2020). A controlled rearing experiment in bugs (male *Tectocoris diophthalmus*; male and female *Murgantia histrionica*) also showed that temperature was a significant factor for melanization: individuals reared in lower temperature were darker than the individuals of higher temperature (Sibilia et al., 2018). In addition, a study on monarch larvae (*Danaus plexippus*) colouration showed that when reared in lower temperature the larvae developed greater portion of black and lower portions of white and yellow, compared to larvae reared in warm temperature (Solensky & Larkin, 2003).

Some of the responses to rearing temperature can result in seasonal polymorphism. For example, *Colias* butterflies, *Papilio machaonin*, and *Pontia* butterflies show seasonally

polyphenic traits that can generate various adaptive phenotypes in response to seasonal environmental variation (Kingsolver, 1995). Distinct wing phenotypes are the most common seasonal polyphenism in butterflies that can influence their thermoregulatory ability (Kingsolver, 1987). For example, environmental manipulation such as altering photoperiodic conditions during the larval stage of the white butterfly (*Pontia occidentalis*), resulted in higher melanin on the dorsal forewings and lower melanin on the ventral hindwings of summer individuals compared with spring individuals (Kingsolver, 1995; Kingsolver & Wiernasz, 1991).

Some insects are also able to change colour reversibly with ambient temperature (Umbers et al., 2013; Huang & Reinhard, 2012; O'Farrell, 1964; Key & Day, 1954). In common blue-tail damselflies (*Ischnura heterosticta*), morphs changed their colour partially and reversibly under controlled laboratory conditions: dull green or grey colour under 12°C and bright blue above 15°C (Huang & Reinhard, 2012; O'Farrell, 1964). In addition, male chameleon grasshopper (*Kosciuscola tristis*) also showed rapid reversible colour change under different laboratory conditions- black to turquoise colouration at 10°C, intermediate colouration from 10 to 15°C and turquoise colouration over 25 °C (Umbers et al., 2013, 2013; Umbers, 2011; Key & Day, 1954). The often-opposing results summarized above indicate that the relationship between insect colour and the thermal environment is complex.

To further understand the experimental evidence of temperature impact on insect colour, we performed a systematic review following PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (Moher et al., 2009). We conducted a literature search on 6th September 2023 using Web of Science database. This search was limited to studies that were published between January 2014 and September 2023. We selected keywords (Insect*)

AND (climate change) AND (colour* OR color* OR thermal melanism OR melanin). Our literature search identified a total of 673 articles, which were then screened to 123 articles based on studies that tested the impact of climate change or temperature variation on insects colour. Then, we further scrutinized to nine articles that experimentally tested the impact of rearing temperature on insects colouration. We summarized our exclusion and inclusion criteria of different studies in supplementary Figure 1. Initially, we aimed to quantify data from these studies, however, this was not possible due to a number of reasons, including the unavailability of data in some studies, lack of sample numbers reported, and the use of different units to quantify colour intensity. Hence, we performed a qualitative analysis and found that generally (six out of nine studies), insects showed high pigmentation or darker colour at colder temperature and low pigmentation or lighter colour as temperatures increase. Some studies report conflicting evidence, where temperature associated melanisation was only found in the wing colour of crickets but not in their hindleg. In contrast, two studies found the opposite results - pigmentation increased with increasing temperature. All our finding is summarized in Table-3. In short, just as field studies provided conflicting evidence, experimental manipulation of ambient temperature in insects is equally reporting inconsistent, possibly species-specific results.

Mechanisms: phenotypic plasticity, microevolutionary response

Populations experiencing new selection pressures may respond in three different ways- they may shift to a more suitable habitat, adjust to changing conditions through phenotypic plasticity, or they may adapt to new conditions through population genetic change (Davis et al., 2005; Holt, 1990). The precise mechanism depends on life history traits, dispersal ability, availability of alternative habitats and the rate of continual environmental change (Gienapp et

al., 2008). Sometimes populations combine these responses to climatic change (Davis & Shaw, 2001).

Individuals can change colour with changing environments (such as temperature and humidity changes) or during transitional developmental stages (Khan, 2020; Khan & Herberstein, 2020a; Nijhout, 2010; Rassart et al., 2008; Vigneron et al., 2007). Plasticity of pigmentation is common among insects and can be expressed temporarily or it can be sustained for a longer time (Nijhout, 2010). Plastic responses are more rapid to new conditions than evolutionary responses (Sgrò et al., 2016). In insects, phenotypic plasticity of color can stem from a change in the colour pigment in the epidermis or the cuticle (Nijhout, 2010). For example, RNA interference (RNAi) mediated treatment of yellow mealworm (*Tenebrio molitor*) showed light brownish colour whereas, enzymes deficient in the cuticle tanning pathway resulted darker pigments (Mun et al., 2020). Similarly, swallowtail butterfly (*Papilio xuthus*) displayed black cuticle colour when epidermal cells expressed tyrosine hydroxylase and dopa decarboxylase enzymes whereas they exhibited reddish-brown colour during the epidermal expression of tyrosine hydroxylase, dopa decarboxylase, and ebony enzymes (Futahashi & Fujiwara, 2005). Phenotypic variation of colour can also occurs in different seasons i.e., polyphenism (Nijhout, 2010) and is known in many insect such as moths (*Orgyia antiqua*) (Sandre et al., 2007), narrow-headed ants (*Formica exsecta*) (Putyatina et al., 2022) and butterflies (species belong to tribe Junoniini) (Clarke, 2017).

Phenotypic plasticity provides an important mechanism to adjust to new environmental conditions. The underlying mechanisms are likely to be up and downregulation of the relevant genes. Insects colour is produced by the expressions of genes, for example, in *Colias crocea* butterflies an increased expression of the BarH-1 gene is responsible for the white wing colour

(Woronik et al., 2019). In *Heliconius* butterflies *optix* and *cortex* genes control red and yellow/white wing patterns (Jiggins et al., 2017). Furthermore, in *Ischnura senegalensis* damselfly the expression of *ebony* and *black* genes is responsible for the reddish-brown colour in the thorax of the gynochrome female (Takahashi et al., 2019). The expression of colour producing genes may vary in response to climate change, however, experimental evidence for such changing gene expressions is limited mostly because of the nature and complexity of the genetic basis for colour (Clusella-Trullas & Nielsen, 2020; Daniels et al., 2014; Roulin, 2014). Recent advancement in genetics and genomics now provide platforms to study the impact of climate on insect colour.

It has been argued that phenotypic plasticity, as described above, is unable to provide long-term solutions for populations (Gienapp et al., 2008; Przybylo et al., 2000). Hence, microevolutionary responses are required to cope with continual environmental change over long periods (Davis et al., 2005; Stockwell et al., 2003). While the heritability of melanism is thought to be high (e.g., Roff & Fairbairn, 2013), potentially setting the stage for rapid evolution, insect melanin is associated with several other physiological mechanisms, such as immunity, sexual selection and desiccation, which could potentially counteract adaptive color evolution in response to a warming climate (Clusella-Trullas & Nielsen, 2020).

Impact of colour change on sexual selection

Sexual selection is an important selective force that can improve population fitness, and can accelerate speciation (Cally et al., 2019; Hugall & Stuart-Fox, 2012). Climatic change may impact life history traits and mating systems that subsequently affect the strength or direction of sexual selection (Maan & Seehausen, 2011; Pilakouta & Ålund, 2021). A recent quantitative genetic model showed that the strength of sexual selection may decrease due to rapid climate

change, which reduces the benefits of sexual selection relative to the survival benefits by adapting to new environmental conditions (Martinossi-Alilibert et al., 2019). For example, temperature can determine the outcome of sexual selection by changing reproductive behaviour, such as mate searching, male-female and male-male interactions (García-Roa et al., 2020). Accordingly a study conducted on ambush bugs, *Phymata americana*, showed that sexual dimorphism in colouration caused by temperature could affect the outcome of mate competition as male bugs with relatively darker color patterns had higher mate-searching success in cool ambient temperature (Punzalan et al., 2008).

