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Complex interactions between temperature, sexual signals and mate choice in a desert-dwelling jumping spider

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Environmental context is a crucial factor that influences sexual communication systems. Particularly in ectotherms, which cannot metabolically regulate their body temperature, temperature has an outsized effect on these intraspecific interactions. Using the desert-dwelling jumping spider *Habronattus clypeatus*, we assessed how temperature impacts various parts of the male signal and female mate choice for the signal. These spiders have multimodal, temporally structured courtship displays that begin with visual-only 'sidling' displays and proceed to multimodal visual and vibratory displays. To examine temperature effects, we performed sequential choice mating experiments ($N = 45$ trials) at two temperature treatments: hot (~50 °C) and room temperature (~25 °C). We found first that variation in the different stages of courtship segregated onto different principal components. The only aspect of male courtship that females expressed preference for was sidling courtship, but only at the higher temperature. Females also preferred to mate with heavier males at all temperatures. Specifically, females preferred to mate with males that performed shorter sidling displays. This is reflected by shorter copulation times in the warm treatment as well. We also found that temperature impacted only vibratory courtship and not sidling courtship. Our results highlight the importance of understanding environmental context in studies of animal communication. We also stress how a holistic, rather than reductive, approach to complex communication systems is vital in order to understand how selection acts upon them.

Sexual communication cannot be understood in isolation from its environmental context. An animal's abiotic and biotic environment can influence how a signal is produced, transmitted, interpreted and acted upon. It has become increasingly clear that assessing how changing environmental dynamics affects signal form and function might not just be an optional or interesting broadening of our understanding, but rather is essential. In other words, without incorporating an analysis of an animal's variable environment, it may be impossible to understand how selection acts on a signal or how it evolved in the first place (Bro-Jørgensen, 2010; Cornwallis & Uller, 2010; Miller & Svensson, 2014). Complex sexual signals in particular must be analysed in light of their variable environmental context for two main reasons. First, changes along a single environmental axis can lead to varying, multidirectional changes in complex signal form (Rosenthal & Elias, 2019). Second, structural changes in the relationships between components of a complex signal can alter the strength and nature of correlated selection on the display as a whole (Chaine & Lyon, 2008; Rosenthal, Wilkins, Shizuka, & Hebets, 2018). Chooser mate choice patterns can also change with variable environments, either in concert with or in opposition to courter signals (Chaine & Lyon, 2015).

Temperature is one environmental factor that is ubiquitous and must be incorporated into studies of communication. As temperature works on the physiological level to alter metabolic processes (Angilletta, 2009; Gillooly, Brown, West, Savage, & Charnov, 2001), all higher-order processes, including behaviour, are influenced by temperature. Endotherms can mitigate these effects by maintaining a constant body temperature. For ectotherms, however, changes in ambient temperature directly affect metabolic rate, and thus the performance of most behaviours (Angilletta, 2009; Hochachka & Somero, 2002). Sexual communication is particularly interesting in this context because temperature directly alters the energetics of courtship, which are often the focus of receiver preferences (Byers, Hebets, & Podos, 2010).

Sexual signals have been known to change with temperature since the first observation of the 'thermometer cricket', from which

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the ambient temperature can be simply calculated based on a cricket's chirp rate (Dolbear, 1897). Since that initial observation, courtship rate has been found to increase at higher temperatures in taxa ranging from frogs (Gerhardt, 1978; Humfeld & Grunert, 2015), to insects (Doherty, 1985; Jocson, Smeester, Leith, Macchiano, & Fowler-Finn, 2019; Mhatre, Pollack, & Mason, 2016; Pires & Hoy, 1992; Ritchie, Saarikettu, Livingstone, & Hoikkala, 2001) and spiders (Brandt, Kelley, & Elias, 2018; Rosenthal & Elias, 2019). Notably, changing temperatures affect not only signaller behaviour, but also receiver responses to those signals. Often these shifts in preference serve to compensate for the effect of temperature on signal production rate, with receivers increasing their threshold of acceptance as temperatures increase (i.e. ‘temperature coupling’: Doherty, 1985; Gerhardt, 1978; Mhatre et al., 2016). However, these changes are not always of the same magnitude as changes in the signal (Gerhardt & Mudry, 1980) and may themselves be complex and potentially nonlinear (Rosenthal & Elias, 2019). Thus, without assessing both signaller and receiver responses, it is therefore difficult to assess the true effects of temperature on the signalling system as a whole.

