



Temperature alters multimodal signaling and mating success in an ectotherm

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Abstract

Temperature affects ectotherms in a variety of ways. These effects can be especially complex in sexual behaviors, as different sexes may be affected differently by temperature. We examined this in the jumping spider, *Habronattus chypeatus*. In this species, males court females using visual and vibratory signals. We tested whether key intersexual behaviors would change with temperature in similar, predictable ways across males and females. We first measured temperature and apparent activity of individuals across the day. We found that *H. chypeatus* are active across a wide range of temperatures (11–56 °C) and are most active at times of day when temperature ranges from 13 to 46 °C. Next, we performed mating experiments across behaviorally relevant temperatures. Females were more likely to allow males to progress to later stages of courtship and had higher mating rates at higher temperatures. Male visual and vibratory courtship behaviors generally became faster, higher-pitched, and lower in amplitude at higher temperatures. This relationship between temperature and signal aspects attained a roughly curvilinear shape, with an asymptote around 40 °C. Intriguingly, mating rates in the lab were highest at temperatures potentially above those during peak spider activity in the field. Our results suggest that temperature's effects on behavior are complex and can affect males and females differently. This work emphasizes that understanding temperature effects on mating is critical to understanding sexual selection patterns particularly in species which use complex signals.

Significance statement

Temperature affects communication in most ectothermic species. Previous research has shown that temperature changes courter signals and chooser choice. However, this has never been investigated in species that use multimodal signals. We investigate how signals and choice change across temperatures in a desert-dwelling jumping spider. Using field temperature/activity modeling and a series of courtship experiments in the lab, we show that male signals and female choice change with temperature across biologically relevant ranges. Our results suggest that the temperatures at which mating is most likely occur at times of the day when animals are least active. These counterintuitive results highlight the importance of understanding how behavior in a controlled lab environment corresponds to natural field conditions as well as the importance of examining the effects of naturally occurring environmental variation on behavior.

Keywords Communication · Temperature · Thermal ecology · Salticidae · Sexual selection · Multimodal signals · Vibratory communication · Biotremology

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Introduction

Sexual signals have long been known to have temperature-dependent properties (Edmunds 1963; Enger and Szabo 1968; Heath and Josephson 1970; Shimizu and Barth 1996). This is especially true in ectotherms, animals whose body temperatures depend primarily on the environment (Abram et al. 2017). For these animals, ambient temperature is directly tied to metabolic rate and thus influences all higher-order functions, such as physiology, immune defense, growth, and

behavior, including sexual behavior (reviewed by Angilletta 2009; Hochachka 2002). Although sexual signals have been studied extensively in this context (Doherty 1985; Pires and Hoy 1992; Ueda et al. 1994; Dunlap et al. 2000), signaling behaviors only represent half of the picture; choice for courtship signals also may change with temperature. During mating interactions, courter and chooser behaviors may change in concert with one another (signal-preference coupling (Pires and Hoy 1992; Dunlap et al. 2000; Greenfield and Medlock 2007) or not (Ritchie et al. 2001), potentially leading to a mismatch across some temperatures.

Studies examining signal-preference coupling have primarily focused on acoustic/vibratory modalities (Gerhardt 1978; Doherty 1985; Ritchie et al. 2001; Greenfield and Medlock 2007; Symes et al. 2017), with fewer studies evaluating visual (Michaelidis et al. 2006; Allen and Levinton 2014), and electric (Dunlap et al. 2000) modalities. However, many animals communicate using signals that involve more than one signaling modality (Partan and Marler 1999) and there has been a dearth of studies that investigate how temperature impacts these multimodal systems (but see Conrad et al. 2017). It is likely that abiotic factors such as temperature will impact the way multimodal signals are produced, transmitted, received, and interpreted. Yet the literature on multimodal signal evolution usually does not explicitly consider such effects (Moller and Pomiankowski 1993; Iwasa and Pomiankowski 1994; Johnstone 1996; Hebets and Papaj 2005; Partan and Marler 2005; Bro-Jørgensen 2010; Higham and Hebets 2013).

Another critical aspect missing from many studies of thermal effects on intersexual communication is ecological data tying activity patterns in the field with temperature. Field activity information is necessary to interpret laboratory data in many instances. For example, studies conducted on temperate species have demonstrated that signals, preferences, and mate choice may shift across temperatures, but animals may be active only within a narrow range of temperatures, e.g., tree frogs (Gerhardt 1978), fruit flies (Ritchie et al. 2001), and tree crickets (Symes et al. 2017). Information about the temperatures that animals naturally experience, and their activity patterns across temperatures, is therefore critical to understanding the relationship between temperature and behavior.

Jumping spiders in the genus *Habronattus* offer a unique study system to address the effects of temperature on mating behavior. *Habronattus* is a speciose (~106 species) genus of jumping spiders found primarily in North America (Leduc-Robert and Maddison 2018). They are known for their striking color, patterning dimorphism, and their elaborate multimodal visual (ornaments and movements) and vibratory displays (Elias et al. 2003, 2005, 2006a, 2012; Taylor et al. 2014). In *Habronattus*, males court while females choose. Male *Habronattus* multimodal displays consist of a series of signal “elements” that are organized in functional units that change in a stereotyped order as courtship progresses (Elias et al.

2012). These male displays are important for mating success (Elias et al. 2005, 2006a), and sexual selection has been suggested to drive diversification in the genus (Maddison and McMahon 2000; Masta and Maddison 2002; Hedin and Lowder 2009; Leduc-Robert and Maddison 2018). We chose *Habronattus clypeatus* as our study species for several reasons. First, *H. clypeatus* males produce complex visual and vibratory signals, but these displays last only for a few minutes in total, making *H. clypeatus* a tractable choice for laboratory study. Second, this species is found in low- to mid-elevation desert scrub in the Sonoran Desert, which is known to be a thermally variable habitat. Finally, females in this species only mate once, meaning that any mating decisions are crucially important to their lifetime fitness (Elias et al. 2006a).

