

Impact of climate on Odonata traits

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DECLARATION

I declare that this thesis, as a whole or in parts, has not been submitted for a higher degree to any other university or institution. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Chapter one is written and formatted as a review article. Tangigul Haque, Md Kawsar Khan, and Mariella Herberstein conceived idea. Tangigul Haque wrote the first draft of the manuscript. Md Kawsar Khan and Mariella Herberstein edited and commented on the drafts and supervised the project.

Chapter two is written and formatted as an original research article. Tangigul Haque, Md Kawsar Khan, and Mariella Herberstein conceived the idea and designed the study. Tangigul Haque collected data, analysed data, and wrote the first draft of the manuscript. Md Kawsar Khan and Donald J. McLean contributed to the data analysis. Md Kawsar Khan and Mariella Herberstein edited and commented on the drafts and supervised the project.

Chapter three is written and formatted as an original research article. Tangigul Haque, Md Kawsar Khan, and Mariella Herberstein conceived and planned the original idea. Tangigul Haque collected data, analysed data, and wrote the first draft of the manuscript. Md Kawsar Khan and Donald J. McLean contributed to the data analysis. Md Kawsar Khan and Mariella Herberstein edited and commented on the drafts and supervised the project.

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No ethics approval was required for this project.

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The thesis has three chapters and these are formatted as manuscripts for submission to the *Biology Letters*, *Journal of Evolutionary Biology*, *Austral Ecology* with some exceptions to meet the requirements of the Macquarie University. This includes the requirement of an abstract of 200 words, 2cm margins, 1.5x line spacing, figures and tables embedded within the text.

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Candidate's statement about the impact of COVID-19 changes on the thesis

Dear Examiner,

Many of our HDR candidates have had to make changes to their research due to the impact of COVID-19. Below you will find a statement from the candidate, approved by their Supervisory Panel, that indicates how their original research plan has been affected by COVID-19 restrictions. Relevant ongoing restrictions in place caused by COVID-19 will also be detailed by the candidate.

Candidate's Statement

Due to covid 19 pandemic and border restrictions, I started my second year Master of Research offsite (Bangladesh). After coming to Australia, I had a plan to collect samples from museums to finish my lab works including DNA extraction, sequencing, and reconstructing a molecular phylogeny. For that purpose, my supervisor contacted the sample collection manager of the Australian Museum and the Director of the National Research Collections Australia, however, both collections were closed, and I was unable to complete this aim for my thesis. An alternative plan to collect samples from different field sites for the molecular phylogeny was also not possible due to the strict timeframe /nature of the Master of Research. This impacted my original research plan to include a phylogeny-controlled analysis. Additional COVID impact include the inability to meet with my supervisors face to face and the restricted times for online meetings due to the different time zones.

ABSTRACT

Insects exhibit diverse colours between and within species that may function in thermoregulation, mate signalling, and predator-prey interactions. Variation in climate along latitudinal gradients may impact insects' traits such as body size and colour. We quantified several phenotypic traits and asked whether variation in these traits can be explained by latitude and local climatic factors (temperature, precipitation, and humidity). We collected Australian odonate photographs from online databases, and measured colour and sexual dichromatism. Furthermore, we measured odonate body size and sexual size dimorphism. Bioclimatic variables were extracted from WorldClim and the Australian Government Bureau of Meteorology databases. Body size of odonates followed Bergmann's (body size increases with latitude) and Rensch's rule (sexual size dimorphism increases with body size when males are larger and decreases with body size when females are larger). We also found a significant correlation between precipitation and male body size. Moreover, body colour of odonates had no relationship with any of our predictors whereas precipitation, humidity, and body size were strongly correlated with sexual dichromatism. Overall, our study provides insight into how climatic factors relate to insect traits and will highlight the consequences of such variations under the changing climate.

CHAPTER ONE

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

Manuscript formatted for the *Biology Letters*

Abstract

Insects exhibit diverse colours that play a crucial role in communication and physiological processes. Global climate change may impact on insect colour and consequently their physiology and behaviour. Insects can respond to these conditions through phenotypic plasticity or genetic modification. We need to understand how the resulting changes in body and wing colour impact survival, reproduction, and interactions with conspecifics and heterospecific (e.g., predator and prey). The aim of this review is to understand the consequences of climate driven colour change on insects. Here, we review the limited contemporary evidence on the impact of climate change on insect colour. First, we discuss the environmental factors that affect insect colours, and then we outline the adaptive mechanisms in terms of phenotypic plasticity and microevolutionary response. Finally, we give an overview of the impact of colour change on sexual selection and whether this colour change has maladaptive or beneficial consequences. We conclude by identifying research gaps and highlight the potential future research areas in this fields.

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 (Fig.1) (Khan, 2020; Khan & Herberstein, 2020b; Wittkopp & Beldade, 2009). Insect 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), intraspecific communication (e.g. signalling), thermoregulation, UV-protection and crypsis including mimicry and camouflage (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 of this species, but may also have an impact on predation risk (Khan & Herberstein, 2020a). On the other hand, abdominal stripes in hornet (*Vespa orientalis*) assist in thermoregulation (Plotkin et al., 2009). Appreciating the complexity with respect to body colours is of utmost important for understanding the species specific ecologies and evolution (Endler & Mappes, 2017).

Contemporary climate change may impact on organisms in many ways such as habitat change and phenotypic changes of individuals, genetic, microevolutionary, and ecological 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 climate factors such as temperature change along with latitude or altitudinal variation and humidity changes (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 insect colour, their relationship 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 sexual selection, and activity (Candolin & Heuschele, 2008). Colour polymorphisms, which refers to the occurrence of two or more discrete colour pattern variants within population due to genetic variation, can enhance the adaptability of an individual to a novel environment, resulting in expansion of population geographical ranges and may

mitigating population extinction (Takahashi & Noriyuki, 2019; Forsman et al., 2016; Wennersten & Forsman, 2012; Forsman et al., 2008). Butterflies and moths, for example, are active flyers who can easily 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).



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

The aim of this review is to discuss 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). Additionally, we highlight the current gaps and propose future directions where further research is required. We believe, our review will provide insights how insect 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 between 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., 2014a). 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, 2014b; 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, and therefore absorb more solar irradiation (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 changing the moth's colour from red to green (Wilts et al., 2019). Also, 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). 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.

Table 1: Studies showing evidence of insect colour change associated with latitude and climatic factors. Study type refers to whether study captured temporal change in colour or geographic change in colour or experimental change in colour.

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)

Species	Study type	Insects' response	Factors associated with colour change	References
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 melanistic 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)

Insect colour functions

Insect colour may provide physical protection, facilitate mimicry, camouflage, thermoregulation and communication (Cott, 1940). In terms of physical protection, darker insect cuticles increase resistance against pathogens and parasites (Armitage & Siva-Jothy, 2005). The 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; Roulin, 2014; 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). A common form of animal camouflage is background matching, for example, 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 (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 (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, 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 black 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 show their unpalatability or toxin signal to predator through their conspicuous warning colouration (Lindstedt et al., 2019).

In addition, colour can function as a form of 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 (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 Batesian mimics of monarch butterfly, wasps and bees, respectively (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 in *Colias meadii* showed that the butterfly wing melanization decreased with increasing temperature in this time period (MacLean et al., 2016). This pattern, however, is not true across space; melanism in *Colias meadii* in the North American geographical regions were studied over the same time period which showed that melanism decreased with increasing temperature in the Northern regions but the opposite pattern (melanin increased with increasing temperature) of wing melanization was found in southern region (MacLean et al., 2019).

Another study provided evidence that European butterflies and dragonflies species were becoming lighter, less melanized in warmer regions and furthermore, darker species shifted their habitats 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 with an increase of spring temperatures (Brakefield & de Jong, 2011). Similarly, darker morphs of leaf beetles (*Chrysomela lapponica*) were strongly declined with increased minimum spring daily temperatures between 1992 and 2018 (Zvereva et al., 2019). Conversely, the frequency of melanistic stick insects (*Timea cristinae*) morphs increased in warmer years (Nosil et al., 2018).

Geographical variation

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 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 where darker colour moths were found at higher elevations, however, this pattern was not consistent across different study sites (Xing et al., 2018). In addition to melanisms, structural colours that cause a metallic appearance also to 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). Variations in colour along latitudinal gradients still a matter of debate, yet few polymorphic systems are understood (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), and 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 (Bishop et al., 2016) 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

Various experimental studies provide support that temperature is related to insects' 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 wing ornamentation when larva was reared at higher temperature than when larva was 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 of this bug: individuals reared

in lower temperature were darker than the individuals of higher temperature (Sibilia et al., 2018). In addition, a study on monarch larval (*Danaus plexippus*) colouration showed larvae that were reared in lower temperature had a greater portion of black, lower portion of white, and yellow colour compared to larvae in warm temperature (Solensky & Larkin, 2003).

Some of the responses to rearing temperature can result in seasonal polymorphism (Chaput-Bardy et al., 2014). 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*), and resulted in high 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; Umbers, 2011; Key & Day, 1954). The often-opposing results summarized above indicate that relationship between insect colour and the thermal environment is complex.

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 (reviewed in Gienapp et al., 2008). Sometimes populations combine these responses to adapt to climatic change (Davis & Shaw, 2001).

Individuals can change colour with changing environments (such as temperature and humidity changes) or during the time of transitional developmental stages (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 permanently (Nijhout, 2010). Plastic responses of an individual are more rapid to new conditions than evolutionary responses (Sgrò et al., 2016). In insects, phenotypic plasticity can arise from color change in the epidermis or the cuticle and may vary with season (polyphenism) (Nijhout, 2010). Although phenotypic plasticity provides an important mechanism to adjust to new environmental conditions, it 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). It is also important to demonstrate the heritability of colour change however, this is not always possible due to the nature and complexity of the genetic basis for colour production (Clusella-Trullas & Nielsen, 2020).

Impact of colour change on sexual selection

Sexual selection is an important factor that contributes to species richness in various ways (Kraaijeveld et al., 2011). 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; Roff, 2013). A recent study on a quantitative genetics model showed that the strength of sexual selection may be decreased 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). A study conducted on ambush bugs, *Phymata americana*, showed that sexual dimorphism in colouration caused by temperature that 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 also come across if intense sexual signaling results in detection by

parasites and predators (Halfwerk et al., 2011; Patricelli & Blickley, 2006; Zuk et al., 2006). In addition, certain sexual signal such as melanized wing interference patterns or patches in drosophila or dragonflies might increase reproductive success but may be physiological detrimental may increase body temperature under the warming climate (Moore et al., 2021; Katayama et al., 2014; Corbet, 1999). Moore et al., (2021) discussed in their review paper that male dragonflies who had higher wing melanization were able to attract more female. However, wing melanization can increase individual body temperature $>2^{\circ}\text{C}$ (Svensson et al., 2020; Moore et al., 2019; Svensson & Waller, 2013). Such thermal effects may confer modest locomotor benefits at low temperature environments but may reduce flight ability, damage wing tissue, and cause death at high temperature environments (Svensson et al., 2020; Moore et al., 2019). This impact may be sex specific as females forage at lower temperature or shaded micro-habitats (reviewed in Moore et al., 2021).