In this study, we investigated the effect of changing temperatures simultaneously on male courtship and female response behaviours in the jumping spider *Habronattus clypeatus*. Jumping spiders in the genus *Habronattus* are a good model for such studies. *Habronattus* signals are unique in the animal world as they combine multimodality with a stereotyped temporal structure across many levels. Visual ‘sidling’ displays precede vibratory courtship, and vibratory signals themselves consist of discrete structures analogous to musical compositions, such as ‘motifs’ and ‘movements’ (Elias, Maddison, Peckmezian, Girard, & Mason, 2012). Many of these species also live in the desert, among the most thermally extreme of terrestrial biomes. Given their intriguing courtship and desert habits, research has begun to explore the relationships between the two (Brandt et al., 2018). In Brandt et al. (2018), the authors first assessed habitat temperatures throughout the day for desert-dwelling *H. clypeatus*. They then selected three relevant environmental temperatures in which to evaluate male courtship signals and female mate choice in the laboratory. They found that most aspects of vibratory courtship and some aspects of visual courtship changed with temperature. Female acceptance rates were also higher in the highest temperature treatment. However, this study measured mating success and courtship signals in two separate experiments, with two different sets of individuals. The causal link between signal and mate choice could therefore not be directly assessed. We sought to expand upon these findings in this study. Using *H. clypeatus*, we measured changes in mate choice and signal structure together to understand how the thermal environment might shape selection on the entire display. Specifically, we predicted the following: (1) since visual and vibratory courtship are both produced by muscular contractions under the same physical constraints, both types of signals would change with temperature in similar ways; (2) if visual and vibratory courtship are both important for mating success, then we would expect females to exert preferences for both at all temperatures.

METHODS

Animal Collection and Maintenance

We collected all spiders during late March and early April 2016 from the Santa Rita Mountains in Pima County, Arizona, U.S.A., from unceded lands of the Tohono O'Odham and Hohokam peoples. No special permits were required to collect spiders from these lands. We captured only sexually immature individuals to ensure that no experimental animals had previously mated. We allowed animals to mature in the laboratory. We housed spiders singly in plastic cages (model 751C, AMAC Plastic Products Corp, Petaluma, CA, U.S.A.). We provisioned animals with adult *Drosophila melanogaster* and first-instar *Gryllodes sigillatus* weekly and provided water as needed. We kept spiders at room temperature (~23–25 °C) on a 12:12 h light:dark cycle with ultraviolet (UV) enriched lighting (Repti-Glo 10.0 Fluorescent Lamp, Exo Terra, Mansfield, MA, U.S.A.) to more accurately simulate their desert habitat. Upon maturation, we confirmed the sex of each spider by assessing the presence of male or female genitalia. Previous studies have shown that females are not receptive to mating earlier than 2 weeks postmaturation (Elias, Hebets, Hoy, & Mason, 2005; Elias, Hebets, & Hoy, 2006). Therefore, we performed experiments only with females that were at least 2 weeks postmaturation (mean: 19 days postmaturation, range 14–48 days). No special protocols or restrictions are required for the handling or collection of spiders for use in behavioural research. However, we took special care to maintain and handle spiders in a safe and ethical manner.

Mate Choice Trials

We staged a total of 80 sequential choice courtship trials at one of two temperatures: room temperature (~23–26 °C) and hot (~50 °C). These temperatures are within field temperatures for *H. clypeatus* during the spring breeding season (Brandt et al., 2018). The experimental set-up consisted of a silicone heater (model SRFG-110/-10P, Omega Engineering, Norwalk, CT, U.S.A.) sandwiched between two 3 mm thick steel plates. We set the heater to either 50 °C (hot treatment) or turned off (room temperature treatment). We placed a piece of white printer paper on top of the plates. We constructed the walls of the courtship arena with a sheet of acetate rolled into a tube, held in place at its bottom with an embroidery hoop. This was placed on top of the paper-covered plates, which served as the floor of the arena. To avoid transferring spider chemical cues between trials, we wiped the plastic walls of the arena with 70% ethanol and changed the paper floor between each trial.

