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Evolutionary interactions between thermal ecology and sexual selection

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Abstract

Thermal ecology and mate competition are both pervasive features of ecological adaptation. A surge of recent work has uncovered the diversity of ways in which temperature affects mating interactions and sexual selection. However, the potential for thermal biology and reproductive ecology to evolve together as organisms adapt to their thermal environment has been underappreciated. Here, we develop a series of hypotheses regarding (1) not only how thermal ecology affects mating system dynamics, but also how mating dynamics can generate selection on thermal traits; and (2) how the thermal consequences of mate competition favour the reciprocal co-adaptation of thermal biology and sexual traits. We discuss our hypotheses in the context of both pre-copulatory and post-copulatory processes. We also call for future work integrating experimental and phylogenetic comparative approaches to understand evolutionary feedbacks between thermal ecology and sexual selection. Overall, studying reciprocal feedbacks between thermal ecology and sexual selection may be necessary to understand how organisms have adapted to the environments of the past and could persist in the environments of the future.

KEYWORDS

climate change, co-adaptation, mate choice, mate competition, mating systems, reciprocal causation,

INTRODUCTION

Organisms must balance many demands as they adapt to their environments (Noordwijk & de Jong, 1986; Reznick et al., 2000; Ricklefs & Wikelski, 2002). Competing for mates, for example, often requires that animals use habitats or express traits that hinder survival (Andersson, 1994; Wiens & Tuschhoff, 2020; Zuk & Kolluru, 1998). Biologists have long understood that these survival costs can offset the benefits of mating success and limit the exaggeration of reproductive characters (Andersson, 1994; Cornwallis & Uller, 2010; Endler, 1980; Fisher, 1958; Gordon et al., 2015; Heinen-Kay et al., 2015; Maan & Seehausen, 2011; Wiens, 2001; Wiens & Tuschhoff, 2020; Zuk & Kolluru, 1998). However, biologists are also increasingly recognising that adapting to the demands of mate competition can involve the evolution of viability-related traits that alleviate these survival costs (Alpedrinha et al., 2019; Fowler-Finn & Hebets, 2011; Fryxell et al., 2019; Hedrick, 2000; Svensson, 2019). Adapting to an environment may therefore entail both reproductive characters evolving to accommodate the demands of survival, and viability-related characters evolving to accommodate the demands of mate competition (Alpedrinha et al., 2019; Lande & Kirkpatrick, 1988; Servedio & Boughman, 2017; Vitousek et al., 2014).

Temperature is one of the most important environmental factors to which organisms must adapt because it influences nearly every biological process

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(Kingsolver, 2009). Decades of research have explored the many ways in which adaptation enhances survival at prevailing thermal conditions (Angilletta et al., 2002; Angilletta, Cooper, et al., 2010; Huey & Kingsolver, 1989; Huey & Stevenson, 1979; Kingsolver, 2009; Levesque & Marshall, 2021). Recent work also shows that adapting to temperature can involve changes to an organism's reproductive ecology (reviewed in García-Roa et al., 2020; Leith et al., 2021). Nonetheless, previous investigations into how viability-related and reproductive traits evolve together as organisms adapt to their thermal environment have only invoked 'good genes' mechanisms (e.g. Gómez-Llano et al., 2021; Martinossi-Allibert et al., 2019; Parrett & Knell, 2018; Yun et al., 2018), whereby sexual selection on condition-dependent traits accelerates local adaptation by indirectly favouring alleles that facilitate resource accumulation (Lorch et al., 2003; Servedio & Boughman, 2017). While 'good genes' mechanisms are one factor that could indirectly cause the correlated evolution of sexual and thermal traits, evolutionary theorists have proposed a variety of more direct mechanisms by which viability-related traits co-adapt with sexual characters to accommodate or enhance the sexual trait's fitness consequences (Bonduriansky, 2011; Husak & Swallow, 2011; Møller, 1996). Our understanding of interactions between sexual selection and thermal adaptation therefore demands a more expansive investigation into how the evolution of reproductive traits reciprocally alters the evolution of thermal physiology and thermoregulation.

Incorporating co-adaptation of the multivariate phenotype—in which the evolutionary trajectory of one trait alters the trajectory of many other traits, and vice versa (Huey et al., 2003; Levins & Lewontin, 1985; Muñoz & Losos, 2018; Svensson, 2018)—yields two overlooked insights regarding temperature's impact on biological diversity. First, variation in thermal biology among taxa should underlie variation in where and when mating occurs as well as how sexually selected traits evolve at different temperatures. Thermoregulatory demands, for instance, may force reproductive rivals or potential mates to aggregate in habitats that contain preferred temperatures (Emlen & Oring, 1977; Trillmich & Trillmich, 1984). Second, the demands of mate competition could, in turn, affect selection on thermal biology when sexual trait expression influences an organism's body temperature or thermoregulatory demands. For example, some colour patterns elevate body temperatures by absorbing more energy from the sun (e.g. Moore et al., 2019; Punzalan et al., 2008; West & Packer, 2002); enlarged ornaments can influence heating and cooling rates (e.g. Darnell & Munguia, 2011; Picard et al., 1999; Shepherd et al., 2008; Taylor, 1966); metabolically demanding courtship and combat behaviour can generate substantial body heat (Chung-Davidson et al., 2013; Erregger et al., 2017; Norris et al., 2010; Villet et al., 2003) and post-copulatory mate guarding can limit opportunities for thermoregulation (e.g. Saeki et al., 2005). Provided sufficient genetic variation and few genetic constraints (Diamond, 2017; Logan et al., 2020), thermal biology and sexually selected traits should evolve together to enhance performance at the body temperatures experienced during mate competition (Box 1).

Given the importance of thermal ecology to individual-, population- and species-level fitness (Buckley et al., 2015; Huey & Berrigan, 2001; Kingsolver, 2009; Sinervo et al., 2010), and the pervasiveness and strength of sexual selection (Hoekstra et al., 2001; Kingsolver et al., 2001; Svensson et al., 2006; West-Eberhard, 1983), reciprocal interactions between thermal ecology and sexual selection could be overlooked features of ecological adaptation. Here, we develop a series of hypotheses for how interactions between temperature and sexual selection promote the correlated evolution of thermal ecology, mating systems and sexually selected traits. (1) Differences in thermal ecology among populations or species can alter mating system dynamics; and (2) Mating dynamics, in turn, can limit opportunities for thermoregulation and affect the evolution of thermal traits. Additionally, the expression of a wide variety of sexual characters can affect body temperatures and thermoregulatory demands, causing: (3) The evolution of thermal biology to constrain and compensate for the evolution of sexual traits and (4) Thermoregulatory and reproductive demands to collectively shape the evolution of multifunctional sexual traits. Importantly, interactions between thermal ecology and sexual selection can arise at any point throughout the progress of mate competition. We therefore discuss our hypotheses in the context of both pre-copulatory and post-copulatory sexual selection. To aid future explorations of the proposed hypotheses, we describe how combinations of experimental and phylogenetic comparative methods could be used to understand evolutionary feedbacks between thermal ecology and sexual selection. Finally, we address how co-adaptation between sexual and thermal traits could promote or forestall physiological adaptation in response to anthropogenic warming.