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	Mate searching	(Punzalan et al., 2008)
Dragonfly (<i>Pachydiplax longipennis</i>)	Temperature	Male flight performance	(Moore et al., 2019)
Common bluetail damselfly (<i>Ischnura elegans</i>)	Higher latitude	Sexual conflict/pre-reproductive selection	(Svensson, Willink, et al., 2020)
<i>Bicyclus</i> butterflies	Temperature	Predator avoidance	(Oliver et al., 2009; Roskam & Brakefield, 1996)
Ambush bugs (<i>Phymata americana</i>)	High temperature	Survival and fecundity (female)	Reviewed in (Punzalan et al., 2008)

Knowledge gaps and proposed future directions

We identified several research gaps that need further exploration. Firstly, the impact of climate on insect colour are derived mostly from long term temporal studies. However, experimental evidence

that the changing climate influences insects colour is scarce. There are empirical studies that observed the consequences on colour after manipulating environmental factors, however, those 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). Short-term experiments are most likely to detect phenotypic plasticity and in addition, we need more long-term experiments over several generations to understand the evolutionary response. Specifically, the fitness impact 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 the potential impact of climate change. Furthermore, there is limited information on the exact genetic and physiological mechanisms resulting in insect colour change. Secondly, there are possible geographic and sex specific biases in the current literatures due the restricted locations or geographic regions of studies that 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. The availability of many advanced techniques such as digital photographs for assessing colour, and computer assisted photographs analysis software also opens the use of museum specimen that may be too fragile for conventional photo spectrometry. Usage of museum specimens provide further opportunity to understand the temporal trend of insect 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 insect colour can impacts physiological functions, intra- and interspecies communication, 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.

Statement of diversity and inclusion

We strongly support equity, diversity and inclusion in science. 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 underrepresented ethnic minority in science.

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CHAPTER TWO

Effects of climate change and body size on body colour and sexual dichromatism in odonates

Manuscript formatted for the *Journal of Evolutionary Biology*

Abstract

Odonates, dragonflies and damselflies, exhibit a diverse array of colour in body and wing that vary depending on their age, sex, dispersal ability, and the geographic area they inhabit. Changes in environmental factors may impact odonate colour, however, general trends of the colour variation and the underlying mechanisms are not well understood. Here, we investigated the impact of climatic factors and body size on colour and sexual dichromatism in Australian odonates. We collected photographs of odonates from several online databases (<http://dragonflypix.com> and <https://www.ala.org.au>) and applied linear mixed effects models to assess whether colour variation and sexual dichromatism of odonates are related to latitude, mean annual temperature, mean annual precipitation, mean annual humidity, and body size. We predicted that odonates' colour would follow the thermal melanism hypothesis; individuals at higher latitudes would be darker compared to the individuals at lower latitudes. We further tested if the extent of sexual dichromatism in odonates is impacted by climate and body size. We found that none of the predictors in our study had a significant effect on body colour whereas body size, precipitation, and humidity were significantly correlated with sexual dichromatism. In contrast to our prediction, body colour in odonates did not follow the thermal melanism hypothesis. Our study provides evidence that sexual dichromatism in odonates can be predicted by local climate and overall body size.

Introduction

Colour is a key phenotypic trait in animals that may function as thermoregulation, physical protection (e.g., parasites and ultraviolet radiation), signalling (attract potential mates and intimidate rivals or predators), and camouflage (Cuthill et al., 2017; Stankowich et al., 2011; Caro, 2005; Cott, 1940). Colour may vary with geography according to ecogeographical rules: (i) thermal melanism hypothesis: darker animals experience a selective benefit in cooler environments through thermoregulation; and (ii) Gloger's rule: darker animals benefit under a warmer and wetter climate as darker colours provide more camouflage in those conditions (Delhey, 2019, 2018; Galván et al., 2018; Clusella Trullas et al., 2007; Gaston et al., 2008; Gloger, 1833). Climate, primarily temperature and precipitation, may impact animals in various ways resulting in changes in distribution, abundance and phenotypes including colour (Dunn et al., 2009; Parmesan, 2007; Bale et al., 2002; Currie & Paquin, 1987). Due to the multidimensionality of climate change, it is complex to predict how animal colour will change in response to future climate (Clusella-Trullas & Nielsen, 2020; Elith et al., 2010). It is thus important to study colour variation, which conveys multiple interactive functions and has a significant impact on the ecology and evolution of populations (Endler & Mappes, 2017).

Insects' colouration play an important role in adaptation, which can change throughout an individual's lifetime (Moore et al., 2021; Khan, 2020; Cortesi et al., 2016; Caro et al., 2016). For example, sexual dichromatism and conspicuous coloration of males and females are under sexual selection in insects (i.e., damselflies and butterflies (Khan & Herberstein, 2021, 2020a; Kronforst et al., 2006; Ellers & Boggs, 2003). As ectothermic animals rely on the environment for maintaining body temperature, changes in ambient temperature may impact thermoregulation (Angilletta Jr & Angilletta, 2009; Huey & Kingsolver, 1989). For example, a temporal study on European butterflies and dragonflies showed that species living in warmer climates were lighter, whereas species that inhabited cooler climates were darker (Zeuss et al., 2014). Similarly, passerine birds and parrots from the tropics are more colourful than birds of the temperate regions, suggesting light colouration provides adaptive benefits to animals in warmer climates (Carballo et al., 2020).

Although colour of both sexes vary across latitudes, males' and females' colour might respond differently to the local climatic factors (Lis et al., 2020; Wilts et al., 2019; MacLean et al., 2019). Natural and sexual selection may act differently to males and females result sexual dichromatism across latitudes (Schreiner et al., 2020; Penney et al., 2012; Allen et al., 2011). For example, *Calopteryx aequabilis* males spend more time in the open arena compared to females therefore selection might favour more elaborated colour in males (Schreiner et al., 2020). The extend of

selection pressure on males and females' colouration might also vary across latitudes because variation of sunlight, and temperature across latitudes may favour different-colour in males and females at different latitudes (Fabricant et al., 2018; Williams, 2007). Additionally, population density and body size might also impact sexual dichromatism (Carballo et al., 2020). In parrot, larger species had lesser sexual dichromatism (Carballo et al., 2020). On the other hand, in high density population, sexual selection might be stronger resulting more conspicuous colouration in males and thereby contributing to greater sexual dichromatism (Khan & Herberstein, 2021, 2020a; Maan & Cummings, 2009). Understanding variations in sexual dichromatism along latitudinal gradients might help to determine the impact of climatic change on animals.

Dragonflies and damselflies exhibit a diverse array of colour similar to the plumage coloration of birds and wing coloration of butterflies (Suárez-Tovar et al., 2022; Delhey, 2018, 2017; Dale et al., 2015; Oliver et al., 2009; Tillyard, 1917). Some species of odonates have a genetically determined colour polymorphism in one or both sexes within a single population (Futahashi, 2017; Mattern & Gossum, 2008; Fincke et al., 2005; Corbet, 1999). Although these colour polymorphisms are mostly prominent in females, male-limited polymorphisms are also found in some odonate species (Willink et al., 2019; Svensson, 2017; Romo-Beltrán et al., 2008; Fincke et al., 2005; Hooper et al., 1999). Female-limited colour polymorphism is mostly found within the Coenagrionidae family, whereas male-limited colour polymorphism is found in the Calopterygidae family (Romo-Beltrán et al., 2008; Fincke et al., 2005; Sirot et al., 2003; Andrés et al., 2002; Hooper et al., 1999).

Climate responses of individuals differ between ectothermic and endothermic species (Buckley et al., 2012). Sex-specific traits such as conspicuous colour can increase reproductive success, however, ornamental colour can also increase visibility to predators and parasites (Halfwerk et al., 2011; Zuk et al., 2006; Endler, 1980). Climatic factors such as temperature can impact the expression of colour, thereby impacting sexual selection and fitness (Moore et al., 2019). For example, in odonates, conspicuous coloration can intimidate rivals or attract mates, and can also increase body temperature to optimum, thereby improving reproductive success at lower temperatures (Moore et al., 2019; Clusella Trullas et al., 2007; Khan & Herberstein, 2021, 2019). However, an increase in body temperature due to sexually selected colour may also affect regular activity (West & Packer, 2002). Anthropogenic activity-driven acceleration of climate change is predicted to impact insects' physiology, including colour, which can influence intra- and interspecific interactions. Understanding how insects' colour responds to climatic factors is important to determine how functions of insects' colour might be impacted and how it contributes to insects' fitness. Latitude is often associated with

climatic factors such as temperature, humidity, and precipitation; latitudinal variation in colour thus provides an excellent platform to determine the impact of climatic factors on insects' colour.

In this study, we investigate the relationship between odonate body colour and sexual dichromatism with body size and latitude. We predict that body colour of odonates would be darker at higher latitudes compared to the body colour of the lower latitudes, in accordance with the thermal melanin hypothesis. We also predict that sexual dichromatism would be higher in smaller species compared to larger species. We also extracted climatic factors (i.e., mean annual temperature, mean annual precipitation, mean annual humidity) where the species occurs and aim to determine if the colour and sexual dichromatism correlates with the local climatic factors. We predicted that colour, and sexual dichromatism would be associated with climatic factors especially with temperature to assist odonates in thermoregulation in which darker odonates would be at lower temperature whereas lighter odonates at higher temperature. We also predict that higher temperature leads to higher sexual dichromatism in odonates than lower temperature.

Materials and methods

Data collection

We collected photographs of 150 species of Australian dragonflies and damselflies, which represents approximately 47% of Australian odonates. These photographs were collected from two online databases (<http://dragonflypix.com> and <https://www.ala.org.au>) between July 2021 and November 2021. These 150 species represent twelve Odonata families: Aeshnidae, Argiolestidae, Coenagrionidae, Corduliidae, Gomphidae, Isostictidae, Lestidae, Lestoideidae, Libellulidae, Libelluloidea, Platycnemididae, and Synthemistidae. We collected photographs of males and females of each species, one to four photographs for each sex, based on the availability in the source database.