For each trial, we paired a female with a male using a random number generator. While still in their respective cages and unable to see, smell or contact one another, we placed a male and a female in the arena for 10 min to allow them to equilibrate to the experimental temperature. After the equilibration period, we introduced the female into the courtship arena, followed by the male a few seconds later. We set a timer for 15 min and allowed the spiders to interact during that time frame. If a male was in the middle of a courtship display at the 15 min mark, we allowed courtship to conclude before ending the trial. If this courtship bout resulted in copulation, this was also allowed to conclude past the time limit. Similarly, if spiders were copulating at the 15 min mark, we allowed this to conclude before ending the trial. We minimized human interference during the trials as much as possible but used a soft paintbrush to prevent spiders from climbing onto the sides of the arena as necessary. We monitored visual displays from both the top and side views using video cameras (CV-3200, JAI Inc., San Jose, CA, U.S.A.) and measured male vibrations with a Laser Doppler Vibrometer (PSV-400, Polytec, Irvine CA) focused on the male's abdomen. We weighed spiders after the trial.

We determined trial outcomes as ‘accept’, ‘reject’ or ‘inconclusive. Accept: the male and female mated. In these trials, copulation duration was calculated from the time the male mounted the dorsum of the female until the time at which he disengaged from her. Reject: the female turned away from or attacked the male three times after courtship had begun. Inconclusive: the male never performed courtship behaviours and/or the female attacked the male prior to any courtship behaviours being observed.

Inconclusive trials were not considered in future analysis, but the spiders were rerun at least 24 h later in the same pairing. Issues with vibrometry recording meant that of the 80 total trials, we performed analyses only with trials that had clear recordings of vibratory courtship ($N = 45$; 19 room temperature, 26 hot).

Analysis of Male Signals

In all observations of *H. clypeatus* to date, the male is the courter and females assess courtship. We followed the methods of Brandt et al. (2018) to analyse both visual and vibratory aspects of male signals. Briefly, *H. clypeatus* visual signals consist of a ‘sidling display’ that involves the male sidling back and forth in front of the female in arcs that shorten in length as he gets closer to her. One courtship trial may include multiple sidling displays. Within each sidling display, the male moves in discrete bursts (movement bouts) and then pauses before commencing the next movement bout. We measured the number and length of sidling and movement bouts. We also calculated the percentage of each sidle that consisted of movement bouts.

After the last sidling display concludes, the male stops in front of the female, approximately one to two body lengths away from her. He then proceeds with the vibratory stage of courtship. Vibrations are produced by either rubbing the cephalothorax against the abdomen (scrapes and thumps) or rapidly vibrating the abdomen (buzzes). Vibratory courtship is also coupled with visual elements such as leg waving. However, because visual aspects are so tightly coordinated with the vibratory signal, we only analysed the vibratory aspects for the sake of simplicity (Elias, Land, Mason, & Hoy, 2006). *Habronattus clypeatus* vibratory displays consist of a series of repeated elements: stridulatory ‘scrapes’, stridulatory ‘thumps’ and tremulatory ‘buzzes’. First, we identified every region of the song consisting of more than five scrapes in a row and calculated the rate of scrapes for each of these regions. We then counted the total number of thumps and buzzes, as well as their duration and peak frequency. A typical *H. clypeatus* vibratory display contains several hundred scrapes, so we calculated the duration and peak frequency of 20 scrapes distributed throughout the song. We selected these exemplar scrapes by evenly sampling them (as much as possible) across each region consisting of five or more scrapes.