Physiologically, a warming climate may enhance the fitness of animals living in cooler temperature and higher latitudes whereas increasing temperature is likely to have detrimental consequences on tropical animals (Deutsch et al., 2008). Behaviorally, animals that display sex specific traits to attract mates or intimidate rivals may also be affected by increasing temperature (Moore et al., 2019). For example, in some environments higher temperatures may increase mating opportunity and reproductive output which may result in a cost of sexual signaling if they are more likely to be detected by parasites and predators (Halfwerk et al., 2011; Patricelli & Blickley, 2006; Zuk et al., 2006). In addition, certain sexual signals such as melanized wing interference patterns or patches in *Drosophila* or dragonflies might increase reproductive success but may be physiological detrimental as they increase body temperature under the warming climate (Moore et al., 2021; Katayama et al., 2014; Corbet, 1999). A recent study provided evidence that male dragonflies with higher wing melanization have greater mating success than males with less melanized wings (Moore et al., 2021). However, wing melanization also increased individual body temperature by $>2^{\circ}\text{C}$ (Svensson et al., 2020; Moore et al., 2019; Svensson & Waller, 2013). Such thermal effects may confer modest locomotor benefits in low temperature environments but may reduce flight ability, damage

wing tissue, and cause death in high temperature environments (Svensson et al., 2020; Moore et al., 2019). This impact may be sex specific as females forage at lower temperatures or in shaded micro-habitats (Moore et al., 2021).

Knowledge gaps and proposed future directions

We identified several research gaps for further exploration. First, the impacts of climate on insects colour are derived mostly from long term temporal studies. However, experimental evidence is scarce. A few recent empirical studies demonstrated the consequences of climatic factors on insects colour by manipulating environmental factors, however, those studies were mostly limited to model species with fewer examples from non-model species. This raises the question whether the model-species responses can be extrapolated to other species or taxonomic groups (Zuk et al., 2014). Second, short-term experiments are most likely to detect phenotypic plasticity and in addition, we argue that more long-term experiments over several generations are necessary to understand the potential for evolutionary response. Specifically, the fitness impact of climate change induced colour change in terms of reproduction, survival, predation, and foraging is mostly unknown. Long term studies have the power to identify multiple factors contributing to colour variations in insects and predict the impact of ongoing climate change. Furthermore, there is limited information on the exact genetic and physiological mechanisms resulting in insect colour change. Third, there are possible geographic and sex specific biases in the current literatures due to the limited geographic regions (mostly temperate) where studies recorded the impact of environmental change on sex-specific colour. Clearly, large-scale geographic surveys on both sexes of multiple species can reduce this bias. Fourth, the availability of many advanced techniques such as digital photographs for assessing colour, and computer assisted image analysis software also opens the use of museum specimen that may be too fragile for conventional photospectrometry.

Usage of museum specimens provides further opportunity to understand the temporal trend of insects colour change under the changing climate. The advancement of genomics, bioinformatics and genetics also broaden the scope to understand the genetic mechanism of climate change induced colour change. In conclusion, the effect of global climate change on insects colour can impact physiological functions, intra- and interspecies communication and sexual selection, all of which may contribute to the global decline of insects. We believe monitoring the impact of global climate change on insect traits based on empirical studies will assist the management of biodiversity and environmental sustainability.

Author contributions

All authors conceived the idea and planned the manuscript. TH wrote first draft of the manuscript. MKK and MEH contributed to the writing and editing of the manuscript and supervised the project.

Funding

TH was supported by International Macquarie University Research excellence scholarship (iMQRES).

Acknowledgements

We acknowledge the Wallumattagal clan of the Dharug nation as the traditional custodians of the Macquarie University land.

Conflict of interest

The authors declare no competing interests.

Statement of diversity and inclusion

434 We strongly support equity, diversity and inclusion in science (Röbler et al., 2020). The authors
435 come from different countries (Bangladesh, Austria, and Australia) and represent different
436 career stages (Masters student, Early career researcher, & Professor). One or more of the
437 authors self-identifies as a member of the LGBTQI+ community. One or more authors are from
438 underrepresented ethnic minority in science.
439

References

- Armitage, S. a. O., & Siva-Jothy, M. T. (2005). Immune function responds to selection for cuticular colour in *Tenebrio molitor*. *Heredity*, *94*(6), 650–656.
<https://doi.org/10.1038/sj.hdy.6800675>
- Badejo, O., Skaldina, O., Gilev, A., & Sorvari, J. (2020). Benefits of insect colours: A review from social insect studies. *Oecologia*, *194*(1–2), 27–40.
<https://doi.org/10.1007/s00442-020-04738-1>
- Berry, A. J., & Willmer, P. G. (1986). Temperature and the colour polymorphism of *Philaenus spumarius* (Homoptera: Aphrophoridae). *Ecological Entomology*, *11*(3), 251–259. <https://doi.org/10.1111/j.1365-2311.1986.tb00301.x>
- Brakefield, P. M., & de Jong, P. W. (2011). A steep cline in ladybird melanism has decayed over 25 years: A genetic response to climate change? *Heredity*, *107*(6), 574–578.
<https://doi.org/10.1038/hdy.2011.49>
- Brakefield, P. M., & Willmer, P. G. (1985). The basis of thermal melanism in the ladybird *Adalia bipunctata*: Differences in reflectance and thermal properties between the morphs. *Heredity*, *54*(1), 9–14. <https://doi.org/10.1038/hdy.1985.3>
- Burg, S. L., & Parnell, A. J. (2018). Self-assembling structural colour in nature. *Journal of Physics: Condensed Matter*, *30*(41), 413001. <https://doi.org/10.1088/1361-648X/aadc95>
- Burghardt, F., Knüttel, H., Becker, M., & Fiedler, K. (2000). Flavonoid wing pigments increase attractiveness of female common blue (*Polyommatus icarus*) butterflies to mate-searching males. *Naturwissenschaften*, *87*(7), 304–307.
<https://doi.org/10.1007/s001140050726>

463 Cally, J. G., Stuart-Fox, D., & Holman, L. (2019). Meta-analytic evidence that sexual
 464 selection improves population fitness. *Nature Communications*, 10(1), Article 1.
 465 <https://doi.org/10.1038/s41467-019-10074-7>

466 Candolin, U., & Heuschele, J. (2008). Is sexual selection beneficial during adaptation to
 467 environmental change? *Trends in Ecology & Evolution*, 23(8), 446–452.
 468 <https://doi.org/10.1016/j.tree.2008.04.008>

469 Caro, T. (2005). The Adaptive Significance of Coloration in Mammals. *BioScience*, 55(2),
 470 125–136. [https://doi.org/10.1641/0006-3568\(2005\)055\[0125:TASOCI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0125:TASOCI]2.0.CO;2)

471 Cezário, R. R., Gorb, S. N., & Guillermo-Ferreira, R. (2022). Camouflage by counter-
 472 brightness: The blue wings of Morpho dragonflies *Zenithoptera lanei* (Anisoptera:
 473 Libellulidae) match the water background. *Journal of Zoology*, 317(2), 92–100.
 474 <https://doi.org/10.1111/jzo.12955>

475 Chapman, R. F., & Chapman, R. F. (1998). *The insects: Structure and function*. Cambridge
 476 university press.

477 Clarke, J. W. (2017). Evolutionary Trends in Phenotypic Elements of Seasonal Forms of the
 478 Tribe Junoniini (Lepidoptera: Nymphalidae). In T. Sekimura & H. F. Nijhout (Eds.),
 479 *Diversity and Evolution of Butterfly Wing Patterns: An Integrative Approach* (pp.
 480 239–253). Springer. https://doi.org/10.1007/978-981-10-4956-9_13

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

484 Clusella-Trullas, S., & Nielsen, M. (2020). The evolution of insect body coloration under
 485 changing climates. *Current Opinion in Insect Science*, 41, 25–32.
 486 <https://doi.org/10.1016/j.cois.2020.05.007>

487 Corbet, P. S. (1999). Dragonflies by Philip S. Corbet | Hardcover. *Cornell University Press*.
 488 <https://www.cornellpress.cornell.edu/book/9780801425929/dragonflies/>

489 Cott, H. B. (1940). *Adaptive coloration in animals*. London,: Methuen.
 490 <http://archive.org/details/adaptivecolorati00cott>

491 Daniels, E. V., Murad, R., Mortazavi, A., & Reed, R. D. (2014). Extensive transcriptional
 492 response associated with seasonal plasticity of butterfly wing patterns. *Molecular*
 493 *Ecology*, 23(24), 6123–6134. <https://doi.org/10.1111/mec.12988>