THERMAL ECOLOGY AND MATING SYSTEM DYNAMICS

Thermoregulation, habitat use, and pre-copulatory drivers of mating system dynamics

Patterns of habitat use related to thermoregulation could affect how mating systems arise in thermally variable environments by altering local density and dictating access to potential mates (Emlen & Oring, 1977; Kokko & Rankin, 2006; Sugita & Ueda, 2013). Heightened thermoregulatory demands can lead to stronger and more frequent biotic interactions by forcing individuals to aggregate

BOX 1 A primer on thermal adaptation

Selection on thermal physiology and thermoregulation stems from exposure to unsuitable body temperatures. In ectothermic animals, these physiological effects are characterised by thermal performance curves (Huey & Stevenson, 1979; Figure 1a) indicating the body temperature where performance is maximised (thermal optimum, or T_{opt}), the range of temperatures where performance is high (performance breadth, or T_{br}) and the maximum and minimum temperatures where performance ceases (critical thermal maximum and minimum, or CT_{max} and CT_{min}). The range of temperatures found between the critical thermal maximum and minimum represent an ectotherm's thermal tolerance range. Selection from extreme temperatures may favour increased heat or cold tolerances, while selection from shifts in intermediate temperatures may favour higher or lower thermal optima. Unsuitable body temperatures can also favour the evolution of habitat use and thermoregulatory behaviour.

In contrast to ectotherms, many endotherms maintain relatively stable body temperatures across a range of ambient temperatures known as the thermal neutral zone (*TNZ*; Figure 1b). Because minimal energy is required to maintain physiological stability within the *TNZ*, endotherms with wider *TNZ*'s are often considered more thermally tolerant (e.g. Khaliq et al., 2014). Increased thermal tolerances in endotherms generally involve adaptations to thermoregulatory physiology, such as cuticular blood flow regulation, as these traits reduce the energy required to generate or dissipate body heat at extreme temperatures (Angilletta, Cooper, et al., 2010; Tattersall et al., 2012). Thus, selection favouring increased heat or cold tolerances in endotherms could cause the evolution of more disparate upper and lower critical temperatures of the *TNZ* (T_{uc} and T_{lc} respectively) and/or shallower slopes of energy expenditure across temperatures outside the *TNZ* (Porter & Kearney, 2009; Riek & Geiser, 2013). However, comparisons of these traits should always be viewed in the context of anatomical and physiological evolution (Levesque & Marshall, 2021).

In both ectotherms and endotherms, changes to an individual's body temperature can influence the number and quality of gametes that they produce (Parratt et al., 2021; Schou et al., 2021; van Heerwaarden & Sgrò, 2021; Wang & Gunderson, 2022). As a consequence, experiencing sublethal body temperatures can still substantially decrease individual- and population-level fitness. The thermal sensitivity of fertility is often characterised using thermal fertility limits, or the upper and lower thermal limits of gamete production or viability (upper *TFL* and lower *TFL* respectively; Walsh et al. 2019,b). Thermal fertility limits are typically estimated at the population level as the temperatures where a fixed proportion of individuals in a population are effectively sterile (e.g. TFL_{50} and TFL_{80}; Parratt et al., 2021; van Heerwaarden & Sgrò, 2021; Figure 1c). However, studying how mate competition affects selection on the thermal sensitivity of fertility requires quantifying how temperature affects the fertility of individuals (Reinhardt et al., 2015). This could be accomplished by creating individual-level gamete thermal performance curves (Wang & Gunderson, 2022; Figure 1a) for the number of gametes produced, morphological indicators of gamete quality (e.g. sperm length and egg size), or gamete performance (e.g. sperm swimming speed).

within smaller patches of thermally suitable habitat (Adolph, 1990; Dell et al., 2014; Magnuson et al., 1979; Mitchell & Angilletta, 2009). Beyond increasing competition for food, nests, or other ecological resources, densely populated habitat patches could also increase the total number of mates that competitors can access or the likelihood that choosers encounter preferred individuals (Kokko & Rankin, 2006). In marine iguanas (*Amblyrhynchus cristatus*) and Galápagos sea lions (*Zalophus californianus wollebaeki*), for example, thermoregulatory requirements cause females to aggregate at high densities, allowing the few successful males to access more potential mates (Trillmich & Trillmich, 1984; Wolf et al., 2005; Figure 2a). How thermoregulation influences movement patterns and encounter rates could also have important effects on mating system dynamics (Kamath & Losos, 2018). For example, to reduce thermal stress, social groups of female proboscis bats (*Rhynchonycteris naso*) relocate among male roosts that differ in temperature, which enables the dominant male at each roost to access mating opportunities (Wilde et al., 2018). Because thermoregulation increases the number of male roosts that a social group visits, narrow thermal tolerances leading to more thermoregulatory activity may influence variance in male mating success and the potential for sexual selection.

Where and when mate competition occurs may also be governed by factors other than thermoregulation, potentially requiring organisms to use thermally demanding habitats in order to access mates. Because time spent thermoregulating outside of thermally demanding mating habitats could reduce mating success, an organism's mating habitat should generate selection on its thermal

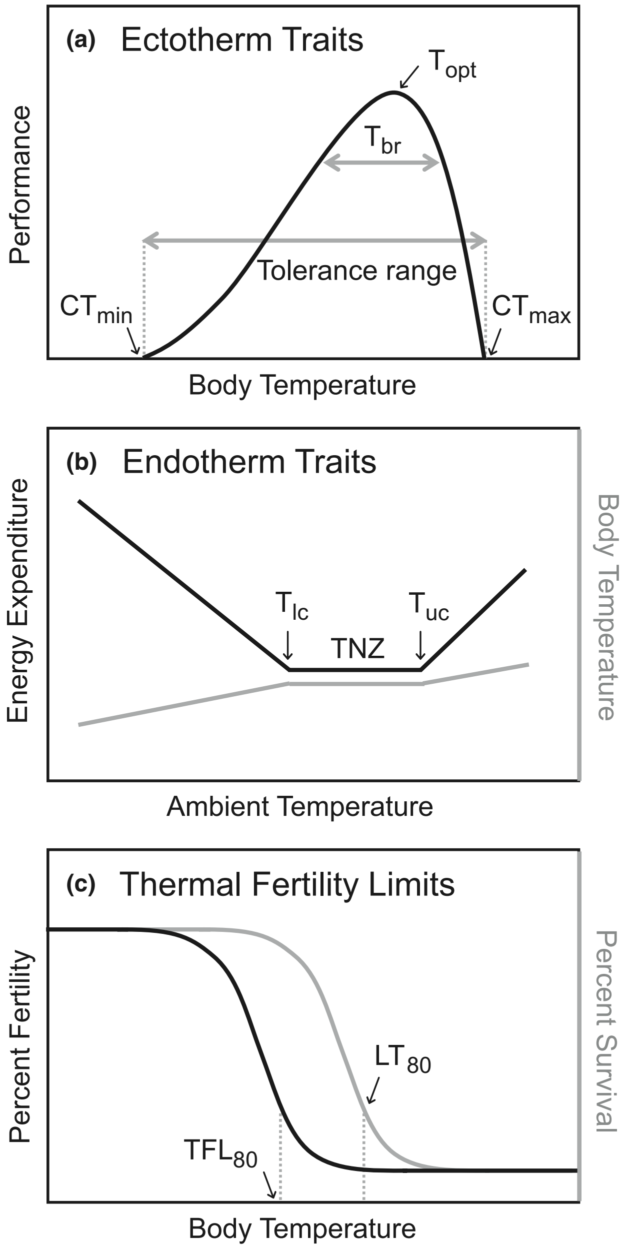

FIGURE 1 Traits relevant to thermal adaptation. (a) For ectotherms, T_{opt} indicates the body temperature where performance is maximised. T_{br} indicates the body temperature range where performance is relatively high compared to maximum performance levels. CT_{max} and CT_{min} represent the high and low body temperatures where performance ceases, with the range between these temperatures being the ectotherm's thermal tolerance range. (b) For endotherms, the *TNZ* represents the range of ambient temperatures where minimum energy is required to maintain physiological performance. T_{uc} and T_{lc} indicate the maximum and minimum ambient temperatures where energy expenditure must increase to maintain physiological performance. (c) For ectotherms and endotherms, the temperature in which gametes are no longer produced or in which gametes are no longer viable is the thermal fertility limit, or *TFL*. At the population level, researchers measure TFL_{80} as the temperature where 80% of individuals are sterilised (analogous to LT_{80}, or the temperature resulting in 80% mortality).