Statistical Methods

All statistical analyses were carried out in R v.3.5.1 (R Core Team, 2018), and plots were generated using the R package ‘ggplot2’ (Wickham, 2016). To reduce the dimensionality of the data set, we first performed a principal components analysis (PCA) on 12 measured courtship components. This included seven vibratory and five visual signal components. The vibratory components included were the average durations of scrapes, thumps and buzzes, average scrape rate and the average frequencies of individual scrapes, thumps and buzzes. The sidling display components included were the time spent sidling and moving, the average duration of a sidling bout and of a bout of moving and the average number of movement bouts per sidle. Two measurements were missing from this data set. We therefore imputed these missing entries using an iterative PCA algorithm implemented using the ‘missMDA’ package in R (Josse & Husson, 2016).

We used the ‘Psych’ R package (Revelle, 2019) to extract three varimax-rotated components that cumulatively explained 85% of the variance in the data set. All six vibratory variables loaded strongly onto PC1 (see Results, Table 1). Scrape, thump and buzz duration loaded negatively, while scrape rate and scrape, buzz and thump frequency loaded positively. Thus, higher values of PC1 primarily indicated shorter vibratory signal durations, with higher vibratory signal production rate and higher vibratory frequencies (i.e. faster, more energetic signals). The average length of sidling and movement bouts and the amount of time spent moving per sidle loaded positively onto PC2. Higher values of PC2 thus represented longer bouts of sidling and a greater proportion of time spent in motion. The total time spent sidling and moving loaded positively onto PC3. Higher values of PC3 indicated more time spent in the visual signalling phase of courtship. For simplicity, we call

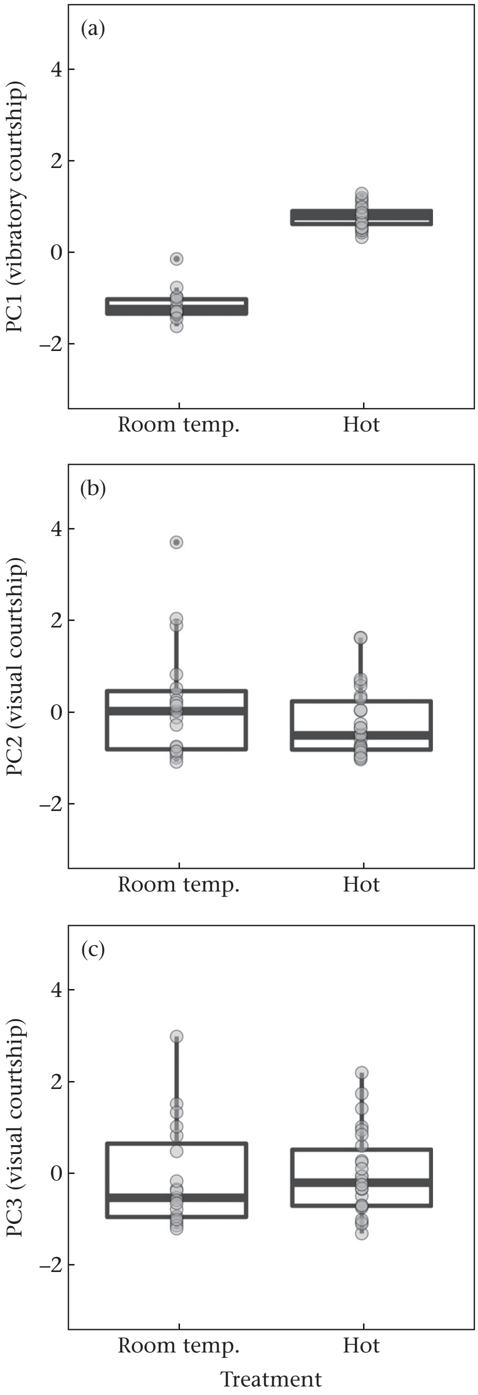

Figure 1. Box plots illustrating the effects of temperature on the first three principal components of *H. clypeatus* courtship: (a) PC1 (vibratory aspects); (b) PC2 (mean sidling components); (c) PC3 (total sidling courtship).

PC1 ‘vibratory aspects’, PC2 ‘mean sidling components’ and PC3 ‘total sidling courtship’.

