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

Md Tangigul Haque[1], Kawsar Khan[1], and Marie Herberstein [1]

[1]Macquarie University

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Abstract

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

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Md Tangigul Haque[1], 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

Abstract

Insects exhibit diverse colours that play a crucial role in communication that directs inter- and intra-species interactions such as predator-prey interactions and sexual selection. Anthropogenic climate change may impact insects colour expression and consequently their physiology and behaviour. Insects can respond to changing climatic through phenotypic plasticity or genetic modification, however it is unclear how any of the resulting changes in body and wing colour may impact interactions with conspecifics and heterospecific (e.g., predator, prey, and mate). The aim of this review is to synthesis the current knowledge of the consequences of climate driven colour change on insects. Firstly, we discussed the environmental factors that affect insect colours, and then we outlined the adaptive mechanisms in terms of phenotypic plasticity and microevolutionary response. Secondly, we conducted a systematic review and performed a qualitative analysis to understand how experimental rearing temperature influences insect colouration. Finally, we gave an overview of the beneficial or maladaptive impact of colour change on sexual selection. We concluded by identifying 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 daker 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 leave 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 (*Sericinus 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^{0}C and bright blue above 15^{0}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^{0}C, intermediate colouration from 10 to 15^{0}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-Allibert 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 >2^0 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.

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Conflict of interest

The authors declare no competing interests.

Statement of diversity and inclusion

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

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

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

Drosophila melanogaster	Experimental	Decreased colour on the thorax and abdomen	Higher temperature	(Gibert et al., 1998)
Planthoppers (*Saccharosydne procerus)*	Experimental	Darker colour	Higher temperature	(Yin et al., 2015)
Dragonflies (*Pachydiplax longipennis*)	Experimental	Increased wing ornamentation	Warmer larval temperatures	(Lis et al., 2020)
Monarch larvae (*Danaus plexippus*)	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 (*Phymata americana)*	Temperature	Dark individuals had higher success rate in mate searching at colder ambient temperature	(Punzalan et al., 2008)
Dragonfly (*Pachydiplax longipennis*)	Temperature	Greater abundance of dark pigment in the wing increased male flight performance at colder temperature	(Moore et al., 2019)
Common bluetail damselfly (*Ischnura elegans*)	High latitude	Darker colours led to increased sexual conflict	(Svensson, Willink, et al., 2020)
Cricket *(Allonemobius socius)*	Short season length	Darker colours led to increased melanin-based immunity	(Fedorka et al., 2013)
Butterflies (*Colias philodice eriphyle*)	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 *(Drosophila nepalensis)*	Abdomen and wing	High percentage of melanin at lower temperature	(Ramniwas & Singh, 2022)
Butterfly *(Aglais urticae)*	Dorsal wing and body	High percentage of melanin at lower temperature	(Markl et al., 2022)
Grasshopper *(Melanoplus sanguinipes)*	Cuticle	Darker individuals at lower temperature	(Srygley & Jaronski, 2022)
Butterfly *(Melitaea cinxia)*	Wing	High Wing melanization at colder temperature	(Rosa & Saastamoinen, 2020)
Dragonfly *(Pachydiplax longipennis)*	Wing	High wing colouration at warmer temperature	(Lis et al., 2020)
Drosophila *(Drosophila simulans)*	Abdomen	High pigmentation at lower temperature	(Negoua et al., 2019)
Harlequin Bug *(Murgantia histrionica)*	Cuticle	High pigmentation at colder temperature	(Sibilia et al., 2018)
Cricket *(Teleogryllus oceanicus)*	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 *(Saccharosydne procerus)*	Body	Increased melanism at high temperature	(Yin et al., 2015)

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