



Temperature impacts all behavioral interactions during insect and arachnid reproduction

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Temperature shapes the processes and outcomes of behaviors that occur throughout the progression of insect and arachnid mating interactions and reproduction. Here, we highlight how temperature impacts precopulatory activity levels, competition among rivals, communication with potential mates, and the relative costs and benefits of mating. We review how both the prevailing temperature conditions during reproductive activity and the temperatures experienced early in life influence mating-related behavior. To effectively predict the consequences of global warming for insect and arachnid mating behavior, we advocate for future work that universally integrates a function-valued approach to measuring thermal sensitivity. A function-valued approach will be especially useful for understanding how fine-scale temperature variation shapes current and future selection on mating interactions.

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Introduction

Temperature influences all biological processes [1,2], including the expression and development of behavioral, physiological, and morphological traits used to coordinate mating [3,4]. Recent work has highlighted the immense range of temperatures that individual insects and arachnids experience [5,6], and this considerable thermal heterogeneity at small spatial scales may be an overlooked factor shaping the outcomes of mating interactions. Despite the importance of mating success for the persistence of insect and arachnid populations, the consequences of global warming for mating-related behavior and sexual communication have been relatively unexplored compared to other

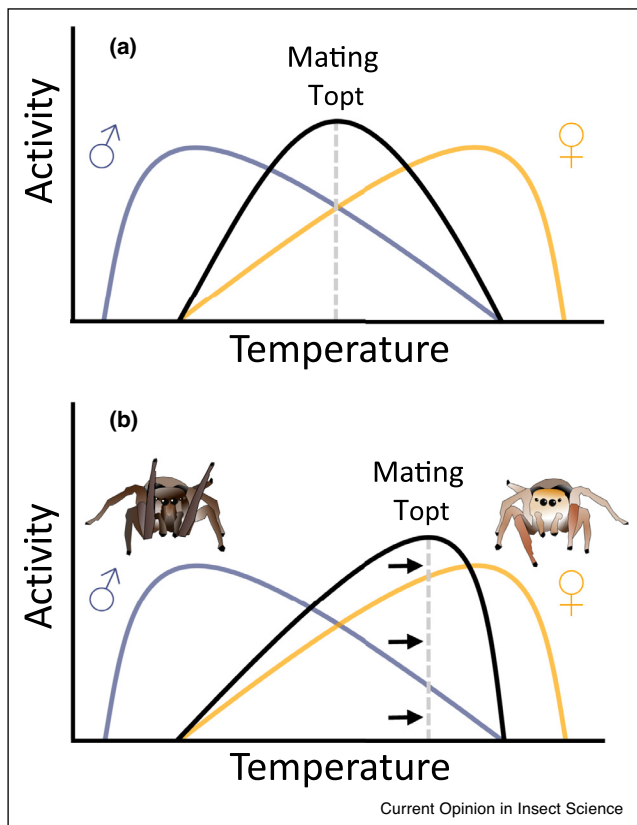
ecologically relevant traits [7,8]. Here, we review how temperature affects (i) precopulatory activity and the likelihood to mate; (ii) intrasexual interactions that mediate competition among rivals; (iii) intersexual communication involved in mate attraction and selection; and (iv) the net fitness consequences of engaging in mating-related behavior. Finally, as function-valued approaches—those which quantify the expression of traits as functions of continuous environmental variation—have advanced our understanding of how temperature impacts ecology and evolution in other contexts [9–13], we conclude by outlining this approach's utility for studying mating interactions in a warming world.

Pre-copulatory activity levels and mating rates

Mating interactions are constrained by the initiation of precopulatory activity. Any thermal sensitivity of activity rates will therefore have outsized consequences for mating interactions. Indeed, recent work reveals that temperature controls the likelihood of an individual engaging in precopulatory activity [14–17,18[•],19[•]], with the highest activity occurring at intermediate temperatures [17,19[•]]. However, the optimal temperatures for arthropod activity often differ between sexes [17,18[•],19[•],20,21]. As a result, the thermal sensitivity of one sex's activity has the potential to disproportionately affect mating rates (Figure 1). For example, in *Habronattus* jumping spiders, females are less choosy at higher temperatures and mating consequently occurs at warmer temperatures than those preferred by males [18[•]]. Similarly, the likelihood of copulation is governed by the thermal sensitivity of male activity rates in *Enchenopa* treehoppers likely because males must seek out and locate the relatively stationary females [19[•]]. Because *Enchenopa* males travel greater distances than females, they likely also encounter a broader range of environmental temperatures [5,6], which may further constrain mate searching at extreme ambient temperatures. Thus, considering how temperature affects the pre-copulatory activity patterns of each sex is key to understanding if, when, and where mating interactions are likely to culminate in copulation.