To assess the effect of treatment on the production of courtship, we then ran three linear models with either PC1, PC2 or PC3 as the dependent variable and both treatment and male mass as independent variables. To assess the relationship between treatment and courtship on copulation success, we ran a logistic regression with trial outcome (copulation success) as the dependent variable and the two-way interactions of treatment and each of the three principal components and male mass as independent variables. To calculate treatment-related differences in copulation rate, we performed an independent two-group *t* test.

RESULTS

Vibratory aspects of courtship (PC1) differed significantly across the temperature treatments, being significantly higher in the hot treatment as compared to the room temperature treatment ($t_{42} = 22.857$, $P < 0.001$; Fig. 1a), but they were not associated with mass ($t_{42} = -0.405$, $P = 0.688$). Mean sidling components (PC2) did not differ across temperature treatments ($t_{42} = -1.381$, $P = 0.175$; Fig. 1b) and were not associated with mass ($t_{42} = -0.211$, $P = 0.834$). Total sidling courtship (PC3) did not differ across temperature treatments ($t_{42} = 0.256$, $P = 0.799$; Fig. 1c) and was not associated with mass ($t_{42} = -0.208$, $P = 0.836$).

Copulation success was not related to vibratory components or mean sidling components (Table 2) but was predicted by a significant interaction of temperature treatment and total sidling courtship (Table 2, Fig. 2). Mating success was associated with lower values of total sidling courtship in the hot temperature treatment (Table 2, Fig. 2a) but not in the room temperature treatment (Fig. 2b). Mating success was also associated with higher male mass (Fig. 3). Of the trials that resulted in copulation, males spent less time copulating in the hot treatment ($t_{42} = 5.000$, $P < 0.0001$; Fig. 4).

Table 1
PC axis loadings for the first two principal components

	PC1 (0.50)	PC2 (0.19)	PC3(0.16)
Scrape duration	**−0.94**	0.24	-0.01
Thump duration	**−0.94**	0.16	0.05
Buzz duration	**−0.91**	0.23	0.04
Scrape rate	**0.95**	-0.24	0.03
Scrape frequency	**0.79**	-0.01	-0.06
Thump frequency	**0.95**	-0.20	0.03
Buzz frequency	**0.94**	-0.07	-0.05
Length of sidling bout	−0.25	**0.81**	0.21
Length of movement bout	−0.11	**0.63**	0.04
Movement time per sidle	−0.15	**0.95**	0.16
Time spent sidling	−0.04	0.12	**0.98**
Time spent moving	0.01	0.22	**0.94**

Parenthetical numbers represent proportion of variance explained by each PC. Highest loadings for each variable are highlighted in bold.

Table 2
Results of logistic regression examining the interacting effects of each principal component and temperature on copulation success

	z	*P*
PC1	1.248	0.212
PC2	0.891	0.373
PC3	−0.182	0.855
Mass	−2.038	**0.042**
Treatment	−1.677	0.094
PC1 × treatment	−0.503	0.615
PC2 × treatment	−1.026	0.305
PC3 × treatment	−2.173	**0.030**

Significant *P* values are highlighted in bold.