physiology. Female *Uca* fiddler crabs, for example, preferentially mate with males that build breeding burrows in the exposed intertidal zone, as these burrows are less likely to collapse when rearing eggs (Christy, 1983). However, surface temperatures outside of these preferred burrows frequently exceed critical thermal limits (Allen et al., 2012; Allen & Levinton, 2014; Darnell et al., 2013, 2015, 2020; Munguia et al., 2017). Because males must remain outside of their burrows to ward off rivals and attract potential mates, fiddler crab mating systems may favour the evolution of higher male heat tolerances to accommodate their reduced thermoregulatory capacity (Darnell et al., 2013, 2020; Figure 2b). Competing individuals may also use specific habitats to increase the efficacy of sexual signals, but to the detriment of thermoregulation. For example, male flycatchers (*Phainopepla nitens*) display and defend their mating territories from exposed perches that are hotter and more physiologically stressful than the surrounding habitat (Rand & Rand, 1943; Walsberg, 1993). Male willow warblers (*Phylloscopus trochilus*) also signal to mates from exposed perches, but instead experience extreme cold temperatures due to exposure to strong winds (Ward & Slater, 2005b). Selection should favour individuals with increased thermal tolerances in these thermally extreme signalling habitats.

Thermal fertility limits and post-copulatory drivers of mating system dynamics

Even if males and females show similar copulation rates, sex differences in thermal fertility limits could generate sex-specific variance in reproductive success at extreme temperatures (Iossa, 2019; Sales et al., 2018; Walsh, Parratt, Atkinson, et al., 2019). For example, in fruit flies (*Drosophila virilis*), male fertility is more heat sensitive than female fertility (Walsh et al., 2021). Heat waves therefore lead to cryptically female-biased operational sex ratios by sterilising many copulating males (Walsh et al., 2021). The few males with high thermal fertility limits would therefore have access to more potential mates and could achieve relatively high reproductive success at extreme temperatures. Thermal fertility limits can also affect remating decisions and sperm competition. High temperatures reduce male fertility in flour beetles (*Tribolium castaneum*) and fruit flies (*Drosophila pseudoobscura*), so females are more likely to mate with multiple males to assure fertilisation under heat wave conditions (Sutter et al., 2019; Vasudeva et al., 2021; Figure 2c). Thus, in extreme thermal environments, the potential for sexual selection may be higher for populations or species with larger sex differences in thermal fertility limits.

Conversely, post-copulatory drivers of mating system dynamics could generate selection on the thermal sensitivity of fertility and general thermal physiology. When

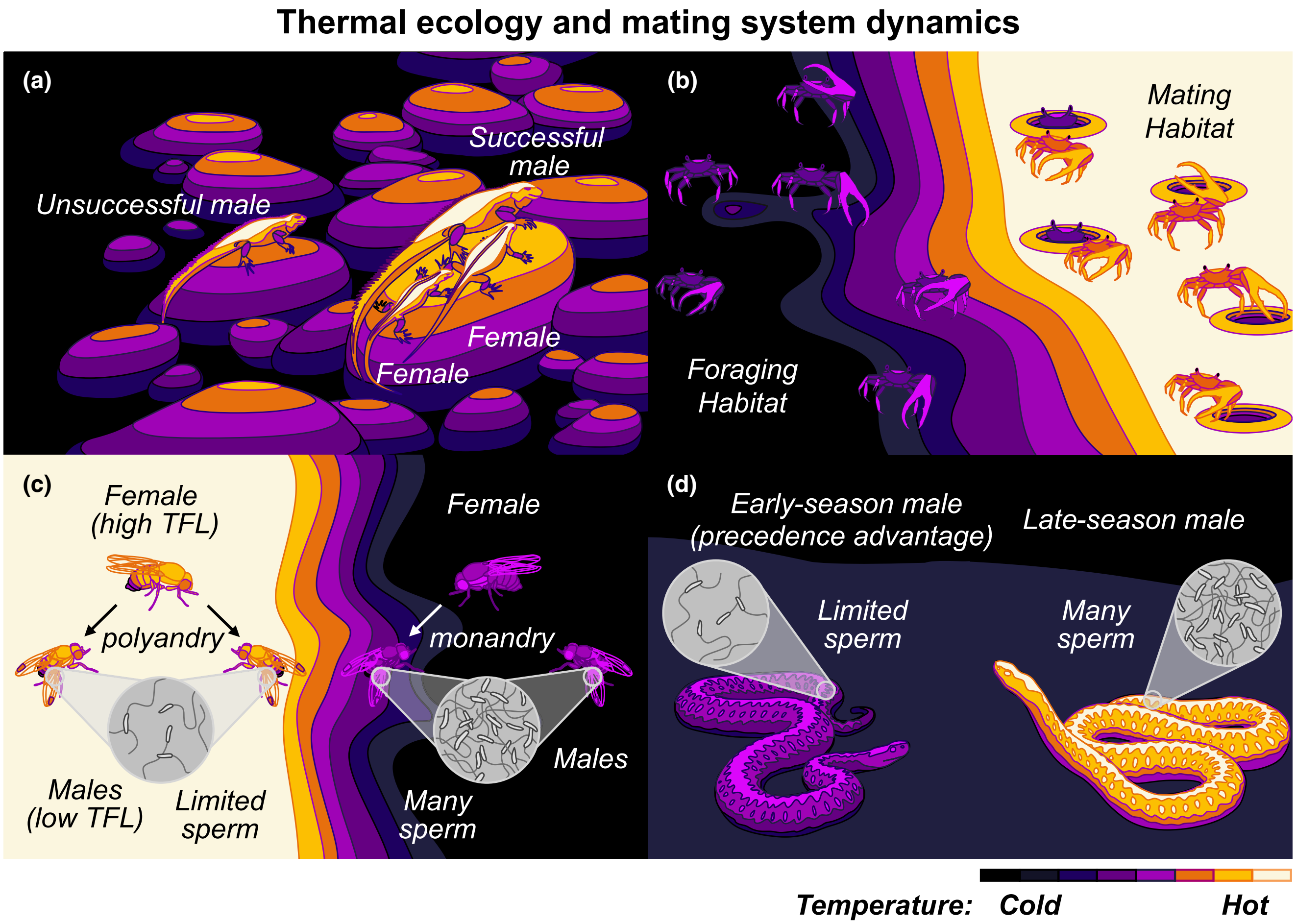

FIGURE 2 Examples of reciprocal interactions between thermal ecology and mating system dynamics. (a) Thermoregulatory demands cause female marine iguanas to aggregate, allowing successful males to access a greater number of available mates (Trillmich & Trillmich, 1984). (b) Male fiddler crabs must expose themselves to extreme thermal habitats while defending breeding burrows, and males that can best tolerate these temperatures should have greater mating success (Allen & Levinton, 2014). (c) Lower thermal fertility limits (*TFL*) in male fruit flies leads females to be more polyandrous under heat wave conditions (Sutter et al., 2019). (d) While polyandry and first-male sperm precedence in European adders favours males that mature earlier in the year, early-maturing males also experience colder temperatures that can hinder sperm production, potentially causing selection to favour more cold tolerant males (Herczeg et al., 2007).

females are more likely to remate as a mechanism for offsetting temperature-induced declines in male fertility (Sutter et al., 2019; Vasudeva et al., 2021), sexual selection may favour the evolution of male thermal physiology for two reasons. First, males with increased thermal fertility limits may be more likely to fertilise a female's eggs at extreme temperatures because they can produce and transfer more sperm (Dickinson, 1986). Second, males with increased thermal fertility limits may produce sperm that are better at competing at extreme temperatures (Reinhardt et al., 2015; Walsh, Parratt, Hoffmann, et al., 2019). Post-copulatory mating dynamics can also influence selection on thermal traits by altering the timing of gamete production. Early-maturing male European vipers (*Vipera berus*) have an advantage in sperm competition due to first-male sperm precedence (Höggren & Tegelström, 2002; Madsen et al., 1992), but also experience colder temperatures that may inhibit physiological performance, including during sperm production (Herczeg et al., 2007; Figure 2d). By favouring earlier-maturing males, polyandry may also favour males with less thermal sensitivity in fertility and males that are generally more tolerant to cool temperatures.