We sought to understand how temperature influences sexual behavior in *H. clypeatus* by testing the following hypotheses: (1) *H. clypeatus* habitats vary in temperature throughout the day, and spiders have distinct patterns of activity across these ranges. (2) Mating rates, courtship progression, and female aggressive behaviors change with temperature. (3) Male visual and vibratory displays change with temperature. Specifically, we predicted that rate and frequency of male signals will increase with increasing temperature. We also predicted that across temperatures where animals are active, mating rates will be similar due to coordination between courter and chooser behavior. By addressing these hypotheses, we hope to gain an understanding of how an abiotic factor impacts a complex behavioral suite that takes place across a wide range of temperatures.

Methods

Field temperature and activity measurements

The breeding season of *H. clypeatus* occurs from April to June. We conducted surface temperature monitoring in April 2011 for 9 days. On each survey day, we measured surface temperature approximately every hour between 0830 and 1500 h for each of the two main substrate types on which spiders were found (rocks and leaf litter). Leaf litter consisted of a mixture of dried oak leaves, sticks, and dirt. We performed these measurements using an IR thermometer (Dual Laser IR Thermometer, Model 42511, Exetech Corp, Nashua, NH). For each substrate type, we measured three exemplars found in sun and shade. Overall, we measured 12 substrate exemplars for each hour of measurement. We recorded surface temperature measurements on a small piece of masking tape placed on each substrate. The emissivity of the IR thermometer was set to 0.95.

We modeled daily patterns of temperature for leaf litter and rock. We performed the modeling with generalized additive

mixed models (GAMMs) in R (v 3.5) using the package *mgcv* (v 1.8.23) (Wood 2006) with time modeled using a thin plate regression spline and a Gamma error structure (to account for positive skew and improve normality of residuals). We estimated a separate smoothed term for each light microhabitat and specified day as a random effect (to account for uneven sampling and clustering of values among days due to weather).

We conducted surveys in the Santa Rita Mountains east of Green Valley, Arizona in April of 2012 at the same time as the temperature measurements. Surveys consisted of 140 directed walk surveys conducted by four observers. Observers walked haphazardly within each plot while recording and capturing all spiders detected. Handheld GPS units (Garmin 60CSx or eTrex Legend Cx) automatically recorded observer location and time of day at 30 s intervals. From this information, we calculated mean walking speed, survey distance, and survey duration for each survey. We modeled apparent activity of *H. clypeatus* as a function of observer, time of day, and survey distance for each survey path using generalized additive models (Wood 2006). We specified a Poisson error structure for these count data, while controlling for any differences in the ability for observers to find spiders. We found spiders in all sites. For the field-based portions of this study, it was not possible to use blinded methods.

Collection and lab maintenance of animals

We collected immature female and adult and immature male *H. clypeatus* in the Santa Rita Mountains in the spring. We housed spiders individually in plastic containers (AMAC) and fed them twice per week on a diet of *Drosophila melanogaster* and first instar *Acheta domesticus*. We kept all animals at room temperature on a 12:12 light cycle with UV-enriched full-spectrum lighting. Pieces of fiberglass window screen were added into the containers to provide environmental enrichment (Carducci and Jakob 2000). Prior studies suggest that females are receptive to mating approximately 2 weeks after maturity (Elias et al. 2005, 2006a), so we waited 2 weeks before running females in any experiments.

Overall experimental design for courtship experiments

The goal for these experiments was to characterize how mating rates, receptivity, and courtship behavior change with temperature. Like other species of *Habronattus*, *H. clypeatus* courtship signals follow a distinct stereotyped progression (Elias et al. 2012). Early-phase courtship begins with visual-only sidling bouts (Fig. 1a). Next, if the female maintains her interest by visually attending to the male and does not attack him, courtship progresses to late-phase (visual + vibratory) courtship when the male is about a body length away (Fig. 1b). See Elias et al. (2003) for a detailed description in

a closely related species. Mating does not occur unless all stages of courtship are completed, and the female allows the male to mate (Elias et al. 2003).

We used two different experiments to assess courtship. Because female feedback is important during the early phases, we measured early-stage courtship using trials with live males and females in a single-choice paradigm. We also assessed mating rates with these trials. However, a high percentage of females never permitted males to advance to late-phase courtship. For this reason, we performed a second set of experiments in which we used live males and euthanized female lures to entice males to produce courtship displays. All males performed courtship in all temperature treatments under these conditions. We performed live courtship trials in 2013 and 2017. We ran courtship trials measuring only late-phase courtship in 2012. All lab experiments were conducted between 1000 and 1500 h to capture when spiders are most active in a lab setting (judged by whether a spider was outside of its silken retreat). We used blinded methods to collect and analyze data to minimize observer bias. Observations were made from video recordings without any information about the treatment.

Mating rate experiments

We conducted trials on 23 cm diameter terracotta platters. We used a fresh piece of circular paper to line the platter for each trial to eliminate the transfer of chemical cues between trials. For all courtship experiments, we measured temperatures of the surface of the arena at various points during the trials using IR thermometers. We recorded the temperature at the beginning of the trial, initiation of courtship, and end of the trial. Only virgin females that matured in the laboratory were used. Both spiders were acclimated to the treatment temperature for 5 min. Preliminary observations on behavior suggested that this acclimation period was sufficient. After the acclimation period, we introduced both spiders into the arena and gave them 5 min to recognize one another, defined here as directly facing each other from less than five body lengths apart. If this did not occur (approximately 20% of trials), one of the investigators used a paintbrush to gently move one of the spiders to face the other. This was done to minimize any errors in recognition that may trigger predatory events.