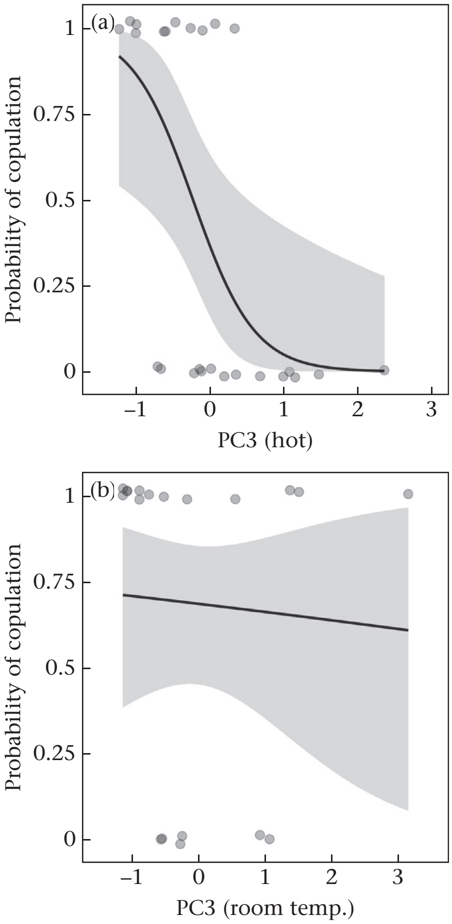

Figure 2. Logistic regression illustrating effects of PC3 (total sidling courtship) on the probability of copulation in *H. clypeatus* at (a) high temperature and (b) room temperature. In both panels, points are jittered slightly in the *Y* direction to prevent overplotting. Shaded area indicates 95% confidence interval.

DISCUSSION

The effect of temperature on *H. clypeatus* courtship varied depending on courtship phase. The early, visual sidling phase was unaffected by temperature, whereas vibratory aspects of the later multimodal phase were significantly temperature dependent, with male courters producing faster, higher frequency vibrations at hotter temperatures (Fig. 1). Temperature itself did not have a direct effect on copulation success in this study (Table 2). Surprisingly, none of the parameters of the vibratory phase appeared to predict mating success, suggesting that male vibratory performance did not predict attractiveness at any of the temperatures measured (Table 2). Conversely, males who spent less time sidling and moving were more likely to mate, but only at high temperatures (Fig. 2). These results suggest that while changing temperatures may significantly alter the production of many aspects of *H. clypeatus* courtship, this does not appear to alter selection on courtship form. Many animals, including vertebrates, use multicomponent and multimodal sexual signals (Candolin, 2003; Møller & Pomiankowski, 1993). The fact that these signals are carefully evaluated by choosers in order to make a mating decision is

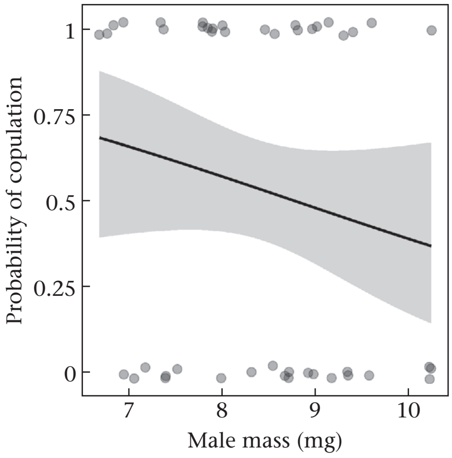

Figure 3. Logistic regression illustrating the effects of male mass on *H. clypeatus* female acceptance rate (probability of copulation). Points are jittered slightly in the *Y* direction to prevent overplotting. Shaded area indicates 95% confidence interval.

generally assumed. It is implicit in the ‘courter–chooser’ framework used for describing intersexual interactions. However, our results suggest that this is not necessarily the case. We discuss the implications of these results in more detail below.

The Effect of Temperature on Courtship Differed Across Courtship Phases

The different phases of courtship had different relationships to temperature. Aspects of vibratory courtship became faster, shorter and higher pitched in the hot treatment, whereas sidling courtship did not change with temperature (Fig. 1). Vibrations are produced by muscular contraction, which is directly influenced by metabolic rate, which itself is tightly coupled to temperature (Hochachka & Somero, 2002). Therefore, temperature-related changes to vibratory courtship are relatively unsurprising. What is more surprising is that *H. clypeatus* maintained properties of their sidling courtship across a wide range of temperatures.