Temperatures experienced during development [22–25], or in early adulthood [26,27], can also affect mating activity. For example, *Plodia* moths reared at hotter temperatures are less likely to mate overall [22]; and adult *Bactrocera* flies exposed to extreme or fluctuating temperatures subsequently have lower mating rates [26]. Alternatively, in other

Figure 1



How sex-specific thermal sensitivity of precopulatory activity can shape mating activity peaks. **(a)** The thermal sensitivity of mating rates is a combination of male and female thermal sensitivity (indicated by the blue and yellow curves, respectively). Thus, mating rates may be highest at the temperature where male and female precopulatory activity overlaps the most (Mating T_{opt} , or thermal optimum). **(b)** The thermal sensitivity of one sex (in this case, females) can disproportionately impact the temperature where mating rates are highest. This is the case for *Habronattus* jumping spiders, where the more choosy females govern the temperatures at which mating occurs [18**].

insects, extreme temperatures experienced earlier in life can prepare individuals for extreme temperatures later in life ('hardening' [28,29]). However, this hardening is not uniformly beneficial. For instance, heat hardening in *Drosophila melanogaster* increases viability and mating activity at hotter temperatures [30], but cold hardening in this species reduces overall mating success [27]. Previously experienced temperatures may also shape the range of temperatures across which mating occurs, which could shape population dynamics in novel thermal environments with important implications for biological control and conservation in a warming world. For example, after the introduction of Brazilian salvinia weevils as a biological control in the United States, thermal acclimation has allowed the population of weevils to mate at previously

unsuitable temperatures and become unintentionally established [31*].

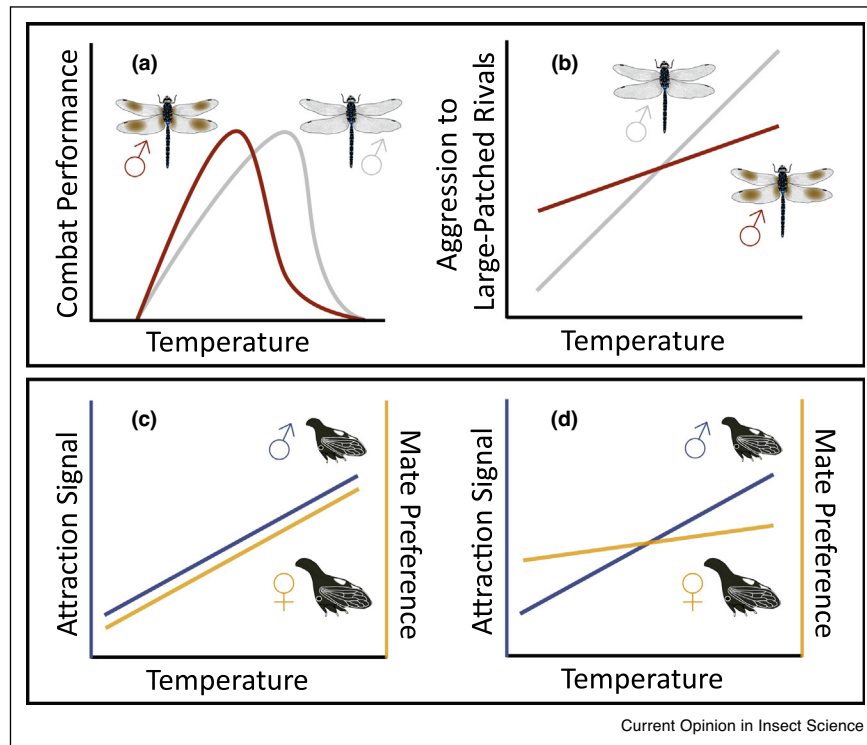
Competition among rivals

Many insects communicate and compete with rivals for access to mates and/or mating territories [32,33]—sometimes engaging in remarkable feats of strength, speed, or endurance [34]. Since the performance of these acts depends on the body temperature of an individual [35], temperature differences between rivals can dramatically affect the outcomes of competitive interactions. In butterflies and damselflies, for example, flight performance is sensitive to body temperature [36,37], and warmer individuals outperform cooler rivals in ritualized combat and territorial defense [38,39]. High thermal variation at the relevant spatial scales for insects and arachnids [5] could therefore affect intrasexual interactions by generating variation in temperature among rivals.