We assigned males and females to one of three treatments: cool (20–23 °C), room temperature (25–28 °C), or warm (34–47 °C). We chose our temperature treatments to reflect the variation of temperatures that spiders experience in the field (Fig. 2a). For the cool treatment, we placed the arena in a refrigerator until it reached approximately 2 °C, measured using an IR thermometer (Dual Laser IR Thermometer, Model 42511, Exetech Corp, Nashua, NH). We then removed the arena and allowed it to warm to about 10 °C. At this point, we placed both the male and female spiders onto the plate

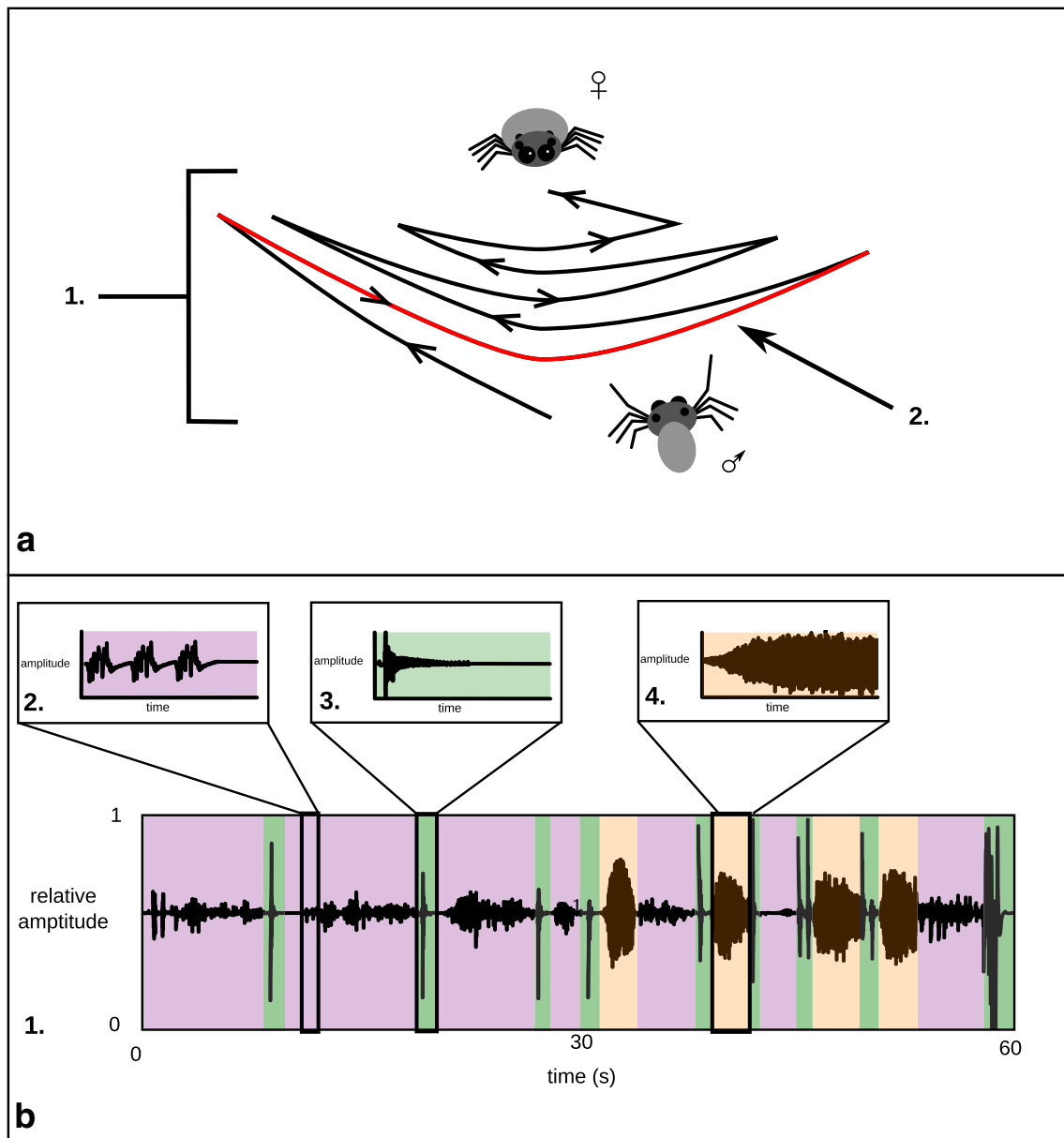


Fig. 1 Early- and late-phase courtship of *H. clypeatus*. **a** Depiction of typical early-phase courtship display. Female (above) remains in place while male walks in a side-to-side zigzag pattern, moving in arcs of shortening length until he is standing ~1 body length away from the female directly in front of her. Illustrated is (1) the entire sidling bout

and (2) a single movement bout. **b** Oscillogram of vibratory aspects of a typical *H. clypeatus* late-phase display. Entire vibratory display is shown in (1). Individual components are indicated in cut-aways: (2) scrapes, (3) thumps, and (4) buzzes

(while still in their cages) to acclimate. Cool trials began when the arena reached approximately 16 °C. We began trials by first releasing the female and then the male directly onto the plate so that they could interact. Only trials in which the arena stayed below 24 °C were included in the cool treatment analyses. For room temperature trials, we kept plates at ambient temperature in the lab, and we placed spiders on the arena for 5 min prior to the trial. Room temperature trials were conducted at 26 °C (range 25–28 °C). For the warm treatment, we placed the arena on an electric griddle (25 cm × 50 cm griddle, Rival Corp, subsidiary of Sunbeam Products Inc., Boca

Raton, FL, USA) until the surface temperature attained approximately 60 °C. Next, we removed the arena from the griddle and allowed it to cool to about 54 °C, at which time the spiders were placed on the plate to acclimate. When the plate attained 49 °C, we began the trial. Only trials in which the arena retained a temperature above 32 °C were included in the warm treatment. We used a total of 37 pairs in these trials: 8 in the cool treatment, 19 in the room temperature treatment, and 10 in the warm treatment. Most individuals were used only once ($n = 35$) although we reused one male each in the warm and room temperature treatments.