CO-ADAPTATION BETWEEN THERMAL BIOLOGY AND SEXUALLY SELECTED TRAITS

Thermal biology constrains and compensates for the evolution of pre-copulatory sexual traits

Expressing ornaments, weapons, and displays sometimes causes body temperatures to surpass an organism's performance limits, causing thermal biology to determine the costs of and limits on those sexual characters (Fisher, 1958; Kotiaho, 2001; Podos, 2021; Zahavi, 1975). Sexual selection often favours the evolution of dark, saturated colour patterns (Cuthill et al., 2017), which absorb more solar radiation and can elevate body temperatures (Clusella-Trullas et al., 2007; Punzalan et al., 2008; Stuart-Fox et al., 2017; West & Packer, 2002). Because dark sexual coloration can cause individuals to heat beyond their performance limits (e.g. Moore et al., 2019; West & Packer, 2002), selection often favours less extensive sexual coloration in warmer climates (Gaudioso-Levita et al., 2017; Moore et al., 2019, 2021; Svensson & Waller, 2013; Watt, 1968). In odonates (dragonflies and damselflies), for example, dark wing coloration is used by males as a signal to ward of rivals and attract potential mates, but also causes heating in temperate lineages (Laakso et al., 2021; Moore et al., 2019; Svensson & Waller, 2013). As a result, many species of temperate odonates have evolved reduced male ornamentation in warmer climates (Moore et al., 2021; Svensson & Waller, 2013). While female lions (*Panthera leo*) prefer males with dark manes, manes are often lighter in warm climates because dark-maned males are hotter, exert greater thermoregulatory effort, and can carry less prey than lighter-maned males (West & Packer, 2002; Trethowan et al., 2017; Figure 3a). Even if individuals do not experience stressful body temperatures during mate competition, long-term thermal costs of sexual traits could still offset their mating advantages and limit their exaggeration. For instance, increased heat load also causes dark-maned male lions to have lower reproductive output even after securing access to mates (West & Packer, 2002). Because thermal biology determines the extent to which many secondary sexual traits can be exaggerated, the evolution of more elaborate sexual characters may be limited to taxa that already possess increased thermal tolerances in many cases.

Organisms can alternatively offset the costs of exaggerated sexual characters if thermal physiology or thermoregulatory mechanisms evolve as compensatory traits (sensu Møller, 1996; Hedrick, 2000; Fowler-Finn & Hebets, 2011; Husak & Swallow, 2011). Larger bodies, ornaments, or weapons favoured by sexual selection can cause heat stress due to slow heat dissipation (i.e. increased 'thermal inertia'; Speakman & Król, 2010; Stevenson, 1985). The evolution of exaggerated sexual size dimorphisms or enlarged ornaments and weapons could therefore favour the evolution of thermal biology to resolve this heat stress. For example, larger male elephant seals (*Mirounga angustirostris*) not only have a mating advantage, but also experience slower cooling rates and endure more stressful body temperatures during intrasexual combat (Norris et al., 2010; Figure 3b). Male elephant seals appear to have adapted to this thermal stress by increasing cuticular blood flow during combat, which accelerates heat dissipation and increases fighting performance (Norris et al., 2010). Similarly, male *Onthophagus* beetles with larger horns prefer cooler habitats to minimise risk of overheating, whereas horn-less males and females prefer hotter temperatures (Shepherd et al., 2008). In each case, individuals that can either tolerate or avoid extreme temperatures will have an advantage in accessing mates. Increased thermal tolerance or thermoregulatory ability may therefore evolve in taxa with exaggerated sexual characters.

Thermal and reproductive demands collectively shape pre-copulatory sexual trait evolution

Many morphological structures serve both thermoregulatory and sexually selected functions. In some cases, structures that initially evolved because they conferred advantages for mate competition may subsequently be altered to enhance their thermoregulatory benefits for growth and survival (Bonduriansky, 2011; Lande & Kirkpatrick, 1988). The horns used by many bovids in intrasexual signalling and combat, for example, also help dissipate heat in warm climates (Taylor, 1966; Picard et al., 1999; Figure 3c). Natural selection due to an organism's thermal requirements may therefore directly favour exaggerated sexual traits in concert with sexual selection. For instance, after emerging from cool burrows, larger male *Uca* fiddler crabs absorb heat at slower rates, allowing them to spend more time defending territories at hot breeding sites and thus strengthening their mating advantage (Allen et al., 2012). The enlarged claws used as sexual signals by males also serve a cooling function in hot environments (Darnell & Munguia, 2011). When male sexual traits facilitate thermoregulation, natural selection may favour females and juveniles that express the same sexual traits for their general thermal advantages in non-reproductive contexts (Bonduriansky, 2011; but see Svensson & Waller, 2013; Moore et al., 2021). Additionally, thermal adaptation can indirectly affect sexual trait evolution if it involves changes to the structures that are used to perform mating behaviours. For example, because beak morphology in Australian songbirds (Meliphagidae) influences both thermoregulation and song production, the evolution of larger and more elongate beaks to dissipate heat in warm climates has indirectly caused the evolution of slower paced and higher frequency songs (Friedman et al., 2019).

Morphological structures and physiological processes that initially provide viability-related thermal benefits may also subsequently be co-opted for and exaggerated by sexual selection (Bonduriansky, 2011; Persons & Currie, 2019). In some cases, sexual selection may exaggerate thermoregulatory traits in ways that hinder their initial function. In non-avian dinosaurs, sexual selection likely drove the evolution of fusiform feathers as sexual signals, but at the cost of reduced insulation (Persons & Currie, 2019). Similarly, while the anatomy of pterosaur head crests resembles heat dissipation structures found in extant animals (Kellner & De Almeida Campos, 2002), detailed analyses suggest that sexual selection may have exaggerated these crests far beyond what was suitable