Temperature can also alter the advantages provided by the sexual characters that mediate communication and other interactions with rivals. For instance, although body size often determines an individual's status among its rivals [40,41], larger insects also heat and cool more slowly [42,43]. This thermal inertia can be detrimental if it prevents large individuals from quickly reaching the optimal temperature range for communicating or competing with rivals [44,45]. Conversely, greater thermal inertia may be advantageous by ensuring that large individuals remain near their thermal optimum during these interactions [46,47]. Temperature can further affect the advantages conferred by ornaments and armaments that evolved to resolve disputes among rivals. For example, dark or saturated color patterns that are used to signal condition or fighting ability often absorb more sunlight, causing the individual to experience hotter body temperatures [37,48]. Any subsequent ornament- or armament-induced heating might improve reproductive performance under cool conditions, but hinder it under warmer conditions ([49,50**]; Figure 2a). As a result, temperature has the capacity to modify the total strength and direction of intrasexual selection on morphological characters, and may affect the evolution of these characters in response to global warming.

One overlooked consequence of the thermal sensitivity of intrasexual signals is that it may also affect how individuals evaluate and respond to a rival's sexual characters. Consider the melanin wing patches of odonates, which signal a male's condition and energetic reserves for battle [51,52]. Because larger patches heat the bearer [50**,53–55], larger patches confer advantageous body temperatures for fighting under cooler conditions ([53]; Figure 2a). Conversely, under warm conditions, heat absorption by large patches may confer body temperatures that are not optimal for fighting ([50**,54]; Figure 2a). The likelihood of defeating a large-patched rival then depends on temperature, and

Figure 2



Examples of how temperature can affect competition among rivals and communication with potential mates. **(a)** Male dragonflies with large patches of wing pigmentation (dark brown curve) absorb more heat from the sun compared to individuals with less pigmentation (grey curve), which is advantageous for combat performance in cool climates but diminishes performance in warm climates [50^{**}]. **(b)** The heating effects of pigmentation could result in less pigmented individuals being more aggressive to large-patched individuals in warm climates [50^{**}]. **(c)** The thermal sensitivity of mate attraction signals can match the thermal sensitivity of mate preferences, resulting in temperature coupling of signals and preferences. This is the case for the male signals (blue line) and female mate preferences (yellow line) of *Enchenopa* treehoppers [67]. **(d)** Mismatches in the thermal sensitivity of signals and preferences can result in absent or incomplete temperature coupling.

selection should favor individuals that avoid large-patched rivals under cool conditions but that are aggressive towards them under warm conditions ([50^{**}]; Figure 2b). In this way, temperature may govern the evolution of how individuals behave in response to their rivals' sexual characters.

Temperatures experienced during development can also affect the expression of intrasexually selected traits in adults. In insects and other ectotherms, warmer temperatures often speed up development and ultimately restrict adult body size [45,56]. However, strong intrasexual selection should favor that the optimal body size is developed irrespective of environmental temperature [57,58]. Consistent selection for large size may explain the canalization of body size across developmental temperatures in dragonflies, which have intense territorial battles, but a lack of body size canalization in damselflies, which primarily engage in scramble competition [59]. When developmental temperatures predict thermal conditions in the adult reproductive environment, some insects might also evolve adaptive plasticity in their thermally sensitive sexual traits [60^{*}]. Although the only

direct test of this hypothesis did not provide support (dragonfly wing patches [61^{*}]), further tests would be valuable given the well-characterized relationships among developmental plasticity, thermal performance, and intrasexual interactions (e.g. lepidopterans [39,62] and coleoptera [63,64]).