494 Davis, M. B., & Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary
 495 Climate Change. *Science*. <https://doi.org/10.1126/science.292.5517.673>

496 Davis, M. B., Shaw, R. G., & Etterson, J. R. (2005). Evolutionary Responses to Changing
 497 Climate. *Ecology*, 86(7), 1704–1714. <https://doi.org/10.1890/03-0788>

498 De Souza, A. R., Turillazzi, S., Lino-Neto, J., & Santini, G. (2017). Colder environments
 499 may select for darker paper wasps. *Biological Journal of the Linnean Society*, 120(3),
 500 700–704. <https://doi.org/10.1111/bij.12910>

501 D’Ettorre, P., & Heinze, J. (2005). Individual Recognition in Ant Queens. *Current Biology*,
 502 15(23), 2170–2174. <https://doi.org/10.1016/j.cub.2005.10.067>

503 Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D.
 504 C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms
 505 across latitude. *Proceedings of the National Academy of Sciences*, 105(18), 6668–
 506 6672. <https://doi.org/10.1073/pnas.0709472105>

507 Dresp, B. (2014). *On the Role of Colour in the Evolution of Selection Behaviour*.
 508 <https://hal.archives-ouvertes.fr/hal-01064670>

509 Edmunds, M. (2005). Crypsis. In *Encyclopedia of Entomology* (pp. 642–646). Springer
 510 Netherlands. https://doi.org/10.1007/0-306-48380-7_1087

511 Ehrlich, R. L., & Zuk, M. (2019). The role of sex and temperature in melanin-based immune
 512 function. *Canadian Journal of Zoology*, 97(9), 825–832. [https://doi.org/10.1139/cjz-](https://doi.org/10.1139/cjz-2018-0323)
 513 2018-0323
 514 Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species.
 515 *Methods in Ecology and Evolution*, 1(4), 330–342. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2010.00036.x)
 516 210X.2010.00036.x
 517 Ellers, J., & Boggs, C. L. (2004). Functional ecological implications of intraspecific
 518 differences in wing melanization in *Colias* butterflies. *Biological Journal of the*
 519 *Linnean Society*, 82(1), 79–87. <https://doi.org/10.1111/j.1095-8312.2004.00319.x>
 520 Endler, J. A., & Mappes, J. (2017). The current and future state of animal coloration research.
 521 *Philosophical Transactions of the Royal Society of London. Series B, Biological*
 522 *Sciences*, 372(1724), 20160352. <https://doi.org/10.1098/rstb.2016.0352>
 523 Evans, D. L., & Schmidt, J. O. (1990). *Insect Defenses: Adaptive Mechanisms and Strategies*
 524 *of Prey and Predators*. SUNY Press.
 525 Fabricant, S. A., Burdfield-Steel, E. R., Umbers, K., Lowe, E. C., & Herberstein, M. E.
 526 (2018). Warning signal plasticity in hibiscus harlequin bugs. *Evolutionary Ecology*,
 527 32(5), 489–507. <https://doi.org/10.1007/s10682-018-9946-3>
 528 Fedorka, K. M., Lee, V., & Winterhalter, W. E. (2013). Thermal environment shapes cuticle
 529 melanism and melanin-based immunity in the ground cricket *Allonemobius socius*.
 530 *Evolutionary Ecology*, 27(3), 521–531. <https://doi.org/10.1007/s10682-012-9620-0>
 531 Fielding, C. A., Whittaker, J. B., Butterfield, J. E. L., & Coulson, J. C. (1999). Predicting
 532 responses to climate change: The effect of altitude and latitude on the phenology of
 533 the Spittlebug *Neophilaenus lineatus*. *Functional Ecology*, 13(s1), 65–73.
 534 <https://doi.org/10.1046/j.1365-2435.1999.00009.x>

535 Figon, F., & Casas, J. (2018). Morphological and Physiological Colour Changes in the
 536 Animal Kingdom. In *eLS* (pp. 1–11). John Wiley & Sons, Ltd.
 537 <https://doi.org/10.1002/9780470015902.a0028065>

538 Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: A
 539 review. *Biodiversity & Conservation*, 7(9), 1221–1244.
 540 <https://doi.org/10.1023/A:1008891901953>

541 Forsman, A., Ahnesjö, J., Caesar, S., & Karlsson, M. (2008). A Model of Ecological and
 542 Evolutionary Consequences of Color Polymorphism. *Ecology*, 89(1), 34–40.
 543 <https://doi.org/10.1890/07-0572.1>

544 Forsman, A., Betzholtz, P.-E., & Franzén, M. (2016). Faster poleward range shifts in moths
 545 with more variable colour patterns. *Scientific Reports*, 6(1), Article 1.
 546 <https://doi.org/10.1038/srep36265>

547 Futahashi, R. (2020). Diversity of UV Reflection Patterns in Odonata. *Frontiers in Ecology*
 548 *and Evolution*, 8. <https://www.frontiersin.org/article/10.3389/fevo.2020.00201>

549 Futahashi, R., & Fujiwara, H. (2005). Melanin-synthesis enzymes coregulate stage-specific
 550 larval cuticular markings in the swallowtail butterfly, *Papilio xuthus*. *Development*
 551 *Genes and Evolution*, 215(10), 519–529. <https://doi.org/10.1007/s00427-005-0014-y>

552 Futahashi, R., & Osanai-Futahashi, M. (2021). Pigments in Insects. In H. Hashimoto, M.
 553 Goda, R. Futahashi, R. Kelsh, & T. Akiyama (Eds.), *Pigments, Pigment Cells and*
 554 *Pigment Patterns* (pp. 3–43). Springer. https://doi.org/10.1007/978-981-16-1490-3_1

555 García-Roa, R., Garcia-Gonzalez, F., Noble, D. W. A., & Carazo, P. (2020). Temperature as
 556 a modulator of sexual selection. *Biological Reviews*, 95(6), 1607–1629.
 557 <https://doi.org/10.1111/brv.12632>

558 Ghiradella, H., Aneshansley, D., Eisner, T., Silberglied, R. E., & Hinton, H. E. (1972).
 559 Ultraviolet Reflection of a Male Butterfly: Interference Color Caused by Thin-Layer

560 Elaboration of Wing Scales. *Science*, 178(4066), 1214–1217.

561 <https://doi.org/10.1126/science.178.4066.1214>

562 Gibert, P., Moreteau, B., Moreteau, J.-C., Parkash, R., & David, J. R. (1998). Light body

563 pigmentation in indian *Drosophila melanogaster*: A likely adaptation to a hot and arid

564 climate. *Journal of Genetics*, 77(1), 13–20. <https://doi.org/10.1007/BF02933036>

565 Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2008). Climate change and

566 evolution: Disentangling environmental and genetic responses. *Molecular Ecology*,

567 17(1), 167–178. <https://doi.org/10.1111/j.1365-294X.2007.03413.x>

568 Gosden, T. P., STOKS, R., & SVENSSON, E. I. (2011). Range limits, large-scale

569 biogeographic variation, and localized evolutionary dynamics in a polymorphic

570 damselfly. *Biological Journal of the Linnean Society*, 102(4), 775–785.

571 <https://doi.org/10.1111/j.1095-8312.2011.01619.x>

572 Guerrucci, M. A., & Voisin, J. F. (1988). Influence of a new environmental factors on the

573 color morphs of *Chorthippus-parallelus* in massif central (France). *Bulletin de La*

574 *Societe Zoologique de France-Evolution et Zoologie*, 113(1), 65–74.

575 Halfwerk, W., Bot, S., Buikx, J., Velde, M. van der, Komdeur, J., Cate, C. ten, &

576 Slabbekoorn, H. (2011). Low-frequency songs lose their potency in noisy urban

577 conditions. *Proceedings of the National Academy of Sciences*, 108(35), 14549–14554.

578 <https://doi.org/10.1073/pnas.1109091108>

579 Hassall, C., & Thompson, D. J. (2012). The effects of environmental warming on Odonata: A

580 review. *International Journal of Odonatology*.