Animals can prevent their courtship signals from changing with temperature in several ways. First, the signal may be produced by a modality that is not affected by acute changes in metabolic rate. One example would be a coloured pattern of plumage in a bird. Second, a signal could be produced by a system that uses mechanical constraints to make the signal temperature insensitive. This is common in the courtship song of crickets. Many species of crickets use what is known as a ‘clockwork mechanism’ that takes advantage of underlying resonant properties of the wing to prevent it from vibrating faster than its resonant frequency, regardless of temperature (Bennet-Clark & Bailey, 2002; Elliott & Koch, 1985). In fact, the ‘thermometer cricket’ uses this mechanism. Whereas the chirp rate does change with temperature, the frequency of each individual chirp is highly constrained to the resonant frequency of the wing (Mhatre, Montealegre-Z, Balakrishnan, & Robert, 2012). In the case of *H. clypeatus*, however, both sidling courtship (which did not change with temperature) and vibratory courtship (which did change with temperature) are produced by muscular contractions that are known to be temperature sensitive. There is also no evidence in either case of any mechanical constraints on production rate. For sidling courtship, muscles in the cephalothorax and legs produce locomotory forces (Foelix, 2010; Zentner, 2013). In vibratory courtship, muscles vibrate the abdomen such that the scraper on the back of the cephalothorax interacts with a file on the front edge of the abdomen (scrapes and thumps) or vibrates the abdomen at fast rates (buzzes) (Elias, Mason, Maddison, & Hoy, 2003).

The fact that these animals can produce some temperature-sensitive and some temperature-insensitive signals using the same basic production mechanism thus suggests that courting males are actively modulating some aspects of their signals to counteract changes in temperature. Although the mechanism is unknown, one example of such a modulation would be if the legs moved faster during movement bouts at hot temperatures but the animals took smaller steps. In Brandt et al. (2018), the authors found that some aspects of sidling courtship did change, but that the changes were driven by a third ‘cold’ treatment. If active modulation is occurring with sidling behaviour, it may break down at the lowest temperatures, leading to this pattern. Alternatively, some of the aspects of sidling courtship that we measured may not be direct measurements of energetic effort, and therefore may not be directly influenced by temperature. Time spent sidling, for example, could reflect the amount of effort spent on sidling, but it could also reflect the amount of time spent in the sidling phase, which might be in part affected by the receptive behaviours of the female. Choosers have been shown to influence courter effort in other species with complex sexual signals, such as bowerbirds (Patricelli, Coleman, & Borgia, 2006; Patricelli, Uy, Walsh, & Borgia, 2002). Future work will explore the possibility that females dynamically influence male signals in *Habronattus.* Additionally, *H. clypeatus* signals are segregated not only by modality (visual versus vibratory) but also by courtship phase and in time. This suggests that these animals' signals are not inherently stuck passively changing with temperature in ways that inconvenience the animals or disrupt patterns of mate choice.

Why males should choose to actively modulate visual, but not vibratory, signalling is unclear. Thermally driven changes in signal form create problems for both signallers and receivers. The visual display occurs first in *H. clypeatus* courtship. Possibly, its function as an attention-grabber (and potentially a species identifier) is more easily disrupted by changes in production rate than are the functions of the vibratory display. As yet, we have no specific data to suggest this, but it is possible that the complex signal performs multiple functions that are each affected differently by changes in temperature.

Female Mate Choice Has a Complex Relationship with Male Courtship and Temperature

Unlike the results of Brandt et al. (2018), we did not find a direct effect of temperature on the likelihood of mating (Table 2). Instead,

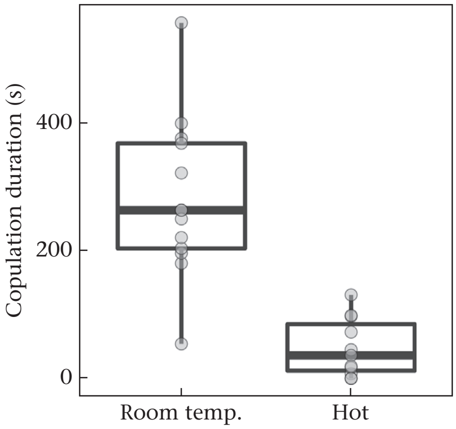

Figure 4. Effect of temperature on *H. clypeatus* copulation duration.