Image processing and analyzing

We imported each photograph to ImageJ (version 1.53) software for measuring standard RGB (Red, Green, and Blue) values (Schneider et al., 2012). Background colours in the imported images were removed and only the body regions were kept for analyses. We checked the quality of the collected photographs and discarded photographs with low quality, shadows, and flash glare. All photographs were collected, quality checked and analyzed by the first author (T.H.) to keep the processing uniform. We manually chose regions on the body that represent different colours of the organism and

extracted RGB values. Based on the percentage of each colour present in each animal, we categorized colours into primary ($> 65\%$), secondary (> 40 and $< 65\%$), tertiary (> 10 and $< 40\%$) and quaternary ($< 10\%$) using the colour threshold in ImageJ software. Finally, we used the values of the primary colour for further analyses, as it represents the highest proportion of patches of each organism (Medina et al., 2020). We used the similar approach with few modifications that was applied to measure the colour variation in butterflies by Medina et al., (2020).

Occurrence data

Odonata occurrence data were downloaded from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>). The GBIF occurrence of each species were extracted by restricting location to Australia, and by setting occurrence status to present, and coordinate status to known only. The downloaded occurrence data included latitudes, longitudes, occurrence status, and collection date. We took a subsample of 15 dragonfly and 15 damselfly (20% of our total samples) randomly, then compared the range maps with field guide to validate the occurrence records.

Colour scores

We calculated mean RGB values and percentage of colour for each species, sex and colour. Mean RGB values were then converted to CIELAB coordinates using the “colorspace” (version 1.4-1) package in R (Zeileis et al., 2020; Tkalcic & Tasic, 2003). This means we had the average values of L, a, and b for each colour in every combination of species, whereby L represents the achromatic channel (colour lightness, black = 0, white = 100); “a” and “b” denote chromatic channels. Coordinate “a” gives the values between green (low) and red (high) colour whereas “b” gives the values between blue (low) and yellow (high).

Sexual dichromatism

Sexual dichromatism was measured for each species by computing the Euclidean distance in CIELAB space between homologous colours on males and females. We then calculated the species dichromatism value by averaging the distances between each of the colours for the species.

Body size measurement

Photographs of the wings of Australian dragonflies and damselflies were collected from an online open accessible photographic library; “Images of Australian Odonata Wings” (Tann, 2021). This

library provides high resolution photographs (~ 9000 x 5000 pixels) of Odonata wings photographed from museum specimens that had been identified accurately by experienced taxonomists. We used the length of the right hindwing as a proxy of body size, since wing size and body size are highly correlated and easy to measure comparing to actual body size (Wonglersak et al., 2020; Corbet, 1999). For each species, we measured the male and female hindwing (horizontally from proximal end to distal end) twice and then used the average of the two measurements to reduce measurement error (Fig. 1). In addition, we performed Pearson correlation between two measurements and found the correlation value $R=0.999$ and $p < 0.001$. ImageJ (version 1.53) software was used for measuring wing sizes (Schneider et al., 2012). Measurements and calculations are in mm.

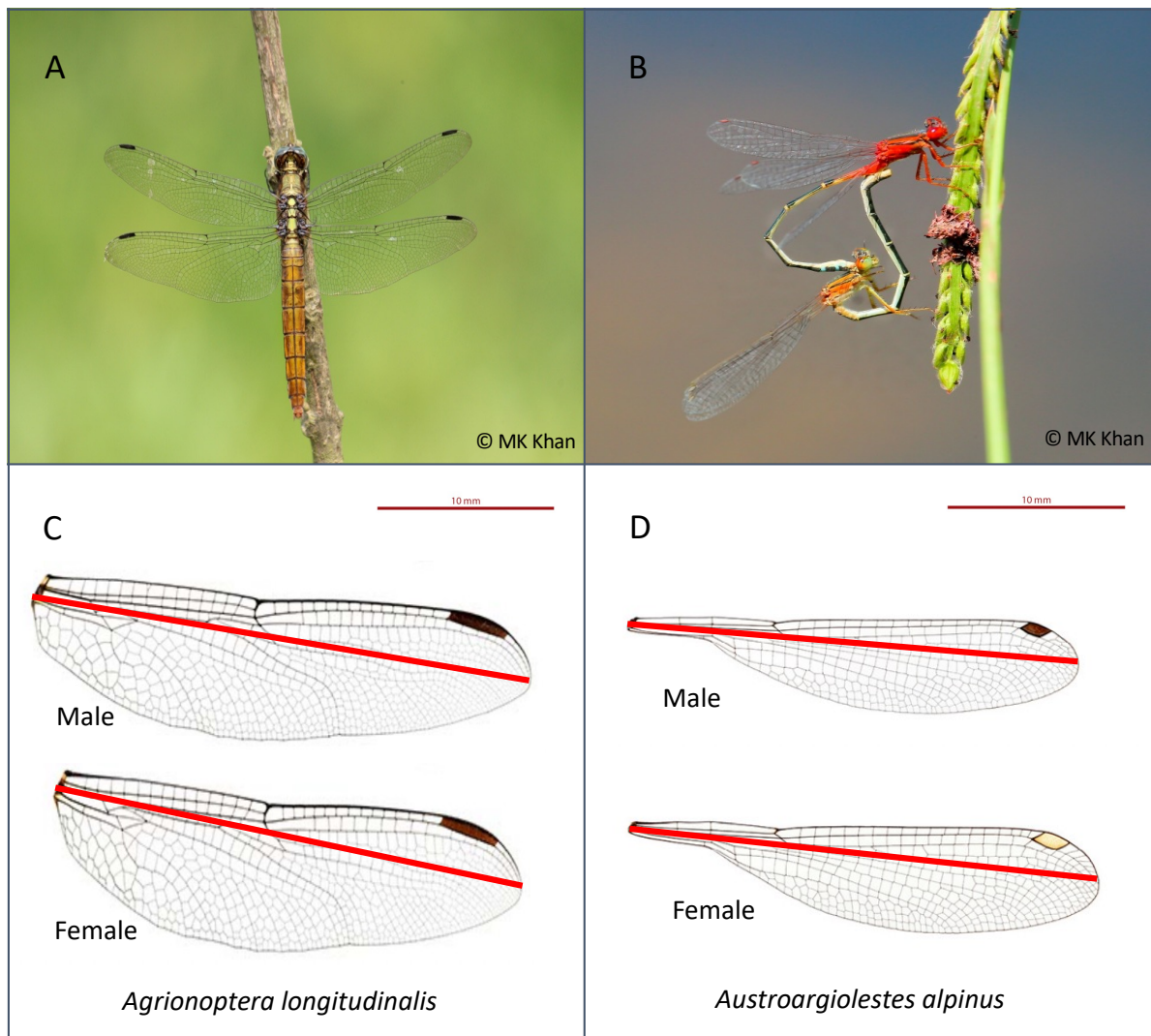


Figure 1: Photograph of an Australian (A) dragonfly; *Pantala flavescens*, male (B) damselfly, *Xanthagrion erythroneurum*, copula, (C) right hindwings of *Agrionoptera longitudinalis* dragonfly (male and female), and (D) right hindwings of *Austroargiolestes alpinus* damselfly, (male and female). Horizontal red lines indicate the measurement of wing length.

Climatic variables

Climatic data were downloaded from WorldClim version 2.1 (<https://www.worldclim.org>) and Australian Government Bureau of Meteorology (<http://www.bom.gov.au>) databases. Records of mean annual temperature (°C) and mean annual precipitation (mm) were downloaded from WorldClim (version 2.1) database in GeoTiff (.tif) file format, with a spatial resolution of approximately ~340 km². We collected thirty years of data spanning from 1970 to 2000. Annual Relative Humidity (RH) data were collected from the Australian Government Bureau of Meteorology (<http://www.bom.gov.au>) in standard text document (.txt) file format over the period of 1976 to 2005. To quantify the climate variables for each species, we defined the species range as the extent of the species occurrences, then averaged the climate variable across all cells that overlapped the species range. All analyses were performed in R (version 4.1.2) (R Core Team, 2021) using the “raster” package (Hijmans & van Etten, 2012).

Statistical analyses

All statistical analyses were performed in R (version 4.1.2) (R Core Team, 2021). We used linear mixed effects models using the *lme4* (Bates et al., 2014) package to determine differences in colour lightness (L), green-red colour index (a), and blue-yellow colour index (b) between males and females. We used coordinates L, a, and b as independent variables, sex as a fixed effect, and colour percentage type (primary, secondary, tertiary and quaternary) as a random factor. We also determined the relationship of colour with latitude and climatic factors, including temperature, precipitation, and humidity, based on sex and primary colour within the species by applying linear mixed-effects models. We fitted all our models using family as a random factor (1|family); colour or sexual dichromatism as a response variable ((colour or sexual dichromatism) ~ (covariates)); and latitude, mean annual temperature, mean annual precipitation, and mean annual humidity as a covariates ((response variable) ~ (latitude or temperature, precipitation, and humidity)). We checked the assumptions of heterogeneity and normality of variance for our model residuals using “performance” R package (Lüdtke et al., 2021).

Results

Effect of climatic factors on odonates colour

We did not find a significant relationship between colour and latitude. Sex-specific responses of colour to latitude were (LMM: ♂: estimate = -0.30 ± 0.24 , $t = -1.28$, $p = 0.20$, Fig. 2(A); ♀: estimate = -0.13 ± 0.28 , $t = -0.47$, $p = 0.64$, Fig. 2(A)). None of the climatic predictors in our study had a relationship with colour. Response of mean annual temperature to colour was (LMM: ♂: estimate = -0.32 ± 0.61 , $t = -0.52$, $p = 0.60$, Fig. 2(B); ♀: estimate = 0.95 ± 0.85 , $t = 1.12$, $p = 0.27$, Fig. 2(B)); mean annual precipitation and colour (LMM: ♂: estimate = -0.001 ± 0.006 , $t = -0.15$, $p = 0.88$, Fig. 2(C); ♀: estimate = -0.01 ± 0.001 , $t = -1.54$, $p = 0.13$, Fig. 2(C)); humidity and colour (LMM: ♂: estimate = -0.31 ± 0.39 , $t = -0.81$, $p = 0.43$, Fig. 2(D); ♀: estimate = 0.27 ± 0.58 , $t = 0.47$, $p = 0.64$, Fig. 2(D)). Summary of the effects of climatic factors on colour is given in Table 1.