581 <https://www.tandfonline.com/doi/abs/10.1080/13887890.2008.9748319>

582 Heidrich, L., Friess, N., Fiedler, K., Brändle, M., Hausmann, A., Brandl, R., & Zeuss, D.

583 (2018). The dark side of Lepidoptera: Colour lightness of geometrid moths decreases

584 with increasing latitude. *Global Ecology and Biogeography*, 27(4), 407–416.
585 <https://doi.org/10.1111/geb.12703>

586 Hinton, H. E., & Jarman, G. M. (1973). Physiological colour change in the elytra of the
587 hercules beetle, *Dynastes hercules*. *Journal of Insect Physiology*, 19(3), 533–549.
588 [https://doi.org/10.1016/0022-1910\(73\)90064-4](https://doi.org/10.1016/0022-1910(73)90064-4)

589 Hodgkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and
590 community responses to altitude. *Biological Reviews of the Cambridge Philosophical*
591 *Society*, 80(3), 489–513. <https://doi.org/10.1017/s1464793105006767>

592 Holt, R. D. (1990). The microevolutionary consequences of climate change. *Trends in*
593 *Ecology & Evolution*, 5(9), 311–315. [https://doi.org/10.1016/0169-5347\(90\)90088-U](https://doi.org/10.1016/0169-5347(90)90088-U)

594 Huang, S.-C., & Reinhard, J. (2012). Color Change from male-mimic to Gynomorphic: A
595 New Aspect of Signaling Sexual Status in Damselflies (Odonata, Zygoptera).
596 *Behavioral Ecology*, 23(6), 1269–1275. <https://doi.org/10.1093/beheco/ars112>

597 Hugall, A. F., & Stuart-Fox, D. (2012). Accelerated speciation in colour-polymorphic birds.
598 *Nature*, 485(7400), Article 7400. <https://doi.org/10.1038/nature11050>

599 Hughes, null. (2000). Biological consequences of global warming: Is the signal already
600 apparent? *Trends in Ecology & Evolution*, 15(2), 56–61.
601 [https://doi.org/10.1016/s0169-5347\(99\)01764-4](https://doi.org/10.1016/s0169-5347(99)01764-4)

602 Injaian, A., & Tibbetts, E. A. (2014). Cognition across castes: Individual recognition in
603 worker *Polistes fuscatus* wasps. *Animal Behaviour*, 87, 91–96.
604 <https://doi.org/10.1016/j.anbehav.2013.10.014>

605 Jiggins, C. D., Wallbank, R. W. R., & Hanly, J. J. (2017). Waiting in the wings: What can we
606 learn about gene co-option from the diversification of butterfly wing patterns?
607 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1713),
608 20150485. <https://doi.org/10.1098/rstb.2015.0485>

609 Joron, M. (2009). Chapter 168—Mimicry. In V. H. Resh & R. T. Cardé (Eds.), *Encyclopedia*
610 *of Insects (Second Edition)* (pp. 633–643). Academic Press.
611 <https://doi.org/10.1016/B978-0-12-374144-8.00177-6>

612 José de Souza, D., Devers, S., & Lenoir, A. (2011). Blochmannia endosymbionts and their
613 host, the ant Camponotus fellah: Cuticular hydrocarbons and melanization. *Comptes*
614 *Rendus Biologies*, 334(10), 737–741. <https://doi.org/10.1016/j.crv.2011.06.008>

615 Kang, C., Stevens, M., Moon, J., Lee, S.-I., & Jablonski, P. G. (2015). Camouflage through
616 behavior in moths: The role of background matching and disruptive coloration.
617 *Behavioral Ecology*, 26(1), 45–54. <https://doi.org/10.1093/beheco/aru150>

618 Katayama, N., Abbott, J. K., Kjærandsen, J., Takahashi, Y., & Svensson, E. I. (2014). Sexual
619 selection on wing interference patterns in *Drosophila melanogaster*. *Proceedings of*
620 *the National Academy of Sciences of the United States of America*, 111(42), 15144–
621 15148. <https://doi.org/10.1073/pnas.1407595111>

622 Kemp, D. J., Vukusic, P., & Rutowski, R. L. (2006). Stress-mediated covariance between
623 nano-structural architecture and ultraviolet butterfly coloration. *Functional Ecology*,
624 20(2), 282–289. <https://doi.org/10.1111/j.1365-2435.2006.01100.x>

625 Key, K. H. L., & Day, M. F. (1954). The physiological mechanism of colour change in the
626 grasshopper *Kosciuscola Tristis* Sjöst. (Orthoptera:Acrididae). *Australian Journal of*
627 *Zoology*, 2(3), 340–363. <https://doi.org/10.1071/zo9540340>

628 Khan, M. K. (2020). Female prereproductive coloration reduces mating harassment in
629 damselflies. *Evolution*, 74(10), 2293–2303. <https://doi.org/10.1111/evo.14048>

630 Khan, M. K., & Herberstein, M. E. (2020a). Ontogenetic colour change signals sexual
631 maturity in a non-territorial damselfly. *Ethology*, 126(1), 51–58.
632 <https://doi.org/10.1111/eth.12959>

633 Khan, M. K., & Herberstein, M. E. (2020b). Ontogenetic habitat shifts reduce costly male–
634 male interactions. *Evolutionary Ecology*, 34(5), 735–743.
635 <https://doi.org/10.1007/s10682-020-10064-y>

636 Khan, M. K., & Herberstein, M. E. (2021). Male–male interactions select for conspicuous
637 male coloration in damselflies. *Animal Behaviour*, 176, 157–166.
638 <https://doi.org/10.1016/j.anbehav.2021.04.006>

639 Khramov, A. V., & Chemakos, M. A. (2022). A New Species of Cretapsychops (Insecta:
640 Neuroptera: Psychopsidae) from the Upper Jurassic of Kazakhstan. *Paleontological*
641 *Journal*, 56(2), 194–198. <https://doi.org/10.1134/S0031030122010087>

642 Kingsolver, J. G. (1987). Evolution and coadaptation of thermoregulatory behavior and wing
643 pigmentation pattern in pierid butterflies. *Evolution*, 41(3), 472–490.
644 <https://doi.org/10.1111/j.1558-5646.1987.tb05819.x>

645 Kingsolver, J. G. (1995). Fitness Consequences of Seasonal Polyphenism in Western White
646 Butterflies. *Evolution*, 49(5), 942–954. [https://doi.org/10.1111/j.1558-](https://doi.org/10.1111/j.1558-5646.1995.tb02329.x)
647 [5646.1995.tb02329.x](https://doi.org/10.1111/j.1558-5646.1995.tb02329.x)

648 Kingsolver, J. G., & Wiernasz, D. C. (1991). Seasonal Polyphenism in Wing-Melanin Pattern
649 and Thermoregulatory Adaptation in Pieris Butterflies. *The American Naturalist*,
650 137(6), 816–830.

651 Kunte, K. (2009). The Diversity and Evolution of Batesian Mimicry in Papilio Swallowtail
652 Butterflies. *Evolution*, 63(10), 2707–2716. [https://doi.org/10.1111/j.1558-](https://doi.org/10.1111/j.1558-5646.2009.00752.x)
653 [5646.2009.00752.x](https://doi.org/10.1111/j.1558-5646.2009.00752.x)

654 Larson, E. L., Tinghitella, R. M., & Taylor, S. A. (2019). Insect Hybridization and Climate
655 Change. *Frontiers in Ecology and Evolution*, 7.
656 <https://www.frontiersin.org/article/10.3389/fevo.2019.00348>

657 Lindstedt, C., Murphy, L., & Mappes, J. (2019). Antipredator strategies of pupae: How to
658 avoid predation in an immobile life stage? *Philosophical Transactions of the Royal*
659 *Society B: Biological Sciences*, 374(1783), 20190069.
660 <https://doi.org/10.1098/rstb.2019.0069>

661 Lindström, L., Alatalo, R. V., Lyytinen, A., & Mappes, J. (2004). The Effect of Alternative
662 Prey on the Dynamics of Imperfect Batesian and Müllerian Mimicries. *Evolution*,
663 58(6), 1294–1302. <https://doi.org/10.1111/j.0014-3820.2004.tb01708.x>

664 Lis, C., Moore, M. P., & Martin, R. A. (2020). Warm developmental temperatures induce
665 non-adaptive plasticity in the intrasexually selected colouration of a dragonfly.
666 *Ecological Entomology*, 45(3), 663–670. <https://doi.org/10.1111/een.12839>