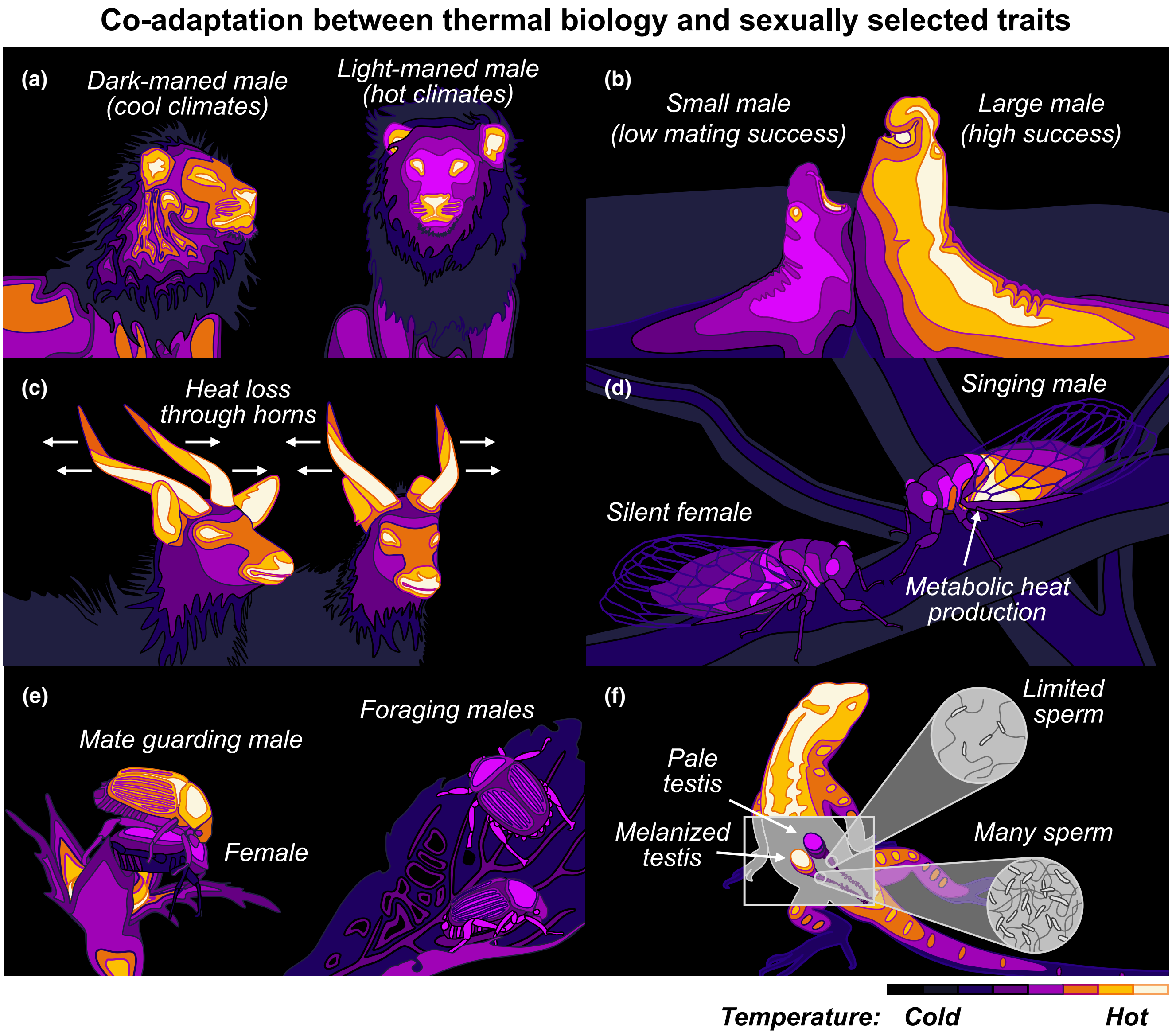

FIGURE 3 Examples showing how interactions between temperature and sexual selection drive the co-adaptation of thermal physiology, thermoregulation, and sexually selected traits. (a) Male lions with darker manes are preferred by females, but dark manes are less likely to evolve in warm climates because they absorb heat from the sun and hinder thermoregulation (Trethowan et al., 2017; West & Packer, 2002). (b) Larger, more dominant male elephant seals incur greater heat stress during combat, but enhanced cuticular blood flow during combat has evolved to compensate for these thermal costs (Norris et al., 2010). (c) In many bovid species, such as the bongo antelope, horns may have initially evolved as intrasexually selected signals and weapons but have secondarily been favoured in warm climates due to their advantages for heat dissipation (Picard et al., 1999; Taylor, 1966). (d) Sexual selection may have favoured the exaggeration of metabolic heat production during acoustic signalling in cicada species due to its advantages for signalling performance (Villet et al., 2003). (e) Thermoregulatory requirements constrain the duration of post-copulatory mate guarding in Japanese beetles (Saeki et al., 2005; Switzer et al., 2008). (f) The melanised left testes of rose-bellied lizards absorb heat from the sun, leading to early sperm production and potential benefits for sperm precedence (Guillette et al., 1983).

for thermoregulation (Tomkins et al., 2010). When the exaggeration of a sexual trait reduces its thermoregulatory function, sexual selection may favour increased thermal tolerances to accommodate this thermal cost. Alternatively, sexual selection may exaggerate thermoregulatory traits that facilitate heat production, insulation, or dissipation due to their thermal advantages during mate competition, just as if they were displays or ornaments. Dark ornamental pigmentation in ambush bugs (*Phymata americana*) is favoured at cool temperatures because it absorbs heat and enhances male mobility, allowing darker males to find and secure mates more quickly (Punzalan et al., 2008). Metabolically generated body heat (Block, 1994; Gillooly & Allen, 2007; Woledge, 1971) can also be co-opted by organisms to aid mate searching (e.g. beetles; Morgan, 1987), or mate attraction (e.g. sea lampreys and crickets, Chung-Davidson et al., 2013; Erregger et al., 2017). For example, metabolic activity during acoustic chorusing in cicadas can elevate body temperatures 20°C to maintain chorusing performance in cool environments (Villet et al., 2003; Figure 3d). Moreover, because organisms that have increased thermal optima can sometimes reach higher maximum performance levels (Angilletta, Huey, & Frazier, 2010; Frazier et al., 2006; Kingsolver & Huey, 2008), the evolution of increased thermal optima may follow the exaggeration of these sexual traits to further enhance their thermoregulatory benefits.

Co-adaptation between thermal biology and post-copulatory sexual traits

Post-copulatory competition and the evolution of post-copulatory sexual traits may be limited by an organism's thermal biology (Suzaki et al., 2018; Vasudeva et al., 2014). For instance, when interactions among gametes occur within the female reproductive tract, thermoregulatory adaptations in females can influence the environment and outcomes of post-copulatory competition (Kekäläinen & Evans, 2018; Reinhardt et al., 2015; Wang & Gunderson, 2022). Some females can bias fertilisations by allocating reproductive fluid to the sperm of specific males (Gasparini et al., 2020; Gasparini & Pilastro, 2011), but these reproductive fluids may only be effective at specific body temperatures (Rossi et al., 2021). Such cryptic mate choice mechanisms may therefore only evolve in lineages where females have already evolved specific thermal preference ranges. Thermoregulatory demands can also affect the evolution of male post-copulatory sexual traits by constraining a male's ability to guard mated females. In Japanese beetles (*Popollia japonica*), males that engage in mate guarding cannot access water for thermoregulation, causing thermoregulatory costs to limit the duration of mate guarding at hotter temperatures (Saeki et al., 2005; Switzer et al., 2008). When extreme temperatures are common, the evolution of mate guarding may be limited to lineages that already possess increased thermal tolerances.

When the advantages to be gained in post-copulatory competition are large, we might also expect the evolution of thermal biology to offset the costs of post-copulatory sexual traits. For instance, the evolution of more heat tolerant male Japanese beetles may compensate for the thermal costs of mate guarding, allowing males to delay thermoregulation, prolong guarding behaviour, and avoid sperm competition (Saeki et al., 2005; Switzer et al., 2008). Under cooler conditions, the evolution of heat absorption mechanisms and other thermoregulatory traits could enhance gamete production and provide advantages during sperm competition. For example, some male *Sceloporus* lizards have evolved a melanised testis that absorbs more heat from the sun, leading to earlier sperm production and potential benefits for sperm precedence or sperm loading (Guillette et al., 1983; Figure 3f). Just as sexual selection has favoured mate guarding, mating plugs, nuptial gifts and a diversity of other strategies of post-copulatory competition (Gwynne, 2008; Parker, 2020; Stockley, 1997; Wedell et al., 2002), post-copulatory sexual selection may favour thermal adaptations that enhance gamete production and a gamete's access to fertilisations.

STUDYING EVOLUTIONARY INTERACTIONS BETWEEN THERMAL ECOLOGY AND SEXUAL TRAITS

Several steps are critical for investigating patterns of reciprocal co-adaptation between thermal biology and sexually selected traits. Researchers should first experimentally determine how expressing a sexual trait or engaging in mate competition influences an individual's body temperature. Phylogenetic comparative methods can then be used to test how thermal biology constrains or compensates for sexual trait evolution, how thermoregulatory and reproductive demands collectively shape the evolution of sexual characters, and the evolutionary consequences of co-adaptation between thermal and sexual traits. Here, we outline useful empirical approaches that could be applied to address each of these steps.