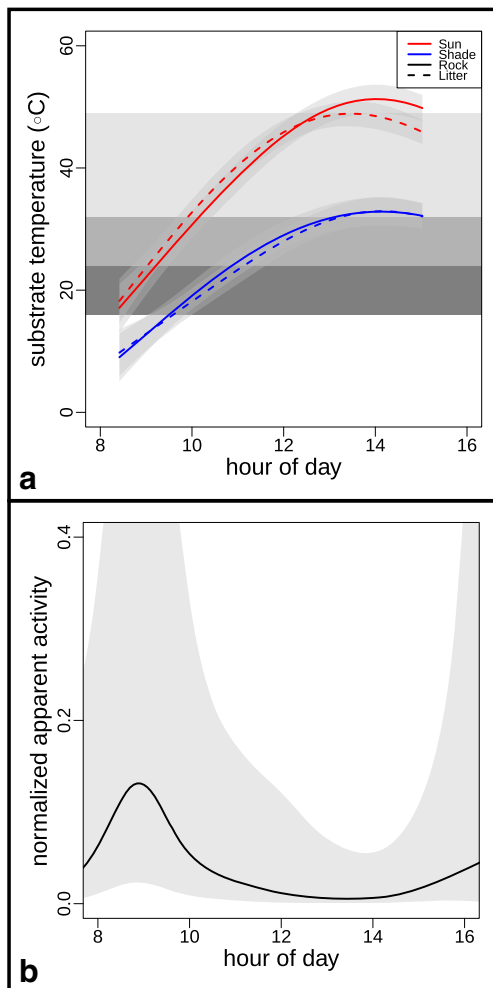


Fig. 2 Habitat temperature and apparent activity of *H. clypeatus*. **a** Surface temperatures of 2 different substrates in *H. clypeatus* habitat in April. Temperatures were taken throughout the day in sun and shade. Solid lines indicate rock, and hashed lines indicate leaf litter. Standard errors are indicated by gray area around lines. Horizontal bars indicate temperature treatments for courtship experiments: cool (20–23 °C), room (25–28 °C), and warm (34–47 °C). **b** Relative apparent activity of *H. clypeatus* individuals throughout the day. Shaded area indicates 95% confidence interval

Once the male began courting, the trial was continued until either (1) the male successfully mated with the female (acceptance) or (2) the female turned away and/or attacked the male three times (rejection). We monitored visual signals with a color video camera (CV-3200, JAI Inc., San Jose, CA, USA) with a macro lens.

In addition to mating rate, we also scored female receptivity and aggression in two ways. First, we recorded whether the male reached the late stage of courtship. Second, we counted how many aggressive behaviors females performed toward males. These behaviors were classified as either (1) *attacks*, in which a female jumped directly at a male, or (2) *grappling bouts*, in which the female attacked the male and remained in contact as she either consumed or attempted to consume him.

To compare mating, courtship progression, and aggression rates between treatments, we used Pearson's chi-squared tests, followed by pairwise nominal independence tests, both implemented in R.

Male courtship

Early-stage courtship

A cartoon of the display is seen in Fig. 1a. The male begins by facing the female, usually at some distance away (~5 body lengths). He waves his first pair of legs in a rhythmic fashion and begins to walk sideways in a shallow arc. As the male sidles back and forth, the arcs shorten, and he moves closer and closer to the female. This movement is not continuous. The male usually completes each arc in a single bout but often pauses at the end of arcs before beginning to move again. We define the entire visual display as a "sidling bout," and a period of time in which the male was moving as a "movement bout" (Fig. 1a). Since the movement bout corresponds to the time that the male is physically moving, we use aspects of the movement bout as a measure of male effort or vigorousness. Similar measures have been used to evaluate courtship in other species of spider (Byers et al. 2010). Females do not move in a manner similar to males. If interested in a male, the female pivots in order to maintain visual contact with the male as he sidles about her but does not move more than about one body length from her initial starting point. Females periodically turn away and then back toward males. Once a male is one to two body lengths away from the female, he stops moving and extends his first pair of legs toward the female as he begins the late phase of his display (see below).

We identified and quantified the following components in early-stage courtship: *sidling bout*, defined as the time from when the male begins moving laterally with respect to the female until he either turns away from the female or begins vibratory courtship, and *movement bouts*, the periods during the sidling bout in which the male is actually moving. Each trial contained 1–12 (mean 3.6) sidling bouts and multiple movement bouts per sidling bout. For each trial, we calculated (1) the total number of sidling bouts divided by the time of the trial (sidle rate), (2) the percent of the trial spent sidling, and (3) the average length of a movement bout. We measured the temperature of the plate surface immediately adjacent to the interacting spiders at three different time points: (1) at the beginning of the trial, (2) at the beginning of courtship behavior, and (3) at the end of the trial. Video analyses were conducted using the Behavioral Observation Research Interactive Software (BORIS) software package (Friard and Gamba 2016).

To model the relationship between temperatures and early-stage courtship signals, we fit GAMMs to each relationship between temperature and courtship components, implemented in R with mgcv. We chose to use GAMMs because they give

detailed models that easily incorporate complexity and non-linearities. We thus compared our GAMMs qualitatively using the estimated 95% confidence intervals. To build our models, we tested each of the following signal components as a dependent variable separately: sidling rate, percent time sidling, and movement bout length. For temperature, we averaged the three different temperature measurements taken during the trial and used the mean as a continuous independent variable in our models. We used a gamma error structure as data were bounded by zero and used $k = 15$ for the number of knots. We also used male identity as a random effect, as we reused one male in each of the warm and room temperature treatments.

Late-stage courtship

Vibratory portions of *H. clypeatus* late-stage courtship consist of three elements: broadband stridulatory *scrapes*, broadband stridulatory/percussive *thumps*, and tonal tremulatory *buzzes* (Fig. 1b). These components are arranged into distinct functional groupings (motifs) (Elias et al. 2012). As the display proceeds, elements are added to motifs creating a distinctive progression.

Male late-stage courtship signals are highly dependent on female feedback. In order to ensure our ability to measure all vibratory signal types, we standardized female feedback by using dead female lures. To construct lures, we used wax to glue a euthanized female to a small dowel inserted into a hole in the arena. A pulley system allowed us to rotate the female in a lifelike manner. This system has previously been effective at stimulating male jumping spiders to court (Girard et al. 2011; Elias et al. 2012). We used 20 males for these trials in a repeated measures design. We ran each male in each of the three temperature treatments for a total $n = 60$ for these trials. We used courtship arenas constructed from 23 cm diameter terracotta platters with a 1-cm hole drilled in the middle of each one where the female lure was placed. A paper liner was used in the arenas as described above. We ran each male in warm, cool, and room temperature treatments in a randomized order.