667 Llaurens, V., Joron, M., & Théry, M. (2014). Cryptic differences in colour among Müllerian
668 mimics: How can the visual capacities of predators and prey shape the evolution of
669 wing colours? *Journal of Evolutionary Biology*, 27(3), 531–540.
670 <https://doi.org/10.1111/jeb.12317>

671 Maan, M. E., & Seehausen, O. (2011). Ecology, sexual selection and speciation. *Ecology*
672 *Letters*, 14(6), 591–602. <https://doi.org/10.1111/j.1461-0248.2011.01606.x>

673 MacLean, H. J., Kingsolver, J. G., & Buckley, L. B. (2016). Historical changes in
674 thermoregulatory traits of alpine butterflies reveal complex ecological and
675 evolutionary responses to recent climate change. *Climate Change Responses*, 3(1), 13.
676 <https://doi.org/10.1186/s40665-016-0028-x>

677 MacLean, H. J., Nielsen, M. E., Kingsolver, J. G., & Buckley, L. B. (2019). Using museum
678 specimens to track morphological shifts through climate change. *Philosophical*
679 *Transactions of the Royal Society B: Biological Sciences*, 374(1763), 20170404.
680 <https://doi.org/10.1098/rstb.2017.0404>

681 Mappes, J., Marples, N., & Endler, J. A. (2005). The complex business of survival by
682 aposematism. *Trends in Ecology & Evolution*, 20(11), 598–603.
683 <https://doi.org/10.1016/j.tree.2005.07.011>

684 Markl, G., Ottmann, S., Haasis, T., Budach, D., Kraus, S., & Köhler, H.-R. (2022).
685 Thermobiological effects of temperature-induced color variations in *Aglaia urticae*
686 (Lepidoptera, Nymphalidae). *Ecology and Evolution*, 12(6), e8992.
687 <https://doi.org/10.1002/ece3.8992>

688 Martinossi-Aliliberti, I., Rueffler, C., Arnqvist, G., & Berger, D. (2019). The efficacy of good
689 genes sexual selection under environmental change. *Proceedings. Biological*
690 *Sciences*, 286(1896), 20182313. <https://doi.org/10.1098/rspb.2018.2313>

691 Mason, C. W. (2002). Structural Colors in Insects. II. *The Journal of Physical Chemistry*.
692 <https://doi.org/10.1021/j150273a001>

693 McCarty, J. P. (2001). Ecological Consequences of Recent Climate Change. *Conservation*
694 *Biology*, 15(2), 320–331. <https://doi.org/10.1046/j.1523-1739.2001.015002320.x>

695 McNamara, M. E., Briggs, D. E. G., Orr, P. J., Noh, H., & Cao, H. (2012). The original
696 colours of fossil beetles. *Proceedings of the Royal Society B: Biological Sciences*,
697 279(1731), 1114–1121. <https://doi.org/10.1098/rspb.2011.1677>

698 Mikhailov, Y. E. (2001). Significance of colour polymorphism in mountain populations of
699 abundant leaf beetles (Coleoptera, Chrysomelidae). *Pirineos*, 156, 57–68.
700 <https://doi.org/10.3989/pirineos.2001.v156.80>

701 Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & PRISMA Group. (2009). Preferred
702 reporting items for systematic reviews and meta-analyses: The PRISMA statement.
703 *PLoS Medicine*, 6(7), e1000097. <https://doi.org/10.1371/journal.pmed.1000097>

704 Moore, M. P., Hersch, K., Sricharoen, C., Lee, S., Reice, C., Rice, P., Kronick, S., Medley,
705 K. A., & Fowler-Finn, K. D. (2021). Sex-specific ornament evolution is a consistent

feature of climatic adaptation across space and time in dragonflies. *Proceedings of the National Academy of Sciences of the United States of America*, 118(28), e2101458118. <https://doi.org/10.1073/pnas.2101458118>

Moore, M. P., Lis, C., Gherghel, I., & Martin, R. A. (2019). Temperature shapes the costs, benefits and geographic diversification of sexual coloration in a dragonfly. *Ecology Letters*, 22(3), 437–446. <https://doi.org/10.1111/ele.13200>

Mun, S., Noh, M. Y., Kramer, K. J., Muthukrishnan, S., & Arakane, Y. (2020). Gene functions in adult cuticle pigmentation of the yellow mealworm, *Tenebrio molitor*. *Insect Biochemistry and Molecular Biology*, 117, 103291. <https://doi.org/10.1016/j.ibmb.2019.103291>

Negoua, H., Chakir, M., David, J. R., & Capy, P. (2019). Climatic adaptation in *Drosophila*: Phenotypic plasticity of morphological traits along a seasonal cycle. *Annales de La Société Entomologique de France (N.S.)*, 55(1), 48–60. <https://doi.org/10.1080/00379271.2018.1540281>

Neville, A. C. (1975). *Biology of the Arthropod Cuticle*. Springer-Verlag. <https://doi.org/10.1007/978-3-642-80910-1>

Nijhout, H. F. (2010). Chapter 6—Molecular and Physiological Basis of Colour Pattern Formation. In J. Casas & S. J. Simpson (Eds.), *Advances in Insect Physiology* (Vol. 38, pp. 219–265). Academic Press. [https://doi.org/10.1016/S0065-2806\(10\)38002-7](https://doi.org/10.1016/S0065-2806(10)38002-7)

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., Del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., Wackers, F. L., Woodcock, B. A., & Santos, A. M. C. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology*, 26, 8–23. <https://doi.org/10.1016/j.baae.2017.09.006>

730 Nosil, P., Villoutreix, R., de Carvalho, C. F., Farkas, T. E., Soria-Carrasco, V., Feder, J. L.,
 731 Crespi, B. J., & Gompert, Z. (2018). Natural selection and the predictability of
 732 evolution in *Timema* stick insects. *Science*, 359(6377), 765–770.
 733 <https://doi.org/10.1126/science.aap9125>

734 O’Farrell. (1964). On physiological colour changes in some Australian odonata. *Journal of*
 735 *the Entomological Society of Australia (N.S.W.)*, 1, 5–12.
 736 <https://doi.org/10.3316/informit.230177224368276>

737 Parkash, R., Rajpurohit, S., & Ramniwas, S. (2008). Changes in body melanisation and
 738 desiccation resistance in highland vs. Lowland populations of *D. melanogaster*.
 739 *Journal of Insect Physiology*, 54(6), 1050–1056.
 740 <https://doi.org/10.1016/j.jinsphys.2008.04.008>

741 Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H.,
 742 Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., &
 743 Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species
 744 associated with regional warming. *Nature*, 399(6736), Article 6736.
 745 <https://doi.org/10.1038/21181>

746 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts
 747 across natural systems. *Nature*, 421(6918), 37–42.
 748 <https://doi.org/10.1038/nature01286>

749 Patricelli, G. L., & Blickley, J. L. (2006). Avian Communication in Urban Noise: Causes and
 750 Consequences of Vocal Adjustment. *The Auk*, 123(3), 639–649.
 751 <https://doi.org/10.1093/auk/123.3.639>

752 Pilakouta, N., & Ålund, M. (2021). Editorial: Sexual selection and environmental change:
 753 what do we know and what comes next? *Current Zoology*, 67(3), 293–298.
 754 <https://doi.org/10.1093/cz/zoab021>