Assessing the thermal consequences of sexual trait expression

Testing how the expression of sexual characters affects an individual's body temperature is required to elucidate the mechanisms driving co-adaptation between sexual and thermal traits. Such tests can be completed by manipulating ornaments and weapons (e.g. Darnell & Munguia, 2011; Moore et al., 2019; Punzalan et al., 2008) or by preventing individuals from performing certain behaviours (e.g. Elias et al., 2006) and then characterising the impact of trait manipulation on body temperatures during mate competition. Other approaches could be used to assess the thermal consequences of sexual trait expression when phenotype manipulations are challenging or impossible. For instance, biophysical models that approximate the size, shape, and material composition of sexual ornaments or weapons can be used to estimate heat absorption and dissipation through these structures (Bakken, 1976; Picard et al., 1999). For research on living animals, recent advancements in thermal imaging offer a minimally invasive method to assess heating and cooling rates of specific morphological characters (Moore et al., 2019; Svensson et al., 2020; Tattersall et al., 2009) and heat generation due to metabolically demanding courtship or combat behaviour (Norris et al., 2010; Ward & Slater, 2005a).

Testing how thermal biology constrains or compensates for sexual trait evolution

To understand how the evolution of thermal biology interacts with the evolution of sexual traits, researchers can first test for the existence of a correlation between these traits at the population- or species-level using phylogenetic comparative methods (Felsenstein, 1985; Harmon, 2018; Revell, 2010). Next, phylogenetic path analyses can assess whether it is most plausible that the evolution of thermal biology has constrained the exaggeration of sexual traits or has accommodated their thermal costs (van der Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013). In cases where both causal directions are supported, a model-averaging approach could assess the relative importance of each direction under reciprocal causation (van der Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013). In Box 2 and Figure 4, we demonstrate how these two methods can be applied to study patterns of co-adaptation between heat tolerance, mating systems, and sexual size dimorphism in cyprinid fishes.

Phylogenetic comparative methods, however, have limited ability to determine causal evolutionary relationships among traits (Losos, 2011). Additionally, current path analysis approaches cannot directly evaluate causal models with reciprocal relationships (Lefcheck, 2016; Pearl & Mackenzie, 2018; Svensson, 2018). In some cases, the relative strength of two reciprocal effects can be assessed indirectly by averaging models that include each causal direction in isolation (van der Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013). When time series data are available, researchers can group the data into discrete time periods and use a series of path analyses to track the causal feedback through time (Greenland et al., 1999; Pearl & Mackenzie, 2018; Svensson, 2018). Time series path analyses, for instance, might be used to test if thermal biology constrained the evolution of sexual traits in an earlier time period, leading sexual selection to cause the evolution of thermal traits in the following period. The most insightful approach would be to pair phylogenetic comparative methods with experiments that test how mate competition generates selection on sexual and thermal traits in tandem (Svensson, 2018; Weber & Agrawal, 2012). Phenotype manipulations and multivariate selection analyses can test how variation in sexually selected traits affects selection on thermal physiology, even when these traits are naturally correlated within the focal population or species. For instance, if sexual selection for heat-absorbing melanisation also favours correlated evolution of

BOX 2 Analysing co-adaptation between thermal and sexual traits in cyprinids

Thermal tolerances may constrain the evolution of sexual size dimorphisms (SSD) by limiting the evolution of body size or guiding the evolution of mating systems. Alternatively, thermal tolerances may evolve to compensate for the evolution of body size or other thermal costs involved in mate competition. To illustrate how researchers might test for these outcomes, we explored the evolution of heat tolerance, body size, SSD, and mating systems in cyprinid fishes (Bennett et al., 2018; Pyron, 1996; Pyron et al., 2013). Sexual selection in cyprinids drives the evolution of behaviours with potential thermal costs, including specialised habitat use and metabolically demanding reproductive behaviour (Ah-King et al., 2005; Mayden & Simons, 2002; Smith, 1991). To test for correlated evolution of heat tolerance and sexual traits, we first conducted a phylogenetic general least squares analysis (see Supporting Information Methods and Results) leveraging data on mating systems, sex-specific body sizes (Pyron et al., 2013), $CT_{\max}$ (Bennett et al., 2018), and the phylogenetic relationships for 25 species (Rabosky et al., 2018). We found that species with higher $CT_{\max}$ are more likely to have pair-spawning mating systems, which intensify sexual selection ($\chi^2_1 = 4.02$, $p = 0.0450$; Table S2; Figure 4a; Pyron, 1996), along with smaller mean body sizes ($\chi^2_1 = 3.90$, $p = 0.0482$; Table S2).

To determine the most plausible causal relationship underlying this correlated evolution, we then used a phylogenetic path analysis (see Supporting Information Methods and Results; von Hardenberg & Gonzalez-voyer 2013; van der Bijl, 2018). We constructed four hypothesised path models: (1) $CT_{\max}$ constrains mating-system and body size evolution, and SSD drives the evolution of mean body size (Figure 4b); (2) $CT_{\max}$ constrains mating system and body size evolution, and mean body size constrains SSD evolution (Figure 4c); (3) $CT_{\max}$ compensates for mating-system and body size evolution, and SSD drives the evolution of mean body size (Figure 4d) and (4) $CT_{\max}$ compensates for mating-system and body size evolution, and mean body size constrains SSD evolution (Figure 4e). The first model received the most support (CICc = 27.3; Table S3), indicating that the evolution of pair spawning, and therefore stronger sexual selection, is likely limited to species that have already evolved higher heat tolerances (Figure 4f). However, while this model suggests that the evolution of male-biased SSD drives the evolution of larger body sizes, it also indicates that evolution of higher heat tolerances constrains body size evolution, leading to smaller mean body sizes (Figure 4f). It is therefore likely that thermal evolution constrains mating system evolution for reasons other than the relationship between pair spawning, male-biased SSD, and mean body size.