Communication with potential mates

Temperature also affects a wide variety of the intersexual communication systems that insects and arachnids use to coordinate mating. Most research to date has focused on the thermal sensitivity of courtship signals, with an emphasis on airborne acoustic communication in orthopterans [65,66^{*}]; substrate-borne vibrational communication in hemipterans and spiders [18^{**},67,68^{**},69^{**}]; visual signaling in spiders and fireflies [18^{**},67,69^{**},70]; and chemical signaling in important lepidopteran pest species [71,72^{*}]. However, in addition to shaping the signals that courtiers use to attract mates, temperature also affects the mating preferences that choosers use to select among courtiers [67,68^{**},73,74,75]. Variation in ambient

temperature could, in response, dramatically affect the strength and direction of sexual selection on intersexual signals [76[•]]. Furthermore, differences in courter and chooser body temperatures due to the considerable thermal heterogeneity found at small spatial scales could be an important overlooked factor shaping mating outcomes [18^{••}]. Overall, thermal variation has high potential to affect many aspects of the mate attraction and selection process.

Temperature can impact intersexual communication across the many signaling modalities—acoustic, visual (i.e. gestural), and chemical—that insects and arachnids use to coordinate mating. Acoustic and visual signals are consistently sensitive to temperature due to thermal constraints on muscle contraction rates during signal production [65,73,77–83]. As a result, increased temperatures generate both temporal and spectral changes in signals. For example, the speed of signaling increases with temperature for acoustic and visual modalities [16,18^{••},66[•],69^{••},84[•]]; and spectral components—like dominant signal frequency—increase at hotter temperatures for acoustic modalities [16,18^{••},66[•],68^{••}]. While not measured as often as other acoustic properties with respect to temperature, acoustic signals can also be quieter at high thermal extremes [16,18^{••}]. Despite the central role of pheromones in insect sexual communication [71,85], relatively few studies have explored the thermal sensitivity of chemical signaling compared to other communication modalities. However, temperature affects chemical signals at all stages of communication—from pheromone production and propagation to signal detection and behavioral responses [71,72[•]]. Because temperature alters the ratio of compounds in pheromone blends used as long-range attractants (reviewed in Refs. [71,72[•]]), long-range chemical communication may be more susceptible to global warming than contact chemical signaling [71]. In response, long-range signalers may increase pheromone production at increased ambient [86] and developmental temperatures [60[•]].

The aspects of mating signals that are sensitive to temperature are often those used by choosers to select mates [68^{••},73–75]. Thus, understanding the relationship between the thermal sensitivities of mating signals and mate preferences is critical for predicting how temperature affects sexual selection and mating outcomes [68^{••},75,80]. Temperature coupling occurs when the thermal sensitivity of mate preferences mirrors that of mating signals ([68^{••},75,83,87,88]; Figure 2c), and can arise when physiological constraints are shared between signal production and signal perception [73] or when selection favors mate preferences that match mating signals [89]. Temperature coupling reinforces the action of sexual selection across temperatures [68^{••}], ensures choosers are likely to identify conspecifics [75], and enables choosers to select high quality mates irrespective of

temperature [90]. However, when temperature coupling does not arise [74] or is incomplete [91], signals and preferences can become mismatched at thermal extremes (Figure 2d). Mismatched signals and preferences could cause breakdowns in sexual communication at extreme temperatures, including the misidentification of heterospecifics as acceptable mates or reductions in mating opportunities if choosers are no longer attracted to the signals of available mates. Absent or incomplete temperature coupling could also induce changes in the strength and direction of sexual selection across environmental temperatures [69^{••},76[•]]. Signals and preferences may have higher variance in a population at extreme temperatures (e.g. *Enchenopa* treehoppers [68^{••}]), which could weaken sexual selection at thermal edges and contribute to the maintenance of genetic variation in variable thermal environments. In addition to direct effects on the expression of sexual signals and preferences, temperature also influences the honesty of signals of quality and the ability for choosers to distinguish among mates [86], sometimes even leading to sexual isolation among lineages reared at different temperatures (e.g. changes in cuticular pheromones in fruit flies [92]). For these reasons, measuring signals and preferences across a wide range of ambient temperatures will be critical for understanding how the increased temperature means and fluctuations accompanying global warming will impact mating success and the temporal dynamics of sexual selection.

Although most research on how temperature affects intersexual communication centers around temperatures experienced during signal production and reception, developmental temperatures can also influence the expression of signals and preferences in adults. This may be most dramatic in seasonal polyphenisms determined by developmental temperatures [80]. The effects of developmental temperature can also mirror those of ambient temperatures during signaling: for example, field crickets reared at hotter temperatures generate faster chirp rates and higher frequency signals than individuals reared at cooler temperatures [66[•]]. Relationships between developmental and mating-season temperatures may become increasingly decoupled and extreme temperature conditions more frequent in a warming world [93]. Thus, previously adaptive patterns of developmental plasticity in signals and preferences may produce less beneficial or even maladaptive phenotypes for individuals communicating in less predictable thermal environments.