755 Plotkin, M., Volynchik, S., Ermakov, N. Y., Benyamini, A., Boiko, Y., Bergman, D. J., &
 756 Ishay, J. S. (2009). Xanthopterin in the Oriental hornet (*Vespa orientalis*): Light
 757 absorbance is increased with maturation of yellow pigment granules. *Photochemistry*
 758 *and Photobiology*, 85(4), 955–961. <https://doi.org/10.1111/j.1751-1097.2008.00526.x>
 759 Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M., & Saarinen, K. (2009). Species traits
 760 explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15(3), 732–
 761 743. <https://doi.org/10.1111/j.1365-2486.2008.01789.x>
 762 Przybylo, R., Sheldon, B. C., & Merilä, J. (2000). Climatic effects on breeding and
 763 morphology: Evidence for phenotypic plasticity. *Journal of Animal Ecology*, 69(3),
 764 395–403. <https://doi.org/10.1046/j.1365-2656.2000.00401.x>
 765 Punzalan, D., Rodd, F. H., & Rowe, L. (2008). Sexual selection mediated by the
 766 thermoregulatory effects of male colour pattern in the ambush bug *Phymata*
 767 *americana*. *Proceedings of the Royal Society B: Biological Sciences*, 275(1634), 483–
 768 492. <https://doi.org/10.1098/rspb.2007.1585>
 769 Putyatina, T. S., Gilev, A. V., Grinkov, V. G., & Markov, A. V. (2022). Variation in the
 770 colour pattern of the narrow-headed ant *Formica exsecta* (Hymenoptera: Formicidae)
 771 in European Russia. *European Journal of Entomology*, 119, 58–68.
 772 <https://doi.org/10.14411/eje.2022.006>
 773 Rajpurohit, S., Peterson, L. M., Orr, A. J., Marlon, A. J., & Gibbs, A. G. (2016). An
 774 Experimental Evolution Test of the Relationship between Melanism and Desiccation
 775 Survival in Insects. *PLOS ONE*, 11(9), e0163414.
 776 <https://doi.org/10.1371/journal.pone.0163414>
 777 Ramniwas, S., & Singh, D. (2022). Maternal melanization defines wing spot area of male
 778 *Drosophila nepalensis*: Supporting evidence through genetic crosses. *Journal of*
 779 *Genetics*, 101(2), 48. <https://doi.org/10.1007/s12041-022-01393-8>

780 Rassart, M., Colomer, J.-F., Tabarrant, T., & Vigneron, J. P. (2008). Diffractive
 781 hygrochromic effect in the cuticle of the hercules beetle *Dynastes hercules*. *New*
 782 *Journal of Physics*, 10(3), 033014. <https://doi.org/10.1088/1367-2630/10/3/033014>
 783 Roff, D. A., & Fairbairn, D. J. (2013). The costs of being dark: The genetic basis of melanism
 784 and its association with fitness-related traits in the sand cricket. *Journal of*
 785 *Evolutionary Biology*, 26(7), 1406–1416. <https://doi.org/10.1111/jeb.12150>
 786 Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A.
 787 (2003). Fingerprints of global warming on wild animals and plants. *Nature*,
 788 421(6918), Article 6918. <https://doi.org/10.1038/nature01333>
 789 Rosa, E., & Saastamoinen, M. (2020). Beyond thermal melanism: Association of wing
 790 melanization with fitness and flight behaviour in a butterfly. *Animal Behaviour*, 167,
 791 275–288. <https://doi.org/10.1016/j.anbehav.2020.07.015>
 792 Rößler, D. C., Lötters, S., & Da Fonte, L. F. M. (2020). Author declaration: Have you
 793 considered equity, diversity and inclusion? *Nature*, 584(7822), 525–525.
 794 <https://doi.org/10.1038/d41586-020-02429-8>
 795 Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change.
 796 *Global Change Biology*, 20(11), 3344–3350. <https://doi.org/10.1111/gcb.12594>
 797 Rowland, H. M., Cuthill, I. C., Harvey, I. F., Speed, M. P., & Ruxton, G. D. (2008). Can't tell
 798 the caterpillars from the trees: Countershading enhances survival in a woodland.
 799 *Proceedings of the Royal Society B: Biological Sciences*, 275(1651), 2539–2545.
 800 <https://doi.org/10.1098/rspb.2008.0812>
 801 Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding Attack: The Evolutionary*
 802 *Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press.
 803 <https://doi.org/10.1093/acprof:oso/9780198528609.001.0001>

804 Sandre, S.-L., Tammaru, T., Esperk, T., Julkunen-Tiitto, R., & Mappes, J. (2007).
 805 Carotenoid-based colour polyphenism in a moth species: Search for fitness correlates.
 806 *Entomologia Experimentalis et Applicata*, 124(3), 269–277.
 807 <https://doi.org/10.1111/j.1570-7458.2007.00579.x>

808 Scali, V., & Creed, E. R. (1975). Influence of climate on melanism in the Two-Spot ladybird,
 809 *Adalia bipunctata*, in central Italy. *Trans R Entomol Soc Lond; (United Kingdom)*,
 810 127:2. <https://www.osti.gov/etdeweb/biblio/6020107>

811 Sgrò, C. M., Terblanche, J. S., & Hoffmann, A. A. (2016). What Can Plasticity Contribute to
 812 Insect Responses to Climate Change? *Annual Review of Entomology*, 61(1), 433–451.
 813 <https://doi.org/10.1146/annurev-ento-010715-023859>

814 Sheehan, M. J., Straub, M. A., & Tibbetts, E. A. (2014). How Does Individual Recognition
 815 Evolve? Comparing Responses to Identity Information in Polistes Species with and
 816 Without Individual Recognition. *Ethology*, 120(2), 169–179.
 817 <https://doi.org/10.1111/eth.12191>

818 Sheehan, M. J., & Tibbetts, E. A. (2009). Evolution of Identity Signals: Frequency-
 819 Dependent Benefits of Distinctive Phenotypes Used for Individual Recognition.
 820 *Evolution*, 63(12), 3106–3113. <https://doi.org/10.1111/j.1558-5646.2009.00833.x>

821 Sibilia, C. D., Brosko, K. A., Hickling, C. J., Thompson, L. M., Grayson, K. L., & Olson, J.
 822 R. (2018). Thermal Physiology and Developmental Plasticity of Pigmentation in the
 823 Harlequin Bug (Hemiptera: Pentatomidae). *Journal of Insect Science*, 18(4), 4.
 824 <https://doi.org/10.1093/jisesa/iey066>

825 Skaldina, O. (2017). *Social insects in biomonitoring*: 75.

826 Söderhäll, K., & Cerenius, L. (1998). Role of the prophenoloxidase-activating system in
 827 invertebrate immunity. *Current Opinion in Immunology*, 10(1), 23–28.
 828 [https://doi.org/10.1016/S0952-7915\(98\)80026-5](https://doi.org/10.1016/S0952-7915(98)80026-5)

829 Solensky, M. J., & Larkin, E. (2003). Temperature-induced Variation in Larval Coloration in
830 *Danaus plexippus* (Lepidoptera: Nymphalidae). *Annals of the Entomological Society*
831 *of America*, 96(3), 211–216. [https://doi.org/10.1603/0013-](https://doi.org/10.1603/0013-8746(2003)096[0211:TVILCI]2.0.CO;2)
832 [8746\(2003\)096\[0211:TVILCI\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0211:TVILCI]2.0.CO;2)

833 Srygley, R. B., & Jaronski, S. T. (2022). Increasing temperature reduces cuticular melanism
834 and immunity to fungal infection in a migratory insect. *Ecological Entomology*, 47(1),
835 109–113.

836 Stanbrook, R. A., Harris, W. E., Wheeler, C. P., & Jones, M. (2021). Evidence of phenotypic
837 plasticity along an altitudinal gradient in the dung beetle *Onthophagus proteus*. *PeerJ*,
838 9, e10798. <https://doi.org/10.7717/peerj.10798>

839 Stavenga, D. G., Leertouwer, H. L., Meglič, A., Drašlar, K., Wehling, M. F., Pirih, P., &
840 Belušič, G. (2018). Classical lepidopteran wing scale colouration in the giant
841 butterfly-moth *Paysandisia archon*. *PeerJ*, 6, e4590.
842 <https://doi.org/10.7717/peerj.4590>

843 Stavenga, D. G., Leertouwer, H. L., & Wilts, B. D. (2014a). Coloration principles of
844 nymphaline butterflies – thin films, melanin, ommochromes and wing scale stacking.
845 *Journal of Experimental Biology*, 217(12), 2171–2180.
846 <https://doi.org/10.1242/jeb.098673>

847 Stavenga, D. G., Leertouwer, H. L., & Wilts, B. D. (2014b). The colouration toolkit of the
848 Pipevine Swallowtail butterfly, *Battus philenor*: Thin films, papiliochromes, and
849 melanin. *Journal of Comparative Physiology A*, 200(6), 547–561.
850 <https://doi.org/10.1007/s00359-014-0901-7>