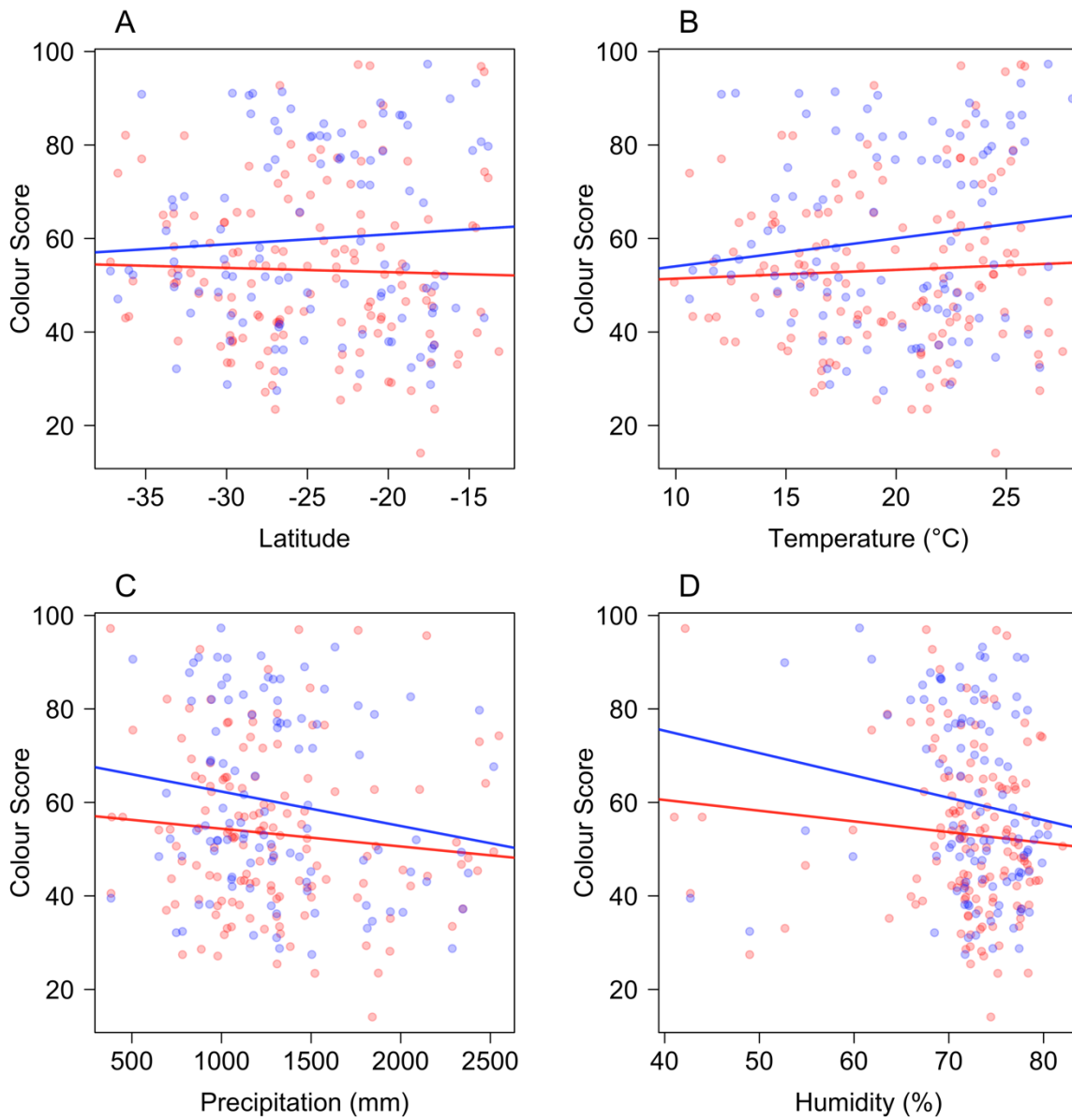


Figure 2: Correlation of climatic factors with colour score (L). No significant relationship was observed between body colour and (A) latitude, and (B) temperature, and (C) precipitation, (D) and

humidity. Y-axis denotes colour score. Orange and blue circles represent male and female data points respectively, where orange solid lines represent linear regression of male body colour with predictor, and blue coloured solid lines represent linear regression of female body colour with predictor.

Table 1: Summary of the effects of climate change on odonates colour.

Sex	Fixed Effects	Estimate	Std. Error	t value	Pr(> t)
Male	Latitude	-0.30	0.24	-1.28	0.20
	Temperature	-0.32	0.61	-0.52	0.60
	Precipitation	-0.001	0.006	-0.15	0.88
	Humidity	-0.31	0.39	-0.81	0.42
Female	Latitude	-0.13	0.28	-0.47	0.64
	Temperature	0.95	0.85	1.12	0.27
	Precipitation	-0.01	0.01	-1.54	0.13
	Humidity	0.27	0.58	0.47	0.64

Sexual dichromatism

We found no significant difference in lightness, L , (LMM: estimate = -0.43 ± 1.46 , $df=573.47$, $t = -0.29$, $p = 0.76$; Fig. 3(A)) or the green-red colour index, a , between males and females (LMM: estimate = -0.21 ± 0.80 , $df=573.86$, $t = -0.26$, $p = 0.79$; Fig. 3(B)). We found a significant difference between the blue-yellow colour index, b , (LMM: estimate = -4.45 ± 1.31 , $df=574.01$, $t = -3.38$, $p = 0.001$; Fig. 3(C)) where females were more likely to be yellow and males were more likely to be blue.

Effect of climatic factors on sexual dichromatism

We fitted linear mixed effects models and found that both precipitation and humidity had a significant relationship with sexual dichromatism (LMM: estimate = 0.01 ± 0.004 , $t = 2.23$, $p = 0.03$, Fig. 4 (A) and estimate = -0.55 ± 0.259 , $t = -2.14$, $p = 0.03$, Fig. 4 (B)) respectively. However, we found weak evidence that latitude was positively (LMM: estimate = 0.08 ± 0.128 , $t = 0.63$, $p = 0.53$, Fig. 4 (C)), and temperature was negatively associated with sexual dichromatism (LMM: estimate = -0.65 ± 0.373 , $t = -1.76$, $p = 0.08$, Fig. 4 (D)). We found that precipitation had a positive correlation with sexual

dichromatism whereas humidity had a negative correlation with sexual dichromatism. We found low correlation coefficient value (0.49) between precipitation and humidity. Summary of the effects of climate on sexual dichromatism is given in Table 2.

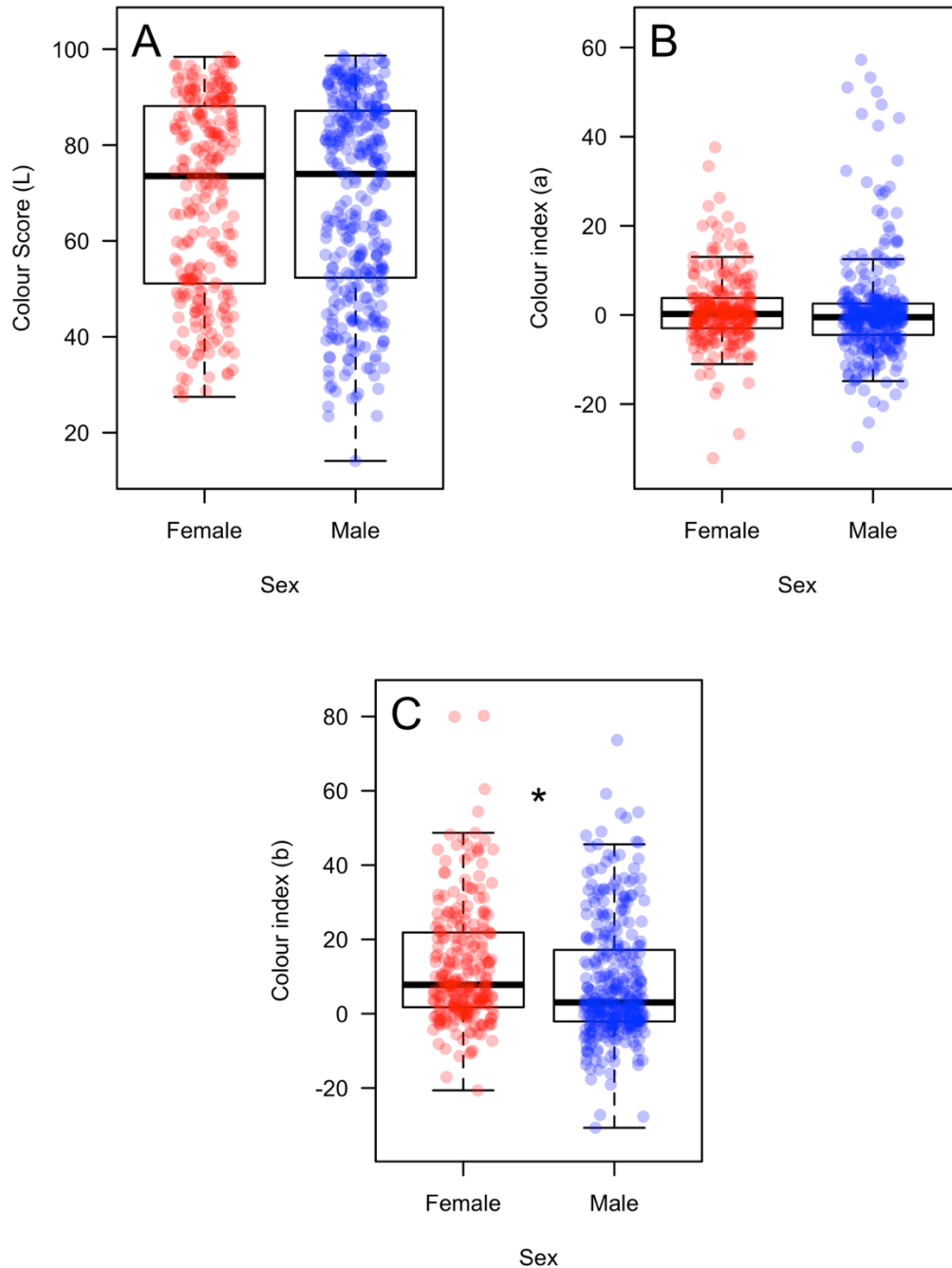


Figure 3: Differences of (A) *L* scores- colour lightness, (B) *a* scores, green to red colour index, (C) *b* scores, blue to yellow colour index, between males and females. The box plots show the median and 25th and 75th percentiles. The whiskers extend to the minimum and maximum but exclude outliers that are beyond 1.5 times the interquartile range. Each dot represents the colour of an

individual species and sex (red circles represent females and blue circles represent males). * indicates $p < 0.05$

Effects of body size on colour and sexual dichromatism

We found that body size had a significant negative correlation with sexual dichromatism (LMM: estimate = -0.43 ± 0.11 , $t = -4.06$, $p < 0.0001$, Fig. 5 (A)), however, it had no relationship with body colour (LMM: estimate = 0.14 ± 0.12 , $t = 1.19$, $p = 0.23$, Fig. 5 (B)).