The fitness consequences of mating interactions

The cost-to-benefit ratio of individual mating events shapes how optimal mating rates evolve, and temperature can be a key regulator of these relationships. Temperature can govern the benefits of mating interactions by affecting copulation and fertilization success [22,94–97],

and thus the degree to which a given mating interaction will increase the net fitness of an individual. Secondary benefits of mating interactions, such as nuptial gift quality [98], can further depend on temperature. If suboptimal temperatures decrease the per-capita fitness benefits of each mating interaction, higher mating rates may be favored to compensate for decreased lifetime reproductive output (e.g. wolf spiders [95,99,100]). Temperature also determines the costs of engaging in a mating interaction by altering the metabolic consequences of courtship and intrasexual interactions (e.g. crickets and cicadas [101–103]), the production costs of nuptial gifts or ejaculates (e.g. butterflies and seed beetles [104,105]), and the harassment experienced from rivals or non-mates (e.g. damselflies [106]). When these cost-benefit relationships are sex-specific, sexual conflict over optimal mating rates can arise [76]. For example, warmer developmental temperatures induce high costs for reproduction in male but not female butterflies, leading to the evolution of seasonality in male choosiness and mating rates [104]. Temperature can also indirectly shape mating systems by altering other proximate drivers, such as breeding season length [107] and operational sex ratios (reviewed in Ref. [76]). However, despite these myriad impacts, relatively few studies integrate the net fitness consequences of temperature on mating rates [108] (but see Refs. [104,105]). Because of the diverse avenues through which temperature can affect mating interactions, it should be a priority to resolve how variation in temperature underlies mating system diversification in insects and arachnids.

Leveraging a function-valued approach for predicting responses to global warming

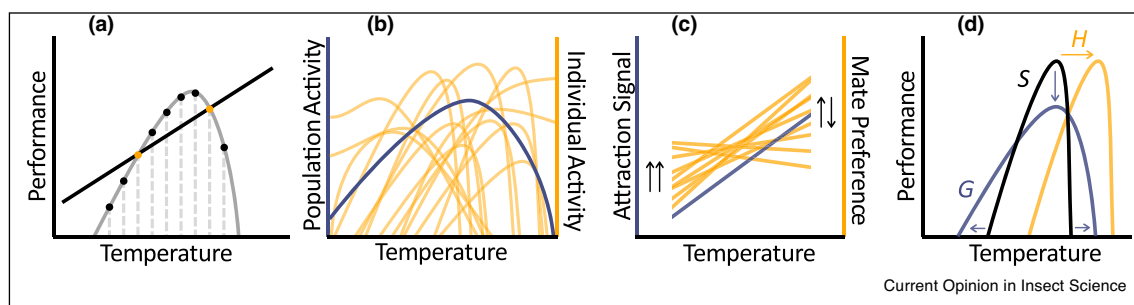
The pervasive thermal sensitivity of mating behaviors suggests that reproduction may be altered or impaired for many insects and arachnids under global warming. Despite the importance of reproduction for population

persistence, few studies have investigated the potential consequences of global warming for mating interactions compared to other behaviors [8]. Future work should therefore prioritize understanding how warming will impact the coordination of mating, as well as the capacity for reproductive interactions to evolve in response to novel temperatures.

One advantageous approach to studying how mating interactions will proceed and evolve in a warming world is to measure the expression of mating behaviors across temperature as a function-valued trait. Function-valued traits are those for which their expression changes as a function of a continuous environmental variable [9–11]—in this case, temperature. Characterizing thermally sensitive mating behaviors as functions of temperature can promote deeper insight into how organisms evolve and interact with variation in their environment [9–11]. For instance, assessing how mating activity changes across temperatures ranging from the minimum and maximum encountered in the environment can allow for more accurate estimates of mating activity peaks (Figure 3a), the detection of more precise differences in thermal sensitivity among mating behaviors, and distinctions among thermal generalists and specialists. Moreover, refining the shape of these functions for both male and female mating behaviors could be valuable for predicting if, and to what degree, different warming scenarios will lead to breakdowns in the coordination of mating [19].