851 Stelbrink, P., Pinkert, S., Brunzel, S., Kerr, J., Wheat, C. W., Brandl, R., & Zeuss, D. (2019).
852 Colour lightness of butterfly assemblages across North America and Europe.
853 *Scientific Reports*, 9(1), 1760. <https://doi.org/10.1038/s41598-018-36761-x>

854 Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S., & Lima, M. (2002).
855 Ecological Effects of Climate Fluctuations. *Science*, 297(5585), 1292–1296.
856 <https://doi.org/10.1126/science.1071281>

857 Stevens, M., & Merilaita, S. (2009). Animal camouflage: Current issues and new
858 perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
859 364(1516), 423–427. <https://doi.org/10.1098/rstb.2008.0217>

860 Stevens, M., & Ruxton, G. D. (2019). The key role of behaviour in animal camouflage.
861 *Biological Reviews*, 94(1), 116–134. <https://doi.org/10.1111/brv.12438>

862 Stewart, A. J. A. (1986). Nymphal colour/pattern polymorphism in the leafhoppers *Eupteryx*
863 *urticae* (F.) and *E. cyclops* Matsumura (Hemiptera: Auchenorrhyncha): spatial and
864 temporal variation in morph frequencies. *Biological Journal of the Linnean Society*,
865 27(1), 79–101. <https://doi.org/10.1111/j.1095-8312.1986.tb01727.x>

866 Stockwell, C. A., Hendry, A. P., & Kinnison, M. T. (2003). Contemporary evolution meets
867 conservation biology. *Trends in Ecology & Evolution*, 18(2), 94–101.
868 [https://doi.org/10.1016/S0169-5347\(02\)00044-7](https://doi.org/10.1016/S0169-5347(02)00044-7)

869 Sugumaran, M. (2002). Comparative Biochemistry of Eumelanogenesis and the Protective
870 Roles of Phenoloxidase and Melanin in Insects. *Pigment Cell Research*, 15(1), 2–9.
871 <https://doi.org/10.1034/j.1600-0749.2002.00056.x>

872 Sugumaran, M., & Barek, H. (2016). Critical Analysis of the Melanogenic Pathway in Insects
873 and Higher Animals. *International Journal of Molecular Sciences*, 17(10), 1753.
874 <https://doi.org/10.3390/ijms17101753>

875 Sun, J., Bhushan, B., & Tong, J. (2013). Structural coloration in nature. *RSC Advances*, 3(35),
876 14862–14889. <https://doi.org/10.1039/C3RA41096J>

877 Svensson, E. I., Gomez-Llano, M., & Waller, J. T. (2020). Selection on phenotypic plasticity
878 favors thermal canalization. *Proceedings of the National Academy of Sciences*,
879 117(47), 29767–29774. <https://doi.org/10.1073/pnas.2012454117>

880 Svensson, E. I., Willink, B., Duryea, M. C., & Lancaster, L. T. (2020). Temperature drives
881 pre-reproductive selection and shapes the biogeography of a female polymorphism.
882 *Ecology Letters*, 23(1), 149–159. <https://doi.org/10.1111/ele.13417>

883 Svensson, E., & Waller, J. (2013). Ecology and Sexual Selection: Evolution of Wing
884 Pigmentation in Calopterygid Damselflies in Relation to Latitude, Sexual
885 Dimorphism, and Speciation. *The American Naturalist*, 182, E174–E195.
886 <https://doi.org/10.1086/673206>

887 Takahashi, M., Takahashi, Y., & Kawata, M. (2019). Candidate genes associated with color
888 morphs of female-limited polymorphisms of the damselfly *Ischnura senegalensis*.
889 *Heredity*, 122(1), Article 1. <https://doi.org/10.1038/s41437-018-0076-z>

890 Takahashi, Y., & Noriyuki, S. (2019). Colour polymorphism influences species' range and
891 extinction risk. *Biology Letters*, 15(7), 20190228.
892 <https://doi.org/10.1098/rsbl.2019.0228>

893 Thompson, M. J., & Jiggins, C. D. (2014). Supergenes and their role in evolution. *Heredity*,
894 113(1), Article 1. <https://doi.org/10.1038/hdy.2014.20>

895 Tibbetts, E. A. (2010). The Condition Dependence and Heritability of Signaling and
896 Nonsignaling Color Traits in Paper Wasps. *The American Naturalist*, 175(5), 495–
897 503. <https://doi.org/10.1086/651596>

898 Tibbetts, E. A., & Dale, J. (2004). A socially enforced signal of quality in a paper wasp.
899 *Nature*, 432(7014), 218–222. <https://doi.org/10.1038/nature02949>

900 True, J. R. (2003). Insect melanism: The molecules matter. *Trends in Ecology & Evolution*,
901 18(12), 640–647. <https://doi.org/10.1016/j.tree.2003.09.006>

902 Tsuchida, T. (2016). Molecular basis and ecological relevance of aphid body colors. *Current*
903 *Opinion in Insect Science*, 17, 74–80. <https://doi.org/10.1016/j.cois.2016.07.005>

904 Umbers, K. D. L. (2011). Turn the temperature to turquoise: Cues for colour change in the
905 male chameleon grasshopper (*Kosciuscola tristis*) (Orthoptera: Acrididae). *Journal of*
906 *Insect Physiology*, 57(9), 1198–1204. <https://doi.org/10.1016/j.jinsphys.2011.05.010>

907 Umbers, K. D. L., Herberstein, M. E., & Madin, J. S. (2013). Colour in insect
908 thermoregulation: Empirical and theoretical tests in the colour-changing grasshopper,
909 *Kosciuscola tristis*. *Journal of Insect Physiology*, 59(1), 81–90.
910 <https://doi.org/10.1016/j.jinsphys.2012.10.016>

911 Vigneron, J. P., Pasteels, J. M., Windsor, D. M., Vértesy, Z., Rassart, M., Seldrum, T.,
912 Dumont, J., Deparis, O., Lousse, V., Biró, L. P., Ertz, D., & Welch, V. (2007).
913 Switchable reflector in the Panamanian tortoise beetle *Charidotella egregia*
914 (Chrysomelidae: Cassidinae). *Physical Review E*, 76(3), 031907.
915 <https://doi.org/10.1103/PhysRevE.76.031907>

916 Viviani, V. R. (2002). The origin, diversity, and structure function relationships of insect
917 luciferases. *Cellular and Molecular Life Sciences CMLS*, 59(11), 1833–1850.
918 <https://doi.org/10.1007/PL00012509>

919 Vukusic, P., & Sambles, J. R. (2003). Photonic structures in biology. *Nature*, 424(6950),
920 852–855. <https://doi.org/10.1038/nature01941>

921 Vukusic, P., Sambles, J. R., & Lawrence, C. R. (2000). Colour mixing in wing scales of a
922 butterfly. *Nature*, 404(6777), 457–457. <https://doi.org/10.1038/35006561>

923 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin,
924 J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent
925 climate change. *Nature*, 416(6879), 389–395. <https://doi.org/10.1038/416389a>

926 Watt, W. B. (1968). Adaptive Significance of Pigment Polymorphisms in Colias Butterflies.
 927 I. Variation of Melanin Pigment in Relation to Thermoregulation. *Evolution*, 22(3),
 928 437–458. <https://doi.org/10.1111/j.1558-5646.1968.tb03985.x>

929 Wennersten, L., & Forsman, A. (2012). Population-level consequences of polymorphism,
 930 plasticity and randomized phenotype switching: A review of predictions. *Biological*
 931 *Reviews*, 87(3), 756–767. <https://doi.org/10.1111/j.1469-185X.2012.00231.x>

932 Williams, P. (2007). The distribution of bumblebee colour patterns worldwide: Possible
 933 significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal*
 934 *of the Linnean Society*, 92(1), 97–118. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8312.2007.00878.x)
 935 [8312.2007.00878.x](https://doi.org/10.1111/j.1095-8312.2007.00878.x)

936 Wilts, B. D., Mothander, K., & Kelber, A. (2019). Humidity-dependent colour change in the
 937 green forester moth, *Adscita statice*. *Biology Letters*, 15(9), 20190516.
 938 <https://doi.org/10.1098/rsbl.2019.0516>