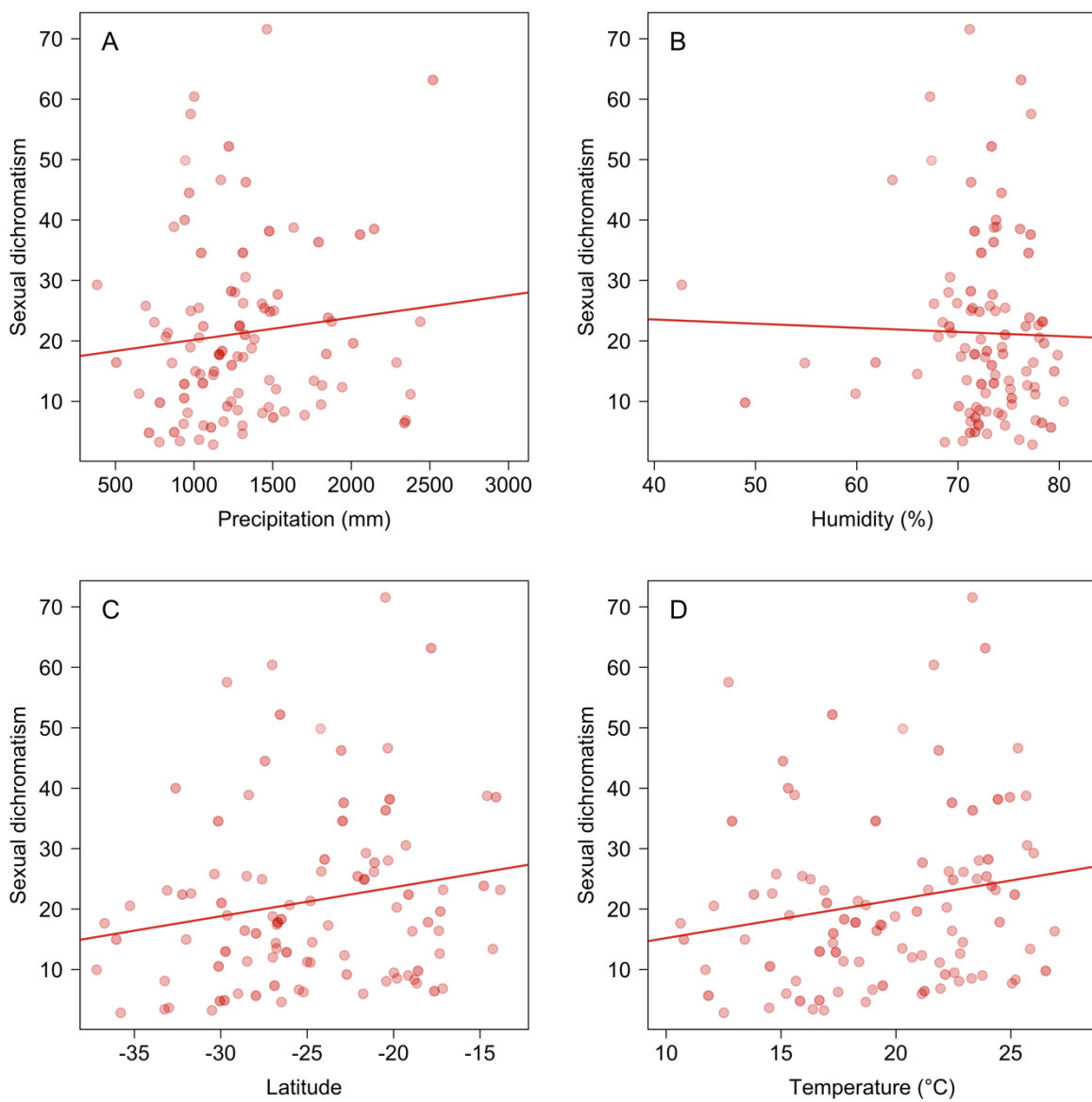


Figure 4: Correlation of climatic factors with sexual dichromatism. (A) Sexual dichromatism increases with mean annual precipitation and (B) decreases with mean annual humidity, whereas there was no relationship with (C) latitude and (D) mean annual temperature. Circles indicate data of sexual

dichromatism for each species, solid lines represent linear regression between sexual dichromatism and predictors. Species sexual dichromatism was calculated by averaging computing Euclidean distances between each of the colours for the species.

Table 2: Summary of the effects of climate on sexual dichromatism. Significant relationships in bold.

Fixed Effects	Estimate	Std. Error	t value	Pr(> t)
Latitude	0.08	0.128	0.63	0.53
Temperature	-0.65	0.373	-1.76	0.08
Precipitation	0.01	0.004	2.23	0.03
Humidity	-0.55	0.259	-2.14	0.03

Discussion

Dragonflies and damselflies exhibit diverse colours across species, and also at different life stages (Suárez-Tovar et al., 2022; Khan & Herberstein, 2020b, 2020a; Khan, 2020). Colours of dragonflies and damselflies, like many other traits, may vary across latitudes and may be impacted by local climatic factors. Here we studied variation of colour and sexual dichromatism in Australian odonates. We found no relationship between odonates' colour and environmental factors, latitude or body size. Our result, however, showed that body size had a strong negative correlation with sexual dichromatism. We also found that climatic factors, such as mean annual precipitation and mean annual humidity, were significantly correlated with sexual dichromatism in Australian odonates.

Latitudinal variation of colour is explained by Gloger's rule; that animals in the tropics benefit from being more colourful than their counterparts in the temperate region as the former environment favours crypsis through the production of more pigmentation (Rensch, 1929). Previous studies on colour variation along latitudinal gradients yielded conflicting results. Some studies found evidence in support of Gloger's rule (i.e., tropical animals are more colourful than temperate) (Carballo et al., 2020; Dale et al., 2015), whereas other studies found the opposite of Gloger's rule (i.e., animals in the temperate region are more colourful than tropics (Dalrymple et al., 2015) or found no correlation between colour and latitudes (Bailey, 1978). Here, like Bailey (1978), we did not find a correlation between colour and latitude in Australian damselflies. While we tested body colour, not wing colour, our findings contrast previous findings that found that wing colour of male dragonflies decreases with

latitude (Moore et al., 2021, 2019). Less melanized wings at higher temperature presumably function as an adaptation to warmer climates through thermoregulation.

We did not find the correlation between body size and latitudes may be due to the smaller body size and slender shape of odonates, which probably do not contribute much to thermoregulation. In support of this argument, Umbers et al., (2013) showed that body colour of the chameleon grasshopper (*Kosciuscola tristis*) had no correlation with thermoregulation. Surface to volume ratio is much larger in wings than bodies, thereby potentially providing a greater relative thermoregulatory function, which could explain why colour is correlated with latitude in wings but not with bodies in small flying insects. Moreover, our result is also contrasted with the result of previous findings (Zeuss, 2014; Pinkert et al., 2017, Acquah-Lampsey 2020).

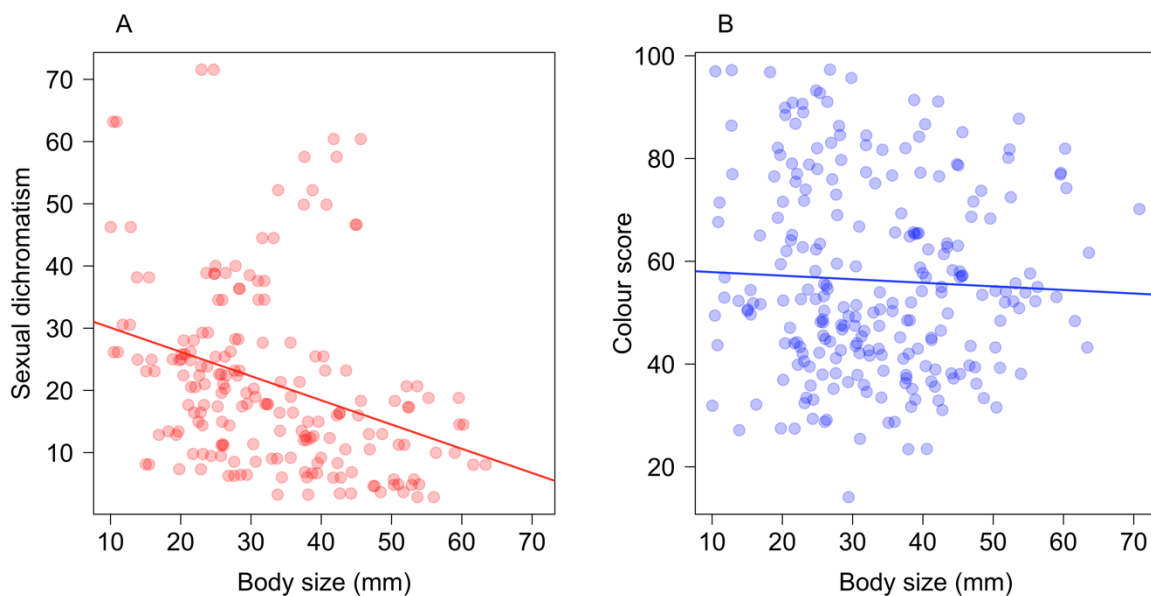


Figure 5: Correlation of body size with sexual dichromatism and colour. (A) Sexual dichromatism decreases with increasing body size. (B) No significant relationship was found between body colour and body size. Each circle represents datum of a species. Solid lines represent the linear regression.

We found no relationship of body colour with climatic factors and body size. Compared to structural and other pigments, melanin pigments provide greater thermoregulatory benefits, therefore resulting in a stronger correlation between melanin based colour, latitude and climatic factors (Badejo et al., 2020). Since we used a photograph-based analysis, we could not differentiate between melanin-based pigment and structural colouration and were unable to determine the impact of colour pigments and latitudes, which might also contribute to our findings. Furthermore, we could not account for ultraviolet and infrared reflectance of body colour, which can also contribute to thermoregulation

(Stuart-Fox et al., 2017; Douglas & Jeffery, 2014; Osorio & Vorobyev, 2008). Finally, we only collected species from Australia and the small geographical region covering small latitudinal range could also account for the lack of observed correlation between colour, latitudes, and climatic factors.

We found that no difference in brightness between males and females, although we did find that males were more likely to be blue and females yellow. Blue colouration in males can function to reduce male-male mating interactions where it is costly, such as in a common mating arena where large numbers of individuals assemble for mating (Khan & Herberstein, 2019; Drury & Grether, 2014). We found that smaller species exhibited a higher level of sexual dichromatism. Our result is consistent with the findings of Carballo et al., (2020) who observed that body size in parrots is negatively correlated with sexual dichromatism. Smaller species have shorter life spans and high population densities, resulting in stronger sexual selection pressure that might drive higher levels of sexual dichromatism (Carballo et al., 2020). In addition, smaller species have lower predation risk than larger species, resulting in relaxed selection on remaining undetected by predators (Penney et al., 2012; Sherratt, 2002; Sheppard & Duncan, 1965), thereby allowing the evolution of more colourful males. However, previous studies found mixed results of sexual dichromatism along latitudinal gradients (Tuomaala et al., 2012; Cardillo, 2002; Bailey, 1978). For example, in the white butterfly (*Pieris napi*), females exhibit greater changes of wing colour than males (Tuomaala et al., 2012). In contrast, in North American dragonfly (*Pachydiplax longipennis*) males but not females wing colour showed significant change across latitudes (Moore et al., 2019). On the other hand, sexual dichromatism showed no variation along latitude in bird taxa (Cardillo, 2002).