All trials were terminated once males attempted to mount and mate with the female model. We excluded one trial from the analysis because the male did not perform all aspects of vibratory courtship. We recorded all vibratory signals with a scanning laser-Doppler vibrometer (PSV-400, Polytec, Irvine, CA). Vibratory signals were recorded directly off the male's abdomen.

H. clypeatus late-stage courtship displays consist of tightly coordinated unique visual movements coupled with unique vibratory signals. There is a tight, one-to-one coordination between visual and vibratory aspects the late courtship display (Elias et al. 2006b), and we did not notice any deviation from this coordination across temperature treatments. Therefore, we analyzed only the vibratory elements of these displays for simplicity. We analyzed the vibratory displays using Audacity v. 2.0.5. Durations were measured for all thumps and buzzes, and for a subsample of scrapes ($n = 20$ per song). We used custom Python scripts to

calculate average durations of thumps, scrapes, and buzzes in the entire song. *Scrape rate* was measured by identifying regions of the display containing multiple repeated scrapes and calculating average scrape rates for each bout. *Frequency* was measured by running an FFT analysis on each signal component and calculating peak (scrape, thump) and fundamental (buzz) frequency using a modified version of the pypeaks Python module. Average root mean square (RMS) amplitude was also calculated for each signal component. All custom software was deposited in a git repository and is available by request.

To statistically model the relationships between vibratory components and temperature, we used GAMMs as described above. We tested each of the following dependent variables separately: scrape, thump and buzz duration, scrape, thump and buzz RMS, scrape rate, scrape and thump peak frequency, and buzz fundamental frequency. For temperature, we used the temperature measured at the time of the beginning of male courtship. Temperature was used as the fixed effect and male identity was a random effect to account for the repeated measures nature of the design. As with the visual signals, we used a gamma error structure and $k = 15$ for the number of knots.

Results

Temperature/activity

H. clypeatus habitat varied in temperature on a daily basis. The range of temperatures throughout the day was 11–37 °C (shade) and 20–56 °C (sun) (Fig. 2a). Apparent activity was bimodal, with a peak around 0900 h and then after 1600 h. Temperatures at these peak activity periods were approximately 13–24 °C in the morning and 32–46 °C in the afternoon (Fig. 2b) (See SI 1 for model statistical details).

Female behavior

Mating rates

In mate choice trials, mating rates differed between the temperature treatments ($df = 2$, $\chi^2 = 24.10$, $p = 5.83 \times 10^{-6}$). Zero percent of pairs mated in the cool treatment, 17% of pairs mated in the room temperature treatment, and 61% of pairs mated in the warm treatment (Fig. 3a). The differences in copulation rate were not significant between cool and room temperature treatments ($p = 0.180$) but were different between cool and warm treatments ($p = 1.65 \times 10^{-4}$) and room and warm treatments ($p = 3.42 \times 10^{-3}$).

Aggression/receptivity

The percentages of trials that contained female attacks were 37%, 26%, and 30% respectively for cool, room, and warm

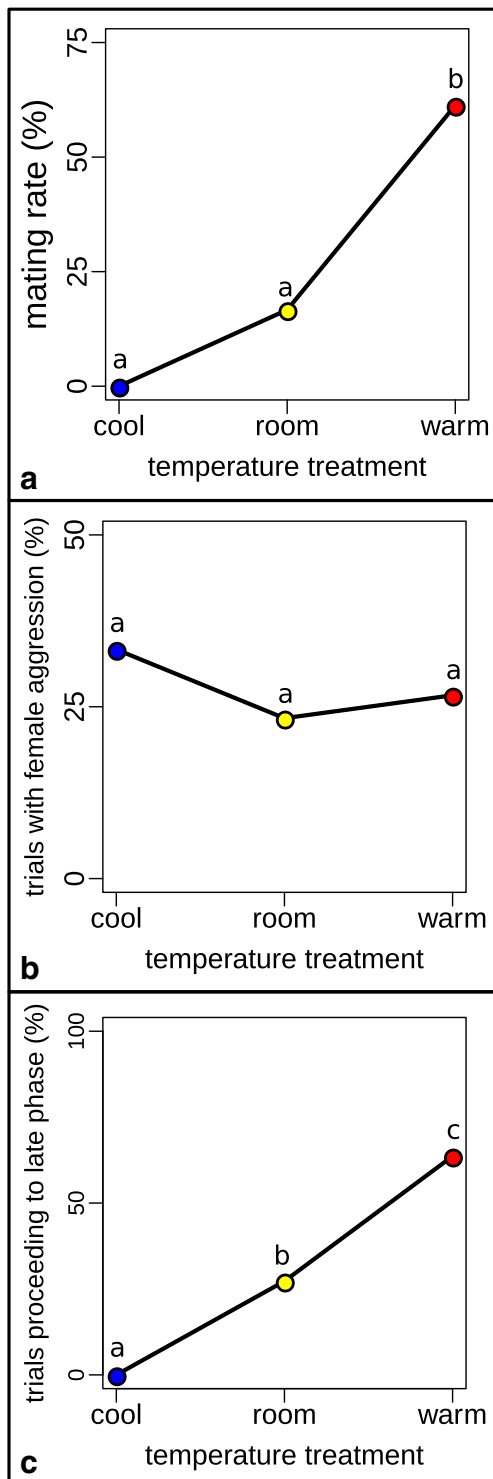


Fig. 3 *H. clypeatus* female behavior across temperature treatments. Different letters within a panel indicate significant differences between treatments ($p < 0.05$). **a** Percent of females mating in three temperature treatments: cool, room temperature, and warm ($n = 37$ pairs, 8 in the cool treatment, 19 in the room temperature treatment, and 10 in the warm treatment). **b** Percent of trials that included aggressive female behaviors. **c** Percent of trials in each temperature treatment that proceeded to late-phase courtship

treatments (Fig. 3b), although these differences were not significant ($\chi^2 = 3.70$, $p = 0.16$). We saw grappling in only two

trials (both in the warm treatment). The outcome of both trials was cannibalization of the male by the female.