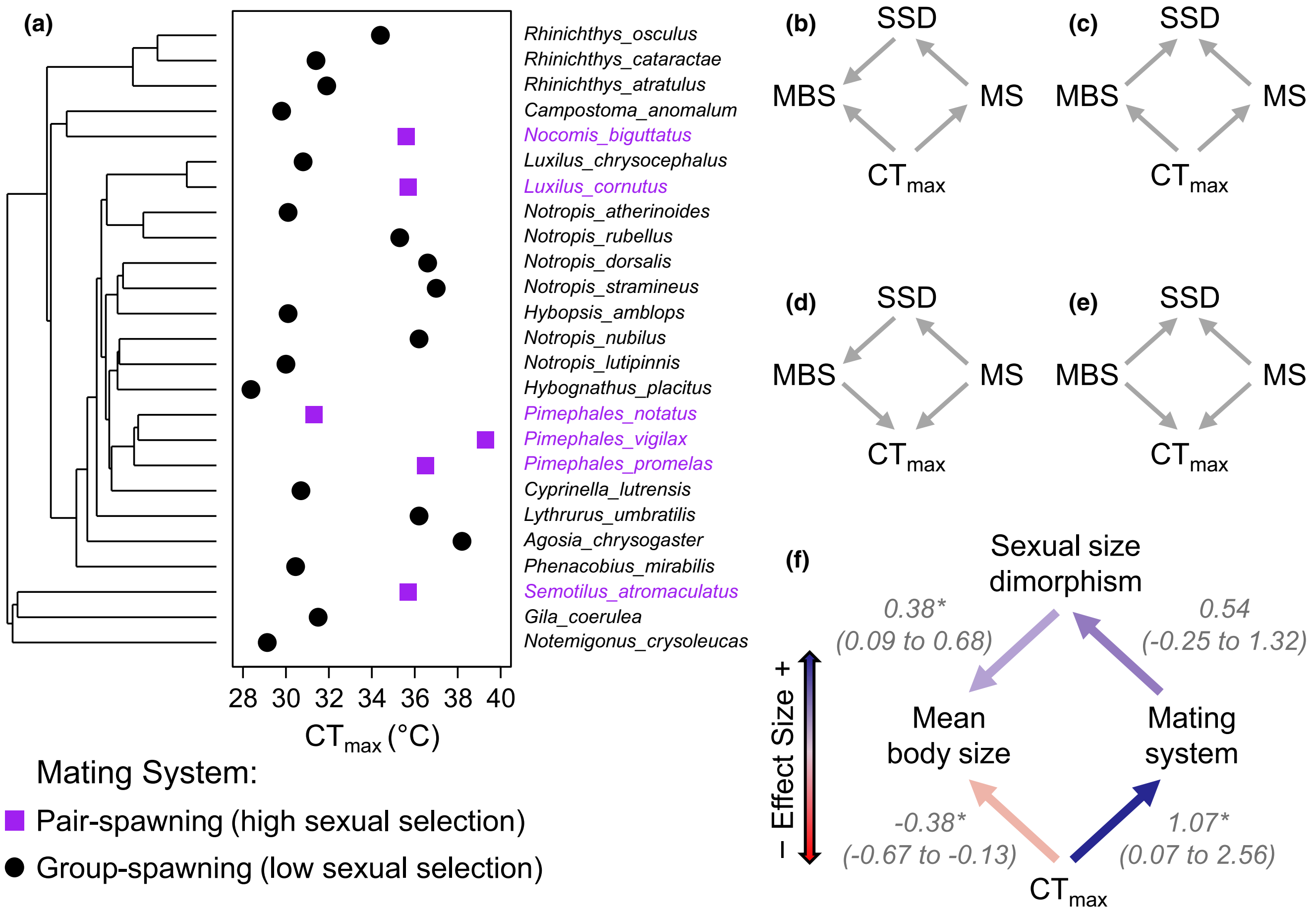

FIGURE 4 (a) Phylogeny illustrating the evolutionary relationship between mating system and heat tolerance (CT_{max}) in cyprinid fishes. Species that have evolved pair-spawning mating systems (i.e. stronger sexual selection; indicated by purple squares and text) have also evolved higher heat tolerances than species with group-spawning mating systems (indicated by black circles and text). Phylogeny obtained from Rabosky et al. (2018) and CT_{max} values reported by Bennett et al. (2018). (b–e) Path diagrams showing hypothesised causal evolutionary relationships among CT_{max}, mating systems (MS), sexual size dimorphism (SSD), and species mean body size (MBS). (f) Path diagram showing the model of causal evolutionary relationships with the best support. The evolution of heat tolerances constrains mating system evolution, with pair-spawning being more likely to evolve in species that already possess increased heat tolerances. Increased heat tolerances and more male-biased SSD have conflicting effects on the evolution of mean body size, suggesting that heat tolerance constrains mating-system evolution for reasons other than the relationship between pair-spawning and male-biased SSD. Blue path arrows reflect positive relationships between traits, while red arrows reflect negative effects. Arrows with more saturated coloration indicate stronger effect sizes. Confidence intervals were obtained from 500 bootstrapped iterations of the best fitting model. Significant parameter estimates indicated with asterisks.

higher heat tolerances, individuals with the highest fitness under warm conditions will be both highly melanised and tolerant of high temperatures. Sexual trait manipulations could also be used to test how trait-induced changes in body temperature affect fitness in other contexts and in the long-term, such as foraging performance and fertilisation success. Additionally, researchers could use heat or cold 'hardening' treatments (González-Tokman et al., 2020; Overgaard & Macmillan, 2017) or genetic lines of high and low thermal fertility limits (Rodrigues et al., 2022) to test how variation in thermal physiology influences selection on the focal reproductive trait.

When possible, it would also benefit researchers to test alternative mechanisms that could underlie the correlated evolution of sexual and thermal traits. For instance, environmental differences in disease risk, predation, or resource availability can favour the evolution of both thermal ecology and sexual characters (Huey & Kingsolver, 2019; Kutch et al., 2014; Landry Yuan et al., 2021; Maan & Seehausen, 2011; Miller & Svensson, 2014; Thomas & Blanford, 2003). The correlated evolution of sexual and thermal traits may therefore instead reflect the repeated adaptation of multiple phenotypic dimensions to local environmental conditions. Such alternative mechanisms could be evaluated by including environmental factors and their potential causal pathways in phylogenetic path analyses, or by conducting the phenotype manipulation experiments described above under altered environmental conditions. In any case, experimental evidence that expressing a sexual character affects selection on thermal tolerances and thermoregulation, or vice versa, would provide strong support for causal relationships between sexual and thermal traits even if their correlated evolution is confounded by environmental differences among taxa.

Understanding how thermal and reproductive demands collectively shape sexual trait evolution

When variation in a sexual trait impacts mating success and thermoregulatory performance, it may be unclear whether the trait first evolved in a reproductive or a viability-related context. Bonduriansky (2011) and Svensson and Waller (2013) offer useful approaches that apply existing phylogenetic comparative methods to explore this question. For instance, researchers could first conduct ancestral state reconstructions to estimate transitions between sexual dimorphism and sexual monomorphism in the focal sexual character, along with transitions between mild and extreme environmental temperature conditions. If the sexual character first evolved via sexual selection and was then co-opted for viability-related thermoregulation, the ancestral state of the sexual character should be dimorphic, followed by a gain of the sexual trait in the less competitive sex (Bonduriansky, 2011). Evolutionary transitions from sexual dimorphism to sexual monomorphism should also be more likely when lineages transition from mild to extreme thermal environments. One can also test if thermoregulatory functions evolved prior to mating functions using the same logic. Ancestral sexual monomorphism followed by exaggeration in the more competitive sex would occur if the character first served viability-related functions and was subsequently co-opted by sexual selection. Tests of these predictions can be accomplished using Pagel's concentrated-changes tests (Pagel, 1994) or hidden Markov models (Beaulieu et al., 2017; Boyko & Beaulieu, 2021).

The relative importance of thermoregulatory and mating-related demands to the evolution of a sexual trait might also change after the trait first evolved in a lineage. In an approach similar to Friedman et al. (2019), phylogenetic path analysis can assess the relative importance of a trait's sexually selected and thermoregulatory functions in shaping its evolution. First, researchers should collect data related to thermoregulatory demands and the strength of sexual selection among populations or species. For instance, the importance of thermoregulation for viability can be indicated by the difference between extreme environmental temperatures and the limits of an organism's physiological tolerance (i.e. ‘thermal safety margins’; Sunday et al., 2014). Variation in mating systems could be used to approximate the potential strength of sexual selection (Krakauer et al., 2011; Shuster, 2009). One would then compare alternative phylogenetic path models to assess if the evolution of the sexual character is most influenced by mating systems (the importance of the trait's reproductive function), thermal safety margins (the importance of the trait's thermoregulatory function), both functions together, or interactions between mating systems and thermal safety margins.

IMPLICATIONS FOR PHYSIOLOGICAL ADAPTATION IN A WARMING WORLD

Recent work has emphasised the potential for anthropogenic warming to modify the process and outcomes of sexual selection (Botero & Rubenstein, 2012; García-Roa et al., 2020; Leith et al., 2021; Miller & Svensson, 2014; Moore et al., 2021; Olsson et al., 2011; Rosenthal & Elias, 2019). There has also been recent interest in how sexual selection could be beneficial for adaptation to environmental change through the purging of deleterious alleles (Cally et al., 2019; Gómez-Llano et al., 2021; Lumley et al., 2015; Parrett et al., 2019; Parrett & Knell, 2018; Yun et al., 2018) or detrimental for adaptation by promoting inbreeding and the evolution of costly traits (Candolin & Heuschele, 2008; Kokko & Brooks, 2003). Here, we expand upon this work by outlining multiple mechanisms through which evolutionary interactions between thermal ecology and sexual selection could promote or impede physiological adaptation to a warming world. Given the particular importance of reproductive performance and thermal tolerance evolution for the persistence of populations under climate change (Diamond, 2018; Hoffmann & Sgrò, 2011; van Heerwaarden & Sgrò, 2021), it should be a priority to understand how the co-adaptation of these phenotypic dimensions influence extinction risk in response to novel temperature regimes.