Using a function-valued approach to measure how individuals, rather than populations, respond to temperature could further enhance our ability to forecast evolutionary responses to global warming. While population-averaged curves can show the temperature at which mating rates are highest in a population, it ignores variation in the patterns of thermal sensitivity among individuals

Figure 3



Graphical depictions of the advantages of a function-valued approach. (a) A hypothetical reaction norm (black line) obtained from sampling mating activity at two temperatures (indicated in yellow). Sampling at additional temperatures reveals a more accurate pattern of thermal sensitivity (grey curve). (b) A population-averaged curve (dark blue) masks individual variation in activity peaks across temperatures (light yellow curves). (c) Individual variation in the thermal sensitivity of mate preferences (light yellow) causes shifts in the direction of sexual selection (black arrows) on mate attraction signals across temperatures (dark blue). (d) Selection from global warming can act on the entire function of thermal responses, potentially favoring the evolution of thermal generalists (G; blue curve) from thermal specialists (S; black curve), and/or horizontal shifts in activity peaks (H; yellow curve). Arrows indicate potential directions of selection generated by environmental warming.

(Figure 3b). This among-individual variation could have important consequences for ecological and evolutionary processes that are obscured when estimating the average function of a population [12]. For example, among-individual variation in the optimal temperature for mating activity could generate assortative mating according to thermal activity curves in spatially and temporally variable thermal environments. Additionally, among-individual variation in the thermal sensitivity of mate preferences can result in weaker selection on male signals at thermal extremes (Figure 3c). Both of these scenarios may contribute to the maintenance of genetic variation in sexual characters in fluctuating and/or heterogeneous thermal environments.

Selection may primarily act on components of a thermal response (e.g. the level of signal production at a focal temperature) or an entire function of a thermal response (e.g. changes in signal production across the range of temperatures encountered in the environment). In either case, evolutionary responses to selection will often depend on the genetic (co)variation underlying the entire function rather than that of its isolated components ([13]; Figure 3d). Consequently, measuring individual-level and genotype-level thermal responses as functions that are subject to selection (e.g. generalist versus specialist curves) will improve our forecasts for evolutionary responses to global warming [9–11]. However, despite its potentially central role in promoting adaptation to novel climates, researchers have yet to estimate heritability in these patterns of thermally sensitivity for mating behaviors.

Integrating individual-level and population-level thermal functions is an ongoing area of research [109,110] and involves multiple empirical challenges. Characterizing how temperature affects an individual's mating behavior can be difficult when individuals cannot be accurately assessed multiple times—for instance, when individuals mate only once, when performance or receptivity diminishes across consecutive mating interactions, or when choosers do not obviously indicate receptivity. In some cases, researchers can circumvent these challenges by measuring responses within genetic lines or among siblings within families [111,112]. When population-averaged curves are most practical, reporting confidence intervals and individual data points on these curves can help approximate levels of variability within populations.

Conclusions

Both the temperatures in the reproductive environment and those experienced during development can affect a wide range of behavioral traits that insects and arachnids use to attract, compete for, and select mates. Measuring changes in mating-related behaviors as continuous functions of temperature—rather than with typical univariate or multivariate approaches—will

enable researchers to accurately estimate peaks in mating activity, distinguish differences in the thermal sensitivity of mating behaviors, and, as a result, predict the outcomes of inter-sexual and intra-sexual interactions across environmental variation. Furthermore, the incredibly variable thermal environments found at small spatial scales [5,6] could create differences in the body temperatures of interacting individuals and generate variation in thermal sensitivity due to developmental plasticity. Understanding how this fine-scale thermal heterogeneity shapes variation in function-valued responses to temperature may provide critical insights into the ecological and evolutionary processes of the Anthropocene. Overall, given the importance of reproduction to population persistence, the thermal sensitivity of the behavioral interactions used to coordinate mating is likely a crucial feature of how insects and arachnids have adapted to climatic conditions in the past. Gaining a mechanistic understanding of the thermal sensitivity of mating behaviors and the information encoded in inter-sexual and intra-sexual signals will also be central to understanding how temperature impacts sexual selection, reproduction, and persistence in a warming world.

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Author contributions

KDF, NTL, and MPM conceived the ideas for the paper. All authors contributed to the writing of the manuscript.

Conflict of interest statement

Nothing declared.

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- of special interest
- of outstanding interest

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