The percentages of trials that proceeded to late-phase courtship were 0%, 32%, and 75% respectively for cool, room, and warm treatments (Fig. 3c). These differences were significant between all three treatments ($\chi^2 = 29.54$, $p = 3.84 \times 10^{-07}$, pairwise: cool-room, $p = 7.53 \times 10^{-03}$, cool-warm, $p = 9.87 \times 10^{-03}$, room-warm, $p = 1.20 \times 10^{-02}$).

Male signals

Early-stage courtship

The rate of sidling bouts that males perform did not change across temperature treatments (Fig. 4a, $p = 0.20$). However, males spent more time per trial sidling as the temperature increased (Fig. 4b, $p = 0.002$). Additionally, the length of each individual movement bout increased with temperature (Fig. 4d, $p = 0.02$), but the total number of movement bouts did not change (Fig. 4c, $p = 0.09$).

Late-stage courtship

Male late-stage courtship signals changed with temperature (Figs. 5 and 6). All measured signal components were temperature-dependent (see Tables 1 and 2 for model details and p values). Durations and amplitudes (RMS) of vibratory components decreased with increasing temperature (Fig. 5), although this relationship was not significant for buzz amplitude. Rates and frequencies of signal components all increased significantly with increasing temperature, although a slight decrease was seen at the highest temperatures (Fig. 6).

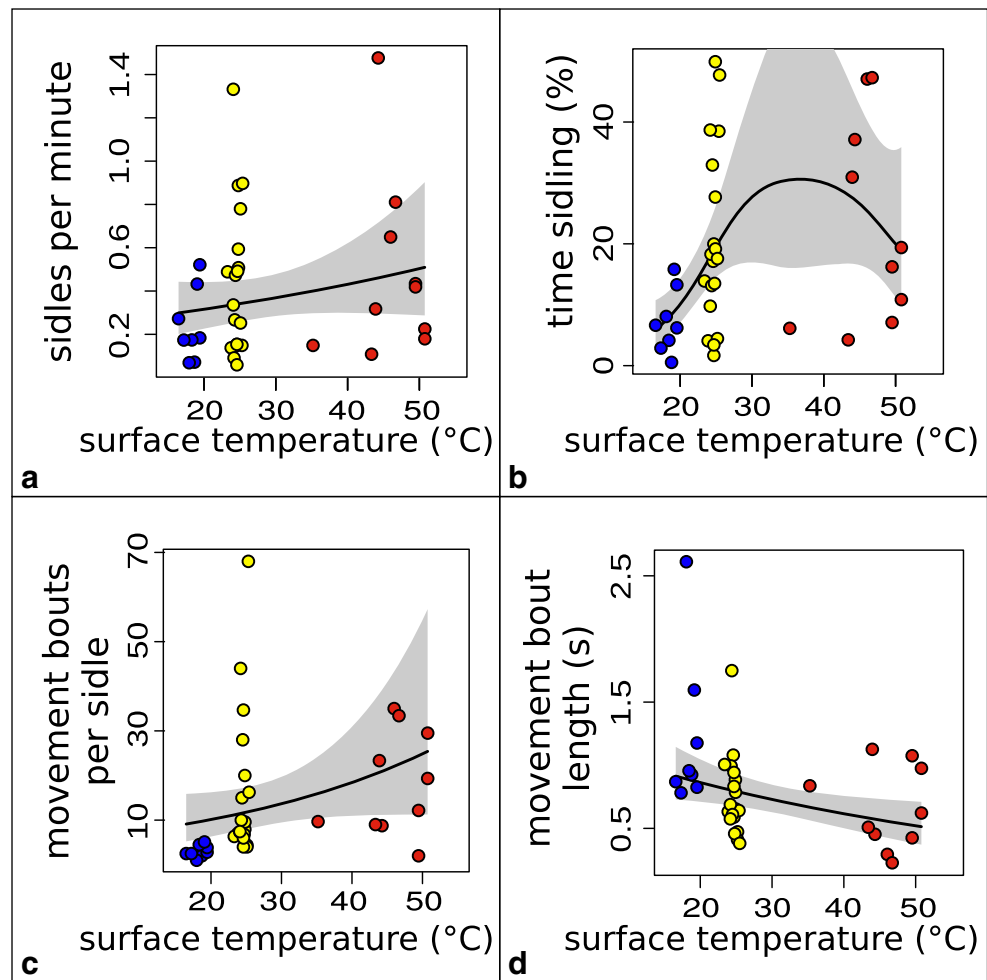
Discussion

We found that temperature has a profound effect on *H. clypeatus* courtship (Figs. 3, 4, 5, and 6). Females exhibit higher mating rates at higher temperatures (Fig. 3). Various aspects of male signals also changed with temperature (Figs. 4, 5, and 6). Importantly and contrary to our predictions, different aspects of courtship have different relationships to temperature. Further complicating this story, females mate at very low rates at temperatures at which spiders are particularly active in the field (in the early morning; Fig. 2). Overall, our results suggest that changes in temperature have dramatic effects on sexual selection.

Mating rates

Mating rates are lowest at the temperatures at which we recorded the highest levels of activity in the field. The fact that females seem not to be engaging in sexual behaviors at

Fig. 4 Early stage *H. clypeatus* male display. **a** Average rate of sidling bouts. **b** Average percent of time spent sidling per trial. **c** Average number of movement bouts per sidling bout. **d** Average length of movement bout per sidling bout ($n = 37$ pairs, 8 in the cool treatment, 19 in the room temperature treatment, and 10 in the warm treatment). Colored dots indicate whether a sample was collected in cool (blue), room temperature (yellow), or warm (red) treatments. Gray areas indicate 95% confidence interval



temperatures corresponding to these times of day is surprising and counter-intuitive. It is important to note that we did not measure operative temperature in our field measurements, so it is difficult to know exact spider body temperatures in the field. Regardless, we do see the trend that spiders are more active at lower field temperatures and tend to mate at higher rates at higher lab temperatures.