In our study, sexual dichromatism increased with mean annual precipitation but decreased with mean annual humidity. Increased rainfall may increase vegetation density resulting in more shaded locations. Females spend most of their time in shaded places (Moore et al., 2021; Ne'eman et al., 2006), so selection should favour darker females to improve thermoregulation, thereby increasing sexual dichromatism. Conversely, closed or forested habitats may be responsible for greater sexual dichromatism as there might be greater selection pressure against conspicuousness in males (Carballo et al., 2020; Marchetti, 1993).

Moreover, carotenoid, a plant based pigment responsible for red and yellow colouration in animals, is taken up through diet (Chui & Doucet, 2009; Delhey, 2015; Olson & Owens, 2005; Prasetya et al., 2020). Males colouration in damselflies function to male-male competition and to reduce unwanted male-male mating (Khan & Herberstein, 2020b). In forest habitat or close canopy where sunlight is little colour signals needs to be more conspicuous for optimal signalling (Théry, 2001). Therefore,

selection should favour more conspicuous colouration in males in the forested habitat with greater canopy coverage.

Insect colour might vary across latitudes as the climatic factors associated with latitude might select colour that maximises thermoregulation. Our large, multi-species analysis does not provide strong evidence that climate impacts the body colour of odonate species *per se* and thus it is difficult to predict how odonate colour will change with global temperature increases. Our study provides evidence that sexual dichromatism is greater in smaller species than larger species, which might have evolved due to intense sexual selection in smaller species. We showed that climatic factors are likely to influence sexual dichromatism, therefore highlighting that the changing climate may impact sexual selection and reproduction.

Author contributions

TH, MKK and MEH 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. DJM contributed to the analysis.

Statement of diversity and inclusion

We strongly support equity, diversity and inclusion in science. 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 underrepresented ethnic minority in science.

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CHAPTER THREE

Impact of climatic factors across latitude on body size in odonates

Manuscript formatted for the *Austral Ecology*

Abstract

Across species, body size and sexual size dimorphism may vary across latitudes and altitudes and may further be impacted by local climatic factors. Body size and sexual size dimorphism may follow macroecological rules such as Bergmann's rule (body size increases with latitudes) or Rensch's rule (sexual size dimorphism increases with body size when males are larger and decreases with body size when females are larger). We tested these macroecological rules in Odonates (damselflies and dragonflies) by comparing body size and sexual size dimorphism across a latitudinal gradient. We further tested if local climatic factors impact body size. We synthesized body size data of Australian Odonata from various online databases and subsequently calculated species-specific sexual size dimorphism. We extracted climatic factors such as mean annual temperature and mean annual precipitation from WorldClim, and mean annual humidity from the Australian Government Bureau of Meteorology. Our mixed effect models found that body size of odonates increases in warmer region which supports the converse Bergmann's rule. We also found a significant relationship between mean annual precipitation and male body size but not with other climatic factors. Further, our data suggest that sexual size dimorphism follows Rensch's rule in Australian odonates. Increase in sexual size dimorphism with body size may be explained by sexual selection, where larger males benefit from greater mating success. The latitudinal and climatic patterns in body size that we observed could be critical in understanding how odonates might be impacted under the rapidly changing climate.

Introduction

Body size affects an individual's behavior, life history and physiology, and impacts ecological and evolutionary processes (Yom-Tov & Geffen, 2011; Chown & Gaston, 2010; Kingsolver & Huey, 2008; Lomolino & Perault, 2007; Wikelski & Romero, 2003). Furthermore, body size bears upon interactions within and across species, such as sexual selection and predator-prey interactions, as well as interacting with fitness indices such as survivability, fecundity, immunity and resistance (Hébert et al., 2016; Sheridan & Bickford, 2011; Russell et al., 2011; Hildrew et al., 2007; Honěk, 1993). Climatic factors, such as temperature and precipitation, have been shown to underpin body size variation across latitudes and altitudes (Wonglersak et al., 2021; Baar et al., 2018; Tseng et al., 2018; Horne et al., 2017). For example, body size of the non-biting midges *Procladius crassinervis* and *Tanytarsus nemorosus* decreases with increasing temperature (Wonglersak et al., 2021). The rapidly changing climate due to anthropogenic activities may impact body size (Gardner et al., 2011; IPCC, 2007; McCarty, 2001) and consequently fitness, which can contribute to the risk of extinction. Understanding variation in body size with respect to environmental factors can therefore identify potential impacts of climate change and guide interventions to maintain biodiversity.

Variation in body sizes across spatial scales may be explained by different biogeographical rules such as Bergmann's rule which states that species are larger at higher latitudes (Bergmann, 1847). However the body sizes of some organisms decrease with latitudes, which is the converse of Bergmann's rule (Mousseau, 1997; Park, 1949). It is debatable that whether Bergmann's rule is well supported in homeothermic animals or not (Riemer et al., 2018). For example, mammals and birds are larger in cooler environments and at higher latitudes (Blackburn et al., 1999; Hawkins & Lawton, 1995; Bergmann, 1847). Invertebrates, on the other hand, often exhibit the converse Bergmann's rule (Shelomi, 2012; Meiri & Dayan, 2003; Mousseau, 1997). For instance, the body size of the cabbage beetle (*Colaphellus bowringi*) decreases with latitude (Tang et al., 2017; Clauss et al., 2013; Ashton, 2002).

Bergmann's rule can be explained by the relationship between body size and latitude in association with ambient temperature, where large animals abundant in cooler regions and small animals in warmer region (Watt et al., 2010; Salewski & Watt, 2017). Larger species can conserve more heat than smaller species due to their lower surface area to volume ratio, with selective benefits for larger organisms in higher latitudes and cooler climates (Tseng & Soleimani Pari, 2019; Bergmann, 1847). This body size and temperature relationship is also known as the temperature-size rule (TSR): the inverse correlation between an animal's body size and temperature (Atkinson, 1994). It has been

shown by both correlative and laboratory studies that there is a strong relationship between body size and temperature (Horne et al., 2017, 2016; Forster et al., 2012; Atkinson, 1994). For example, a negative relationship between body size and temperature was observed in ectotherms (Angilletta, 2004; Kingsolver & Huey 2008). Similarly, the body size of beetles decreased by 95% when reared at high temperatures (Tseng et al., 2018). In contrast, a positive correlation between wing length and mean annual temperature was found in butterflies (Na et al., 2021).

Sexual size dimorphism, predominant among animals, refers to the differences in body size between males and females, and can vary among species and populations (Fairbairn, 2005; Fairbairn & Preziosi, 1994; Manier, 2004; Meiri et al., 2005). Female-biased sexual size dimorphism (larger females) is common in most ectotherms whereas male-biased sexual size dimorphism (larger males) is predominant in many birds and mammals (Blanckenhorn et al., 2007; Fairbairn, 2007; Székely et al., 2004; Blanckenhorn, 2000; Fairbairn, 1997; Cabana et al., 1982). This general view, however, is not consistent, as variation in sexual size dimorphism is common (Colwell, 2000; Székely et al., 2000). Selective processes that may be responsible for sexual size dimorphism in animals include (i) intense competition of one sex over access to mates compared to the other sex (ii) ecological processes and (iii) fecundity selection (Andersson, 1994; Owens & Hartley, 1998; Serrano-Meneses, Córdoba-Aguilar, Azpilicueta-Amorín, et al., 2008a). It is hypothesized that sexual size dimorphism increases with body size in species with male-biased sexual size dimorphism and decreases with body size in species with female-biased sexual size dimorphism (Rensch, 1950). A large number of animal taxa follow this allometric relationship, known as Rensch's rule (Raihani et al., 2006; Serrano-Meneses & Székely, 2006; Colwell, 2000; Fairbairn, 1997).

Odonata is an old insect order that is widely used as a model system to understand ecological and evolutionary processes such as the evolution of body size. Biogeographical patterns of Odonata have been tested in European species, which showed that odonates are smaller at lower latitudes and higher temperatures (Zeuss et al., 2017). A similar study in British Odonata showed a negative correlation between body size and mean seasonal temperature for Zygoptera (damselflies), with no relationship for Anisoptera (dragonflies; Wonglertsak et al., 2020). Some studies found that body size showed a U-shaped (curvilinear) pattern with latitude (Johansson, 2003; Outomuro et al., 2021). The application of body size rules to Odonata has, until now, been largely tested in Northern hemisphere species, with mixed results – some patterns supported Bergmann's rule while others did not.

In this study, we aim to determine the relationship of body size with latitude and other ecological factors (temperature, precipitation, and humidity) in Australian Odonata. We tested Bergmann's and

Rensch's rules. To do so, we collected digital images of odonate wings from an online open library, "Images of Australian Odonata Wings", and measured wing size (a proxy for body size) for our analyses (Tann, 2021).

Materials and methods

Wing size measurement

We used hindwing size as a proxy for body size, as they are strongly correlated (see also Wonglersak et al., 2020; Bai et al., 2016; Corbet, 1999; Haas & Tolley, 1998). We obtained high resolution photographs (~ 9000 x 5000 pixels) of Australian Odonata from the online open access photographic library "Images of Australian Odonata Wings" (Tann, 2021). These images were photographed from taxonomically identified and validated specimens from museum collections. Hindwing length was determined by measuring each wing horizontally from proximal end to distal end. Each wing was measured twice and then averaged to reduce measurement error. In addition, we performed Pearson correlation between two measurements and found the correlation value $R = 0.999$ and $p < 0.0001$. We measured hindwing of 318 species, male ($n=312$) and female ($n=302$). We used ImageJ (version 1.53) software for measuring wing sizes (Schneider et al., 2012). Measurements and calculations are in mm.

Occurrence Data

The Odonata occurrence data used to construct species' ranges were downloaded from the Global Biodiversity Information Facility (GBIF, <https://www.gbif.org>). The GBIF occurrence of each species were extracted by restricting location to Australia, and by setting occurrence status to present, and coordinate status to known only. The downloaded occurrence data included each species' latitudinal position, longitudinal position, occurrence status, collection date, and availability in state.

Climatic Variables

Bioclimatic data were downloaded from WorldClim version 2.1 (<https://www.worldclim.org>) and Australian Government Bureau of Meteorology (<http://www.bom.gov.au>) databases. Mean annual temperature (°C) and mean annual precipitation (mm) data from 1970 to 2000 were downloaded from WorldClim (version 2.1) database with a spatial resolution of approximately 340 km². Annual relative humidity data were collected from the Australian Government Bureau of Meteorology over the period

of 1976 to 2005. To quantify the climate variables for each species, we defined the species range as the extent of the species occurrences, then averaged the climate variable across all cells that overlapped the species range. All analyses were performed using R version 4.1.2 (R Core Team, 2021) and the package “raster” (Hijmans & van Etten, 2012).