Sexual selection could increase the efficacy of thermal adaptation by constraining behavioural thermoregulation during mate competition (Andersson, 1994; Darnell et al., 2013, 2020; Saeki et al., 2005), thereby exposing genetic variation in physiological traits to selection. Behavioural thermoregulation is generally thought to conceal genetic variation in thermal physiology and slow evolutionary responses to natural selection (Grigg & Buckley, 2013; Huey et al., 2003; Muñoz, 2021; Muñoz & Losos, 2018), potentially leaving populations vulnerable to extinction in changing climates (Buckley et al., 2015). However, when mate competition requires the use of physiologically extreme habitats or the expression of thermally costly sexual characters, it simultaneously makes thermal physiology highly relevant to fitness and limits opportunities for behavioural thermoregulation. In these cases, engaging in mate competition would reveal variation in thermal physiology and expose it to selection. Future investigations of the thermal consequences of reproductive behaviours may therefore reveal interesting examples in which behaviour ends up potentiating, rather than forestalling, physiological adaptation during environmental change.

Mate competition could also generate directional selection on thermal traits that is aligned with selection from anthropogenic sources, thereby accelerating adaptation to changing environments. For many of the examples described in the previous sections, sexual selection is predicted to favour traits that accommodate warmer body temperatures and increased tolerance to thermal extremes. Similarly, as climates continue to change, both warmer mean environmental temperatures and more extreme climatic events are expected to favour traits that enable organisms to withstand such thermal conditions (Collins et al., 2013; Coumou & Rahmstorf, 2012; Fischer & Knutti, 2015; Meehl et al., 2007). The aligned effects of natural and sexual selection would increase the overall intensity of selection on thermal physiology and behaviour (Arnold & Wade, 1984a, 1984b), potentially resulting in faster rates of adaptation to novel thermal environments. For instance, post-copulatory sexual selection favouring increased thermal fertility limits may complement natural selection on gamete production in warming climates (Schou et al., 2021; van Heerwaarden & Sgrò, 2021; Walsh, Parratt, Hoffmann, et al., 2019).

When the demands of mate competition complement selection from anthropogenic change (e.g. both favour higher $CT_{\max}$ or greater thermoregulatory efficiency), sexual selection could further promote adaption to warming environments by pre-adapting populations to increased body temperatures. In warming climates, fragmented forest patches, or urban heat islands, sexual characters that elevate body temperatures might become increasingly costly, and selection may favour their reduction (Clusella-Trullas & Nielsen, 2020; Moore et al., 2019, 2021; Svensson & Waller, 2013). However, because these sexual traits are likely to be co-adapted with thermal ecology, the populations that possess them may already be well suited to warmer conditions because of their pre-adapted thermal physiology and thermoregulatory strategies. As a result, even if thermally relevant sexual characters become lost or reduced, the pre-existing physiological advantages of these populations may give them a leg-up on thermal adaptation during environmental change.

Alternatively, exceedingly costly sexual characters may inhibit or slow adaptation to global warming. Extreme thermal events are becoming more frequent and intense with climate change (Collins et al., 2013; Coumou & Rahmstorf, 2012; Fischer & Knutti, 2015; Meehl et al., 2007), and sexually selected traits that elevate body temperatures may exacerbate the ensuing physiological challenges. For example, although body sizes are predicted to decrease for many species under future climate conditions (Gardner et al., 2011; Ryding et al., 2021; Sheridan & Bickford, 2011), sexual selection may promote the maintenance of large individuals and thus oppose adaptation to future environments. Sexual characters that enhance thermoregulatory function could also cause maladaptation by delaying or inhibiting the evolution of thermal tolerances (Cotto et al., 2019; Diamond & Martin, 2020; Huey et al., 2003). While these characters may initially buffer populations from extreme temperatures (Huey & Tewksbury, 2009), they could cause physiological adaptation to lag behind temperature changes and ultimately increase extinction risk (Buckley et al., 2015; Huey et al., 2003).

As is often the case during adaptation, a single evolutionary problem can favour a variety of phenotypic solutions (Gould & Lewontin, 1979; Jacob, 1977). Researchers should therefore consider how adaptations to climate change involving other trait dimensions may affect the correlated evolution of thermal physiology and sexual characters. For instance, the evolution of earlier reproductive seasons and altered life histories in response to warming environments (Chick et al., 2019; Møller, 2004) may also ameliorate the thermal costs of mate competition and weaken selection on thermal tolerances. Even in unchanging thermal environments, earlier reproductive seasons could evolve in lieu of increased heat tolerance to accommodate sexual traits that induce heat stress. Nevertheless, compared to other possible adaptations, the co-adaptation of thermal and reproductive traits may have outsized benefits for population persistence in a warming world. The demands of mate competition already require populations to perform near their physiological thermal limits, making the evolution of thermal tolerances a more direct route compared to life-history evolution for avoiding extinction at increased temperatures (Hoffmann & Sgrò, 2011). Additionally, the evolution of thermal tolerances related to reproductive performance, such as thermal fertility limits, is often more closely linked to extinction risk and geographic range limits than the evolution of viability-related thermal tolerances (Parratt et al., 2021; van Heerwaarden & Sgrò, 2021).

SUMMARY AND CONCLUSION

Evolutionary interactions between thermal ecology and sexual selection are likely widespread and reciprocal. An organism's thermal biology may constrain the potential for sexual selection and limit the evolution of sexual characters. Sexual selection, in turn, can feed back to affect thermal adaptation by favouring individuals that can accommodate or co-opt the thermal consequences of bearing sexual traits and engaging in mate competition. Our reciprocal hypotheses can be re-framed in the context of other viability-related traits and expanded to unify sexual selection and broader aspects of eco-physiological adaptation. For instance, the evolution of an organism's foraging efficiency may influence the energetic costs and benefits of producing sexual traits, and the evolution of energetically expensive sexual traits may favour the compensatory evolution of increased foraging efficiency. The intersection of sexual selection and physiological adaptation therefore presents a clear path towards studying reciprocal causation during evolution, a concept which is deeply rooted in evolutionary ecology (Levins & Lewontin, 1985) but which currently lacks a strong empirical foundation (Svensson, 2018).

Here, we have identified multiple processes that could drive the co-adaptation of thermal ecology and sexual characters. Incorporating these processes of co-adaptation will advance our understanding of how sexual selection drives thermal adaptation beyond the adaptive benefits of good genes and genic capture mechanisms. Given the taxonomically pervasive relationships between thermal ecology and sexual selection, we suspect that the processes outlined here may have played an under-appreciated role in shaping the diversification of both thermal biology and sexually selected traits. Furthermore, as humans continue to dramatically alter existing thermal environments via global warming, urbanisation and deforestation, the effects we have detailed indicate that sexual selection should have a larger impact on adaptation in the Anthropocene than is currently recognised. Considering feedbacks between thermal ecology and sexual selection may be necessary to understand how organisms have adapted to the environments of the past and could persist in the environments of the future.

AUTHOR CONTRIBUTIONS

NTL, MPM, and KDFF conceived the idea. NTL conducted the literature review and wrote the manuscript with input from KDFF and MPM. NTL and MPM performed the analyses. NTL created the figures and artwork.

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DATA AVAILABILITY STATEMENT

We agree to the data sharing policy and have uploaded our data and code to Dryad (doi:10.5061/dryad.70rxwdbzx) as “Private for Peer Review”, which can be accessed using the following link: https://datadryad.org/stash/share/vjsLnWnAnOanSrk9dcVo797403OERAcV17tv73DRhHY

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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