Lower mating rates at lower temperatures could be the result of several factors. First, temperature may directly affect a female's ability to mate. We consider this unlikely, given that important behaviors such as foraging occur at the lower temperatures included in this study, suggesting that animals are physiologically able to perform important tasks at these temperatures. Also, males were able to perform courtship behavior at these lower temperatures suggesting that females would also likely be able to perform sexual behaviors. Second, females may be unwilling to mate at lower temperatures, potentially because this behavior carries certain environment-dependent risks. For example, females may experience increased predation risk or other hazards while assessing courting males. This risk may be increased at cool

temperatures, since females presumably have slower reaction times and a hindered ability to flee danger, as has been found in other ectotherms (Weatherhead and Robertson 1992; Cooper 2000; Carlson and Rowe 2009).

Third, temperature may alter the attractiveness of male signals. If females prefer faster, higher pitched male courtship, cold temperatures will reduce the attractiveness of all males. If this is the case, males that display in a warmer environment may be at an advantage, regardless of their quality and ability to produce multimodal signals. We might therefore expect that males will preferentially court in warm temperatures. This has been found in crickets, which prefer to call from warm locations which allow them to generate a more appealing call (Hedrick et al. 2002). A more extreme version of this principle has been seen in fiddler crabs, which choose to court at temperatures that are dangerously near their thermal limit but improve their courtship signal (Allen and Levinton 2014). In systems like *H. clypeatus*, females only mate once; thus, there are potentially large fitness consequences for females that choose mates with misleading signals. In most species in which this has been studied, animals have been shown to use signal-preference coupling to coordinate signaling changes

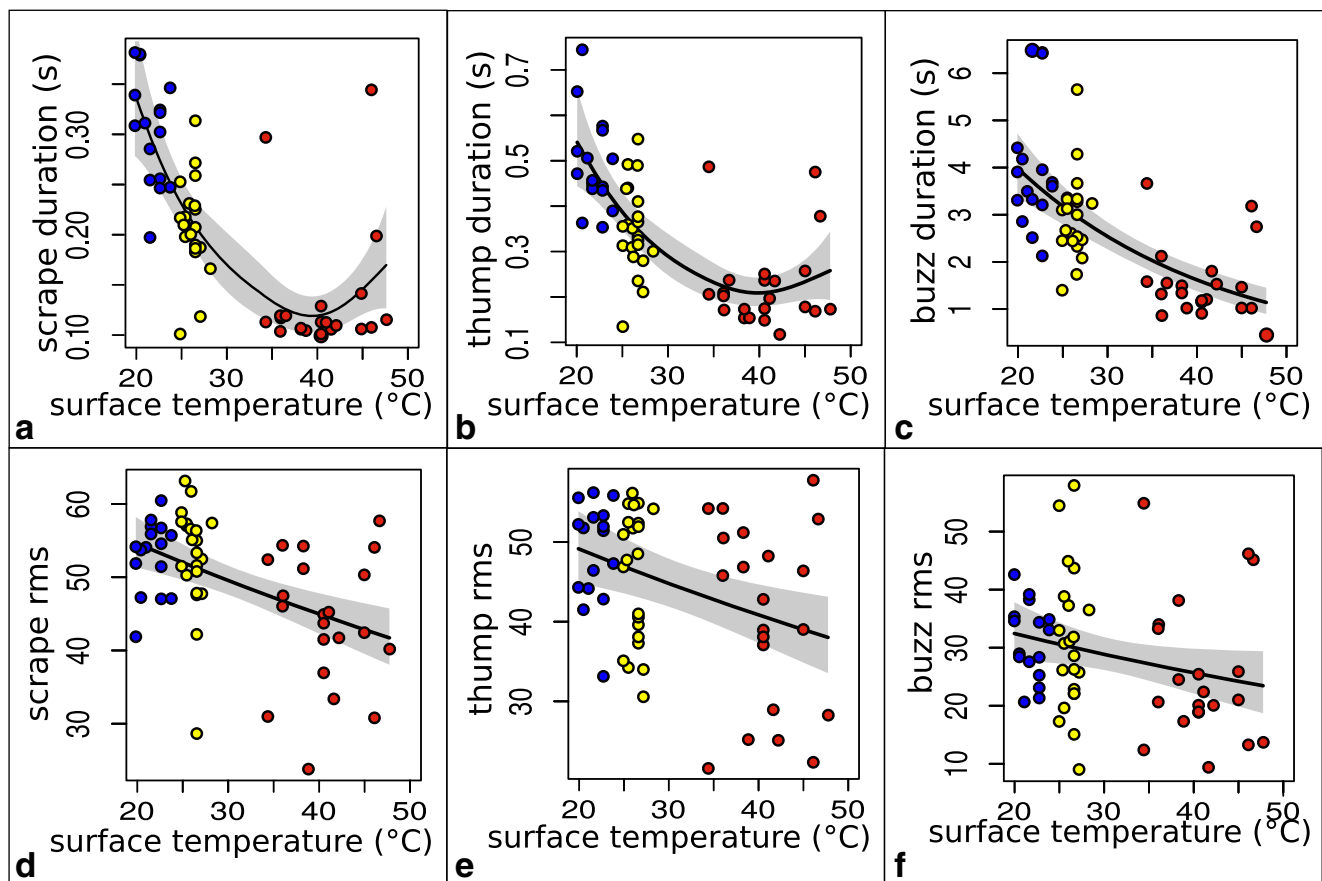


Fig. 5 Durations and amplitudes of vibratory aspects of *H. clypeatus* male late-phase display. **a** Average scrape duration. **b** Average thump duration. **c** Average buzz duration. **d** Average scrape RMS. **e** Average thump RMS. **f** Average buzz RMS. ($n = 60$ trials, 20 each for cool, room

temperature, and warm treatments). Colored dots indicate whether a sample was collected in cool (blue), room temperature (yellow), or warm (red) treatments. Gray areas indicate 95% confidence interval