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

942 Woronik, A., Tunström, K., Perry, M. W., Neethiraj, R., Stefanescu, C., Celorio-Mancera, M.
 943 de la P., Brattström, O., Hill, J., Lehmann, P., Käkälä, R., & Wheat, C. W. (2019). A
 944 transposable element insertion is associated with an alternative life history strategy.
 945 *Nature Communications*, 10(1), Article 1. [https://doi.org/10.1038/s41467-019-13596-](https://doi.org/10.1038/s41467-019-13596-2)
 946 [2](https://doi.org/10.1038/s41467-019-13596-2)

947 Xing, S., Bonebrake, T. C., Ashton, L. A., Kitching, R. L., Cao, M., Sun, Z., Ho, J. C., &
 948 Nakamura, A. (2018). Colors of night: Climate–morphology relationships of
 949 geometrid moths along spatial gradients in southwestern China. *Oecologia*, 188(2),
 950 537–546. <https://doi.org/10.1007/s00442-018-4219-y>

- Yin, H., Shakeel, M., Kuang, J., & Li, J. (2015). An Opposite Pattern to the Conventional Thermal Hypothesis: Temperature-Dependent Variation in Coloration of Adults of *Saccharosydne procerus* (Homoptera: Delphacidae). *PLOS ONE*, 10(5), e0128859. <https://doi.org/10.1371/journal.pone.0128859>
- Yoshioka, S., & Kinoshita, S. (2006). Structural or pigmentary? Origin of the distinctive white stripe on the blue wing of a *Morpho* butterfly. *Proceedings of the Royal Society B: Biological Sciences*, 273(1583), 129–134. <https://doi.org/10.1098/rspb.2005.3314>
- Zeuss, D., Brandl, R., Brändle, M., Rahbek, C., & Brunzel, S. (2014). Global warming favours light-coloured insects in Europe. *Nature Communications*, 5(1), 3874. <https://doi.org/10.1038/ncomms4874>
- Zheng, X.-L., Yang, Q.-S., Hu, Y.-W., Lei, C.-L., & Wang, X.-P. (2015). Latitudinal variation of morphological characteristics in the swallowtail *Sericanus montelus* Gray, 1798 (Lepidoptera: Papilionidae). *Acta Zoologica*, 96(2), 242–252. <https://doi.org/10.1111/azo.12072>
- Zuk, M., Garcia-Gonzalez, F., Herberstein, M. E., & Simmons, L. W. (2014). Model Systems, Taxonomic Bias, and Sexual Selection: Beyond *Drosophila*. *Annual Review of Entomology*, 59(1), 321–338. <https://doi.org/10.1146/annurev-ento-011613-162014>
- Zuk, M., Rotenberry, J. T., & Tinghitella, R. M. (2006). Silent night: Adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters*, 2(4), 521–524. <https://doi.org/10.1098/rsbl.2006.0539>
- Zvereva, E. L., Hunter, M. D., Zverev, V., Kruglova, O. Y., & Kozlov, M. V. (2019). Climate warming leads to decline in frequencies of melanic individuals in subarctic leaf beetle populations. *Science of The Total Environment*, 673, 237–244. <https://doi.org/10.1016/j.scitotenv.2019.03.458>

977 **Table 1:** Evidence of insect colour change associated with latitude and climatic factors. Study
978 type refers to whether the study used temporal, geographic or experimental evidence of colour
979 change.

980

Species	Study type	Insects' response	Factors associated with colour change	References
Montane butterfly (<i>Colias meadii</i>)	Temporal	Decreased wing melanization	Warmer temperature	(MacLean et al., 2016)
Montane butterfly (<i>Colias meadii</i>)	Temporal	Increased wing melanization	Higher temperature	(MacLean et al., 2019)
Butterflies and dragonflies	Temporal	Decreased melanization	Higher temperature	(Zeuss et al., 2014)
Ladybird beetle, (<i>Adalia bipunctata</i>)	Temporal	Decreased frequency of melanic morph	Higher spring temperatures	(Brakefield & de Jong, 2011)
Leave beetles (<i>Chrysomela lapponica</i>)	Temporal	Decreased darker morphs	Higher spring daily temperatures	(Zvereva et al., 2019)
Stick insects (<i>Timea Cristine</i>)	Temporal	Increased frequency of melanic morphs	Warmer temperature	(Nosil et al., 2018)
Ladybird beetles (<i>Adalia bipunctata</i>)	Geographical	Decreased frequency of melanic morphs	Altitude	(Scali & Creed, 1975)
Beetle (<i>Oreina sulcata</i>)	Geographical	Green colours	Lower elevations	(Mikhailov, 2001)
Beetle (<i>Oreina sulcata</i>)	Geographical	Darker and more reflective metallic morphs	Higher elevations	(Mikhailov, 2001)
<i>Colias</i> butterflies	Geographical	Darker hindwing (undersides)	Higher latitude	(Watt, 1968)
Bumblebees	Geographical	Darker colour	Lower latitude	(Williams, 2007)

<i>Drosophila melanogaster</i>	Experimental	Decreased colour on the thorax and abdomen	Higher temperature	(Gibert et al., 1998)
Planthoppers (<i>Saccharosydne procerus</i>)	Experimental	Darker colour	Higher temperature	(Yin et al., 2015)
Dragonflies (<i>Pachydiplax longipennis</i>)	Experimental	Increased wing ornamentation	Warmer larval temperatures	(Lis et al., 2020)
Monarch larvae (<i>Danaus plexippus</i>)	Experimental	Greater portion of black and a lower portion of white and yellow colour	Lower temperature	(Solensky & Larkin, 2003)

Table 2: Impact of climate driven colour change on sexual selection

Species	Factors associated with colour change	Impact	References
Ambush bugs (<i>Phymata americana</i>)	Temperature	Dark individuals had higher success rate in mate searching at colder ambient temperature	(Punzalan et al., 2008)
Dragonfly (<i>Pachydiplax longipennis</i>)	Temperature	Greater abundance of dark pigment in the wing increased male flight performance at colder temperature	(Moore et al., 2019)
Common bluetail damselfly (<i>Ischnura elegans</i>)	High latitude	Darker colours led to increased sexual conflict	(Svensson, Willink, et al., 2020)
Cricket (<i>Allonemobius socius</i>)	Short season length	Darker colours led to increased melanin-based immunity	(Fedorka et al., 2013)
Butterflies (<i>Colias philodice eriphyle</i>)	Elevation	Lighter males had reduced flight activity at high elevation	(Ellers & Boggs, 2004)

Table 3: Experimental studies of linking rearing temperature to insect colouration

Study system	Body parts/region of study	Direction of colour change	References
Fruit fly (<i>Drosophila nepalensis</i>)	Abdomen and wing	High percentage of melanin at lower temperature	(Ramniwas & Singh, 2022)
Butterfly (<i>Aglais urticae</i>)	Dorsal wing and body	High percentage of melanin at lower temperature	(Markl et al., 2022)
Grasshopper (<i>Melanoplus sanguinipes</i>)	Cuticle	Darker individuals at lower temperature	(Srygley & Jaronski, 2022)
Butterfly (<i>Melitaea cinxia</i>)	Wing	High Wing melanization at colder temperature	(Rosa & Saastamoinen, 2020)
Dragonfly (<i>Pachydiplax longipennis</i>)	Wing	High wing colouration at warmer temperature	(Lis et al., 2020)
Drosophila (<i>Drosophila simulans</i>)	Abdomen	High pigmentation at lower temperature	(Negoua et al., 2019)
Harlequin Bug (<i>Murgantia histrionica</i>)	Cuticle	High pigmentation at colder temperature	(Sibilia et al., 2018)
Cricket (<i>Teleogryllus oceanicus</i>)	Wing cuticle and hindleg	Reduced wing colour at warmer temperature, however, lighter hindleg at mid temperature (29 °C) than lower (26°C) and higher temperature (32°C)	(Ehrlich & Zuk, 2019)
Planthopper (<i>Saccharosydne procerus</i>)	Body	Increased melanism at high temperature	(Yin et al., 2015)



1013 **Figure 1:** Insects exhibit diverse colours that are produced from pigments, structural-based
1014 colour or a combination of both. A) *Danaus genetica*, B) *Ceriagrion cerinorubellum*, C)
1015 *Tectocoris diophthalmus*, D) *Coccinella transversalis*, E) *Trithemis aurora*, F) *Taxila*
1016 *haquinus*. Photo © MK Khan