Sexual size dimorphism (SSD)

There are several methods to measure sexual size dimorphism in animals and we applied the following formula:

$$\log_{10}(\text{male body size}) - \log_{10}(\text{female body size})$$

where a positive value indicates male-biased (male > female) sexual size dimorphism and a negative value indicates female-biased (female > male) sexual size dimorphism (Serrano-Meneses, Córdoba-Aguilar, & Székely, 2008; Fairbairn, 2007; Lovich & Gibbons, 1992).

Statistical analyses

All statistical analyses and illustrations were performed in R (version 4.1.2). We applied linear mixed-effects models (LMM) using the R package lme4 (Bates et al., 2014) to determine the relationship of body size with latitude and climatic factors (e.g., temperature, precipitation and humidity) for males and females. First, to determine the relationship between body size and latitude, we fitted a model using body size as the response variable, latitude as a fixed effect and family as a random factor. We then applied a model with body size as the response variable, mean annual temperature, mean annual precipitation, and mean annual humidity as fixed effects and family as a random factor, to determine correlation between body size and the climatic factors. We checked the assumptions of heterogeneity and normality of variance for our model residuals using the “performance” R package (Lüdtke et al., 2021).

We used major-axis regression to determine the relationship (isometric or allometric) between sexual size dimorphism and body size using the “lmodel2” package in R (Legendre, 2018; Rohlf & Sokal, 1981). We plotted \log_{10} male against \log_{10} female wing length to test whether Rensch’s rule is evident in Odonata or not. If the slope value is greater than 1, it follows Rensch’s rule (Fairbairn, 1997).

Results

Relationship between body size and environmental factors

We found a significant correlation of male body size with latitude; male body size increased with latitude (LMM: 0.214 ± 0.087 , $t = 2.48$, $p = 0.01$; Fig. 1A; Table 1). We further found that male body size is correlated with mean annual precipitation (LMM: 0.003 ± 0.002 , $t = 2.07$, $p \leq 0.05$; Fig. 1B; Table 1) but not with mean annual temperature (LMM: 0.034 ± 0.192 , $t = 0.18$, $p = 0.86$; Fig. 1C; Table 1) nor mean annual humidity (LMM: -0.067 ± 0.124 , $t = -0.54$, $p = 0.59$; Fig. 1D; Table 1).

We similarly observed a significant positive correlation between body size and latitude in females (LMM: 0.229 ± 0.089 , $t = 2.56$, $p \leq 0.05$; $p = 0.01$; Fig. 1A; Table 2). Female body size, however, was not correlated with mean annual precipitation (LMM: 0.002 ± 0.002 , $t = 1.17$, $p = 0.24$; Fig. 1B; Table 2), mean annual temperature (LMM: 0.135 ± 0.212 , $t = 0.64$, $p = 0.52$; Fig. 1C; Table 2), or mean annual humidity (LMM: -0.012 ± 0.135 , $t = -0.09$, $p = 0.93$; Fig. 1D; Table 2).

Table 1: Summary of the linear mixed-effects models for male body size with climatic factors. Bold results indicate a significant association.

Fixed Effects	Estimate	Std. Error	df	t value	Pr(> t)
Latitude	0.214	0.087	245.94	2.475	0.014
Temperature	0.034	0.192	243.70	0.176	0.860
Precipitation	0.003	0.002	241.27	2.074	0.039
Humidity	-0.067	0.124	240.20	-0.535	0.593

Table 2: Summary of the linear mixed-effects models for female body size with climatic factors. Bold results indicate a significant association.

Fixed Effects	Estimate	Std. Error	df	t value	Pr(> t)
Latitude	0.229	0.089	237.05	2.562	0.011
Temperature	0.135	0.212	235.30	0.638	0.524
Precipitation	0.002	0.002	232.85	1.173	0.242
Humidity	-0.012	0.135	231.79	-0.091	0.928

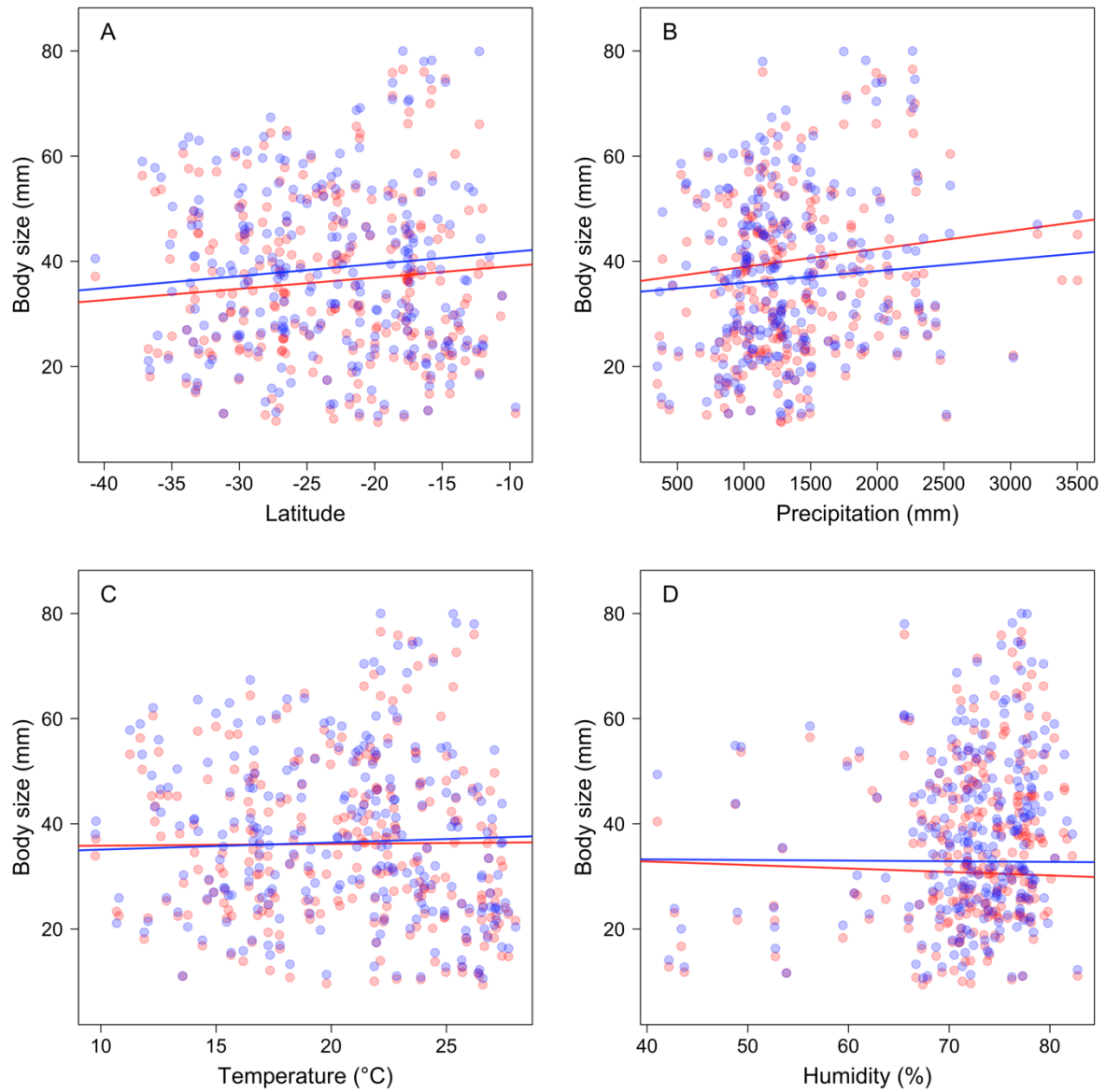


Figure 1: Body size (A) increases with latitude, and (B) increases with precipitation in males only, and (C) does not relate to temperate, and (D) does not relate to humidity. In all panels, orange and blue circles represent male body size and female body size data points respectively. Orange-coloured solid lines represent linear regression of male body size with predictor whereas blue-coloured solid lines represent linear regression of female body size with predictor.

Sexual size dimorphism (SSD) and body size

Odonates exhibited both male- and female-biased sexual size dimorphism, although female-biased sexual size dimorphism was predominant (female wing length, mean \pm SE: 38.11 \pm 0.86mm, N= 302; male wing length, mean \pm SE: 36.29 \pm 0.81mm, N=312; mean difference = 1.82, Wilcox one-sample test, V = 5320, P < 0.0001; Fig. 2). Our result provides evidence that Australian odonates follow

Rensch's rule as the major axis slope between $\log_{10}(\text{male body size})$ and $\log_{10}(\text{female body size})$ is significantly greater ($\beta = 1.024$, $N = 296$) than one (95% CI [1.004–1.043]; Fig. 3).

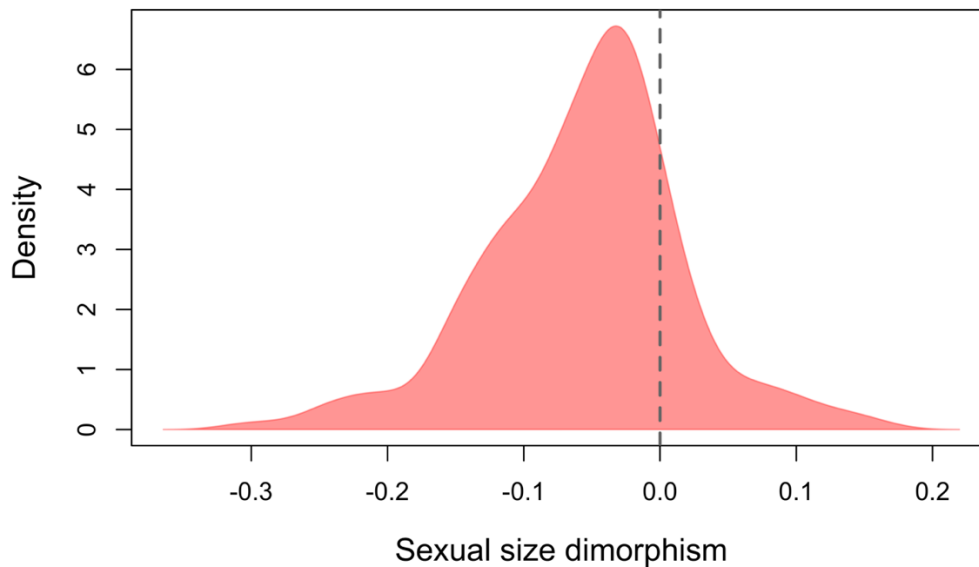


Figure 2: Distribution of sexual size dimorphism in wing length in odonates. The vertical grey line indicates monomorphism. Positive values indicate male-biased sexual size dimorphism and negative values indicate female-biased sexual size dimorphism. This plot also represent that our study species showed comparatively more female-biased sexual size dimorphism than male-biased sexual size dimorphism.

Discussion

Variation of body size across latitudes and how the local climatic factors impact this size variation as well as population fitness is important to determine species extinction risk under the rapidly changing climate. In this study, we analyzed the relationship of sex-specific body size with latitude and climatic factors (mean annual temperature, mean annual precipitation, mean annual humidity) in Australian odonates. We found a significant relationship between body size and latitude in both males and females. Our data supports the opposite pattern of Bergmann's rule. In addition, male body size increased with mean annual precipitation and female body size did not correlate with any of the climate factors we tested. We also found odonate body size showed both male- and female-biased sexual dimorphism and followed Rensch's rule.

Our analysis revealed a significant correlation between odonate body size and latitude which supports the opposite pattern of Bergmann's rule: larger size odonates in warmer region. Our result is

consistent with other insect studies including stick insect-*Dares murudensis* (Büscher, 2014), fly-*Drosophila subobscura* (Huey et al., 2000), beetles-Graptodytes and Hydroporus genus (Pallarés et al., 2019), and geometrid moths (Brehm et al., 2004). Animal's growth during seasonal time may be linked converse Bergmann's rule (Roff, 1980). Insects have longer time for growth at lower latitude compared to higher latitude, as seasonal length are longer at warmer region. Also, extreme heats at lower region may contribute to converse Bergmann's rule (Winterhalter et al., 2008). Though birds and mammals strongly follow Bergmann's rule, in insects, evidence for this rule is highly variable. Mixed responses were found in beetles for example, with larger sized beetles having a positive relationship with latitude (Bergmann's rule) and smaller sized beetles having a negative relationship with latitude – the converse of Bergmann's rule (Tseng & Soleimani Pari, 2019). In addition, Baranovská & Knapp (2018) observed a declining pattern of *Silpha carinata* (beetle) body size (both sexes) with increasing altitude. Large body size is often linked to an organism's fitness whereby large body size in females results in greater fecundity, attracts more males, and has an advantage in collecting resources (Blanckenhorn, 2000; Honěk, 1993; Khan, 2020; Lighton et al., 1994; Rivero & West, 2002) and larger males have greater mating success through male-male competition and female choice (Lindenfors et al., 2002; Székely et al., 2000). The benefits of larger body size may, however, change based on resource allocation, acquisition pattern, and selection pressure (Kemp & Alcock, 2003). For example, damselflies with an intermediate body size have greater mating success than larger or smaller damselflies (Thompson & Fincke, 2002; Stoks, 2000; Gribbin & Thompson, 1991). Variation in body size may stem from phenotypic plasticity and could be adaptive, yet the adaptive significance has rarely been tested (Hassall et al., 2014; Huey et al., 2000). Furthermore, environmental variation across latitudes may impact physiological processes at the cellular level thereby affecting body size variation along latitudinal clines (Atkinson & Sibly, 1997; van der Have & de Jong, 1996).

Latitude can affect a range of climatic factors including temperature, photoperiod, humidity and rainfall (De Block et al., 2008; De Block & Stoks, 2003) and our observed correlation between body size and latitude could be due to those climatic factors. Indeed, we found a significant correlation between male body size and mean annual precipitation. More precipitation results in denser vegetation thereby creating more feeding opportunities for odonates, which potentially leads to larger male size. Climatic factors may have sex-specific impacts in odonates, as mean annual precipitation had an impact on male body size but not on female body size. Our result in males is consistent with a previous finding in beetles that found a significant relationship between body size and mean annual precipitation (Baar et al. 2018). We, however, did not observe a significant relationship between male body size and temperature or humidity. Moreover, in females, we did not find a significant relation

between female body size and mean annual temperature, mean annual precipitation, or mean annual humidity. While our results for females are consistent with previous findings where no relationship between body size and mean annual temperature was observed (Baar et al., 2018; Hassall et al., 2014), they contradict the observed significant relationship between body size (both sexes) and temperature in beetles, chironomids, and butterflies (Na et al., 2021; Tseng et al., 2018; Wonglersak et al., 2021). This may be due to the semi aquatic life history of Odonata that may affect the response of body size to environmental factors (Hassall et al., 2014). For example, Forster et al. (2012) observed that the response of the temperature size effect in aquatic species is greater than terrestrial species. Even between odonate groups, environmental differences may have different impacts. For example, in damselflies (Zygoptera) wing length had a positive relationship with seasonal temperature whereas in dragonflies (Anisoptera) wing length had no relationship with seasonal temperature (Wonglersak et al., 2020). Clearly, in odonates, sex, species, and suborder can affect the magnitude of temperature and body size responses. We believe more studies are required both at the inter- and intra-specific level to understand the complex relationship between body size and climatic factors.

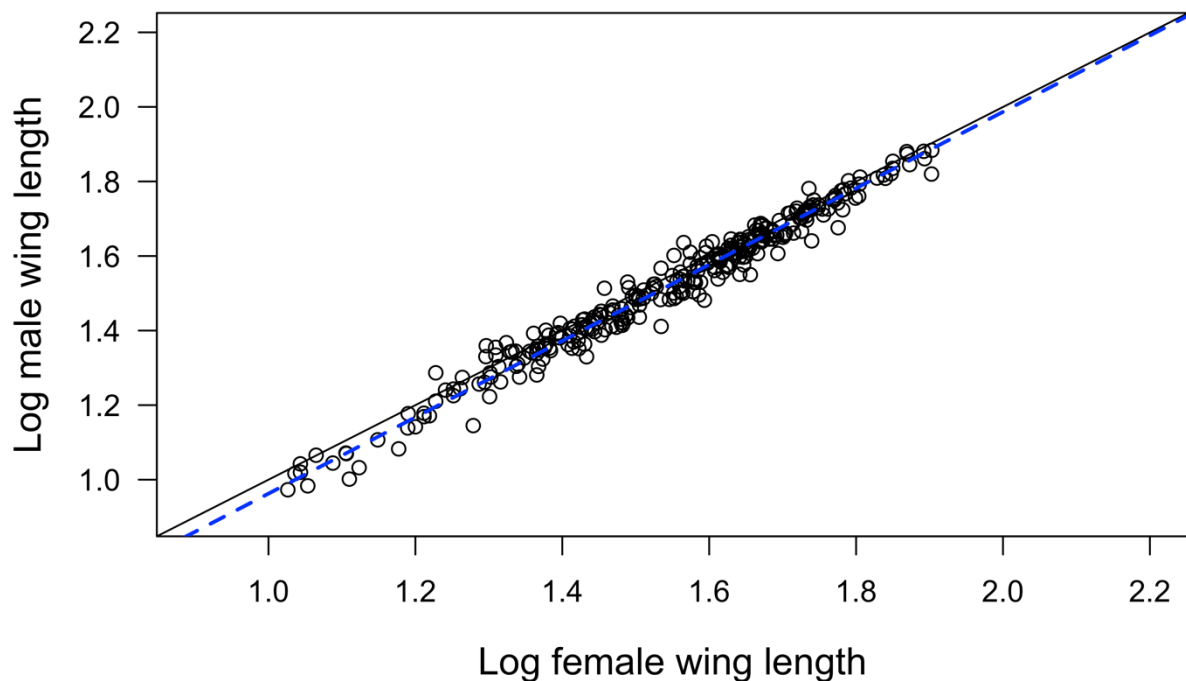


Figure 3: Log₁₀ male wing length on log₁₀ female wing length in Odonata. Continuous solid line represents isometric (size of males is equal to size of females) relationship whereas dashed line indicates the fitted relationship using major-axis regression

Our study found that odonates show both male-biased and female-biased sexual size dimorphism. Our result is consistent with previous findings, which also reported both male-biased sexual size dimorphism and female-biased sexual size dimorphism in European odonates (Serrano-Meneses, Córdoba-Aguilar, & Székely, 2008). In support of Rensch's rule, in Australian odonates, sexual size dimorphism increased with body size in species with larger males and decreased with body size in species with larger females (Rensch, 1950). A similar result was found in a previous study (Johansson et al., 2005), however, the result varied (across suborders) in another study (Serrano-Meneses, Córdoba-Aguilar, Azpilicueta-Amorín, et al., 2008a). Small male size may enhance male agility and help males to compete over females (Serrano-Meneses & Székely, 2006; Raihani et al., 2006; Hernández & Benson, 1998; Andersson & Norberg, 1981). This small male advantage could be further selected if females prefer agile and small males; selection may thus result in female-biased sexual size dimorphism (Blomqvist et al., 1997; Figuerola, 1999; Foellmer & Moya-Laraño, 2007; Hakkarainen et al., 1996; Neems et al., 1998). A previous study on the territorial damselfly, *Lestes viridis*, showed that small sized males have higher mating success than larger sized males if the smaller male had a high flight performance (De Block & Stoks, 2007). In line with this evidence, male agility was found to influence sexual size dimorphism in territorial odonates, whereby agile males benefitted from being small (Serrano-Meneses et al., 2008). Sexual selection may favor larger male size when mating success is related to territoriality (Fairbairn & Preziosi, 1994). Larger male odonates have a greater capability to protect or defend their territories and therefore a higher mating success (Johansson et al., 2005). The reason may be related to a higher proportion of reserves (e.g., lipids) stored in larger males (Serrano-Meneses et al., 2007; Córdoba-Aguilar & Cordero-Rivera, 2005). In summary, sexual selection, natural selection, and ecological factors may all contribute to sexual size dimorphism in odonates.

To our knowledge, this is the first study to perform comparative analyses of body size with climatic factors in Australian odonates. We believe more work (e.g., phylogenetically corrected analyses and experimental studies with large numbers of samples) is required to understand the general geographic trend of body size along environmental gradients. Moreover, we think it is important to focus on factors other than body size, such as voltinism, photoperiods, and genetic effects that may be associated with variation in species body size and sexual size dimorphism in odonates. Finally, experiments such as “common garden experiment” are required for understanding how species grow and develop at various latitudes.

Our comparative analysis provides evidence that latitudinal variation and climatic factors such as precipitation strongly influence Odonata body size. Our study highlights that climatic factors impact

insects' body size, which consequently impacts fitness, thereby contributing to species extinction risks. Anthropogenic activities are accelerating climate change, so we need a broader understanding of how climate change might contribute to insects' body size changes and extinction risks.

Author contributions

TH, MKK and MEH 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. DJM contributed to the analysis.

Statement of diversity and inclusion

We strongly support equity, diversity and inclusion in science. 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 underrepresented ethnic minority in science.

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