in temperature (Gerhardt 1978; Doherty 1985; Pires and Hoy 1992; Symes et al. 2017). Signal-preference coupling predicts that across temperatures, mating rates should be similar, as the same quality males would be selected even as signaling behavior shifts. Signal-preference coupling is not supported in this study, similar to a few studies in flies and frogs (Gerhardt and Mudry 1980; Ritchie et al. 2001). In these studies, it was suggested that reproductive behavior only occurs in a subset of thermal conditions. Ectotherms are well known to exhibit temperature shuttling in which they move between different temperature regimes in their environment to maintain a narrow range of preferred body temperature (Casey 1981; Martin and Huey 2008; Kearney et al. 2009; Clissold et al. 2013). We suggest that females may select particular thermal microhabitats to accurately assess males. This would represent an alternative solution to environment signal-preference mismatch that obviates the need for physiological coupling. Future work will examine whether signal-preference coupling based on microhabitat selection is occurring.

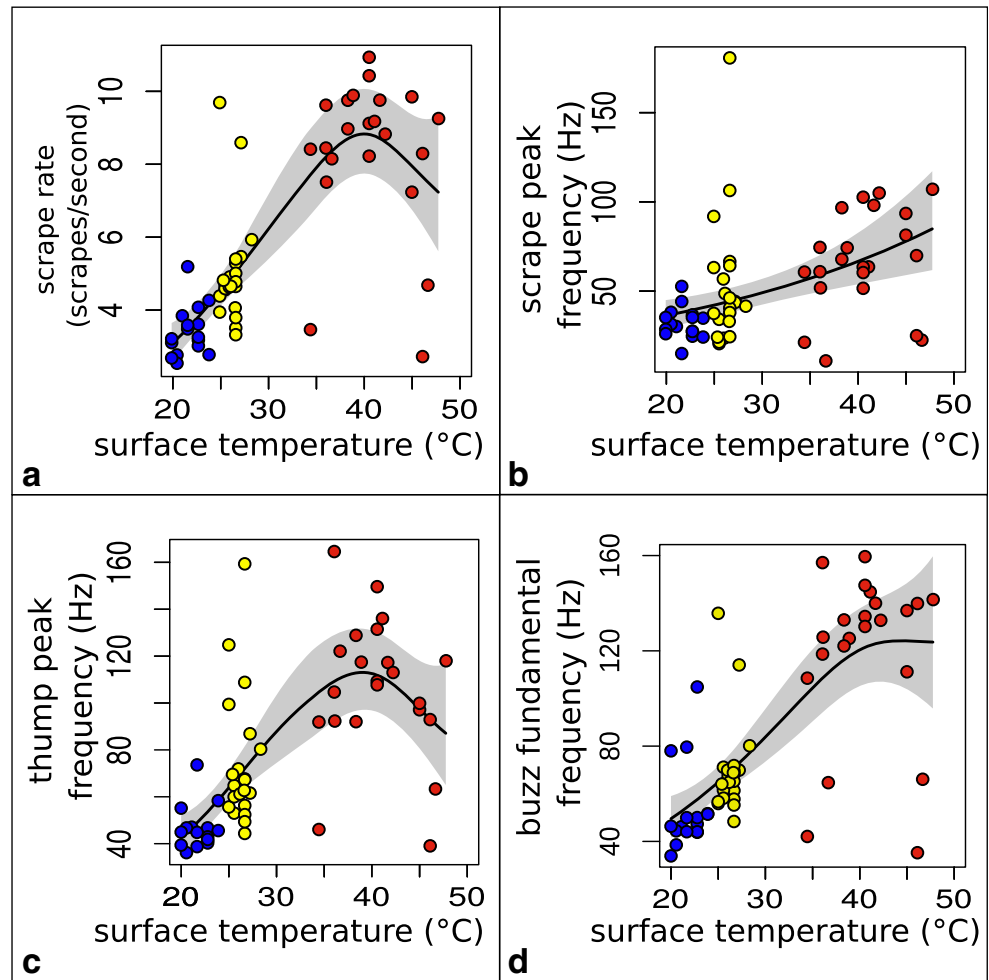
In this study, we observed differences in how far courtship progressed for the different temperature treatments (i.e., early phase, late phase). None of the cool trials progressed beyond the early phase, whereas most of the warm trials did. For many

jumping spider species including those in the genus *Habronattus*, female attention is critically important for male success (Elias et al. 2005, 2006a; Lim et al. 2007, 2008). Female receptivity in the form of attention is predicted to drive the progression through distinct phases. This study suggests that temperature changes the likelihood that females will allow males to progress through the necessary phases. Overall, these data suggest that although female mate choice behaviors are affected by male courtship behaviors, female behavior is affected by temperature in substantially different ways than male behavior. In other words, female behaviors do not simply get “faster” as a result of increases in temperature like males. Instead, variance in the numbers of males selected changes with temperature suggesting complex shifts in mate choice mechanisms (i.e., preference and choosiness).

Male signals

In addition to mating rate, we also looked at male visual and vibratory signaling and how they responded to temperature. In general, male signal components decreased in duration, increased in speed, and increased in frequency with increasing temperature

Fig. 6 Rates and frequencies of vibratory aspects of *H. clypeatus* male late-phase display. **a** Rate of scrapes. **b** Average peak frequency of scrapes. **c** Average peak frequency of thumps. **d** Average fundamental frequency of buzzes ($n = 60$ trials, 20 each for cool, room temperature, and warm treatments). Colored dots indicate whether a sample was collected in cool (blue), room temperature (yellow), or warm (red) treatments. Gray areas indicate 95% confidence interval



(Figs. 4 and 5). This occurred in both visual and vibratory modalities. These relationships broadly attained a curvilinear shape,

in which rates and frequencies increased to a point, and then flattened out or decreased slightly. This pattern suggests a

Table 1 Statistical details for parametric portion of GAMM models for male visual and vibratory components. $k = 15$ for all models. $*P < .05$

	Estimate	S.E.