we found that females preferred to mate with males who spent less time overall sidling and moving, but only at high temperatures (Fig. 2). In fact, these were the only aspects of male courtship that influenced female mate choice. Our choice for temperature treatments were well within temperatures at which these animals can be found performing courtship behaviour in the wild (Brandt et al., 2018). However, the hot treatment was also within the range of thermal stress for this species (Brandt, Roberts, Williams, & Elias, 2020). At these temperatures, females may prefer to mate with males performing short sidling displays due to the accumulating effects of thermal stress and the need to complete courtship and copulation as quickly as possible. Pairs also concluded copulations more rapidly in the hot treatment (Fig. 4), which lends support to this hypothesis. As females were unable to retreat to a cooler temperature during the courtship trial, this could represent a trade-off between a choice to mate with a particular male and the need to alleviate thermal stress. A similar trade-off between mating behaviour and thermal stress has been seen in fiddler crabs (Allen & Levinton, 2014). Pairs in the wild may respond differently, as females have the option to seek out other environments. However, females interested in mating with a courting male must still choose how much time to allocate to the encounter given the environment they are in.

Vibratory courtship had no influence on mate choice, regardless of temperature (Table 2). This is surprising, as vibratory courtship is known to be essential for mating success in other *Habronattus* species. In *Habronattus dossenus*, a sister species to *H. clypeatus,* female acceptance rates are drastically reduced when males are unable to produce or transmit vibratory signals (Elias, Mason, & Hoy, 2004; Elias et al., 2005). Vibratory courtship is also essential in other jumping spider genera with multimodal signals, such as *Maratus* and *Phidippus* (Girard, Elias, & Kasumovic, 2015; Sivalinghem, Kasumovic, Mason, Andrade, & Elias, 2010). Vibration frequency is one specific area in which we might expect evidence of strong female choice. Vibration frequency is often considered an honest signal of male body size, which is often correlated with greater mating success in spiders, even in other species of jumping spiders (Sivalinghem et al., 2010). Although male body size did correspond to higher female acceptance (Fig. 3), vibratory courtship did not. One possible explanation is that paper substrate does not transmit vibratory signals as well as other substrates used in previous studies, such as nylon (Elias et al., 2004). However, paper is likely more similar to objects in the spiders' natural habitat (i.e. leaf litter) than nylon. Future studies using more sophisticated methods of temperature control will explore the relationship between substrate, temperature and vibration transmission.

Common reductionist approaches to the study of complex signals often assume that each part of a complex display carries nuanced information that a chooser can then assemble into a detailed view of a potential mate's quality. Yet our findings suggest that even though vibratory courtship is temporally complex and necessary for mating success, females do not appear to ‘pay attention’ to its specifics or use it to select a specific mate over another. Alternatively, higher-order aspects of the signal may be more important for mate choice than the simple durations, rates and frequencies of individual components. Like notes in a symphony, the progression and alternation of signal components may be important, rather than the total number of notes played, or the tempo alone. Supporting this notion, PC3 (i.e. total sidling courtship), the only principal component that describes time spent in one phase of courtship, is also the only principal component that predicted mating success at any temperature (Fig. 2). Future work will further disentangle the nuanced, multilevel temporal structure of these signals.

Conclusions

The majority of published work on ectotherms suggests that increasing temperature increases courtship production rate. This study adds to the body of literature demonstrating that the response of multicomponent signals to thermal changes is much more complex and nuanced than previously considered (see Martin, Gray, & Cade, 2000; Rosenthal & Elias, 2019). It is particularly striking that changes in temperature so strongly altered behaviour in one phase of courtship yet had no effect on others. This is despite the fact that all aspects of courtship are generated using muscular contractions that should be similarly affected by temperature. This suggests the possibility that males are actively moderating the effects of temperature on some, but not all, phases of courtship. Additionally, while these significant differences in response to changing temperatures have the potential to strongly reshape selection on courtship form, we found surprisingly little evidence of mate choice with respect to male phenotype at any temperature. Many arthropods produce complex sexual signals that may include the repeated production of a series of specific movements and vibrations. Such signals are most often analysed in terms of production rate, loudness or duty cycle (i.e. ‘vigour’, Byers et al., 2010), which are often the target of receiver preferences. Our results, however, suggest that this is not always the case. Either these signals have evolved and are maintained through some other process, or it is the relationships between components that are of interest, rather than the rates and frequencies of the components themselves. These findings caution against accepting a simplistic characterization of selection on complex displays and empower researchers to embrace environmental variability in such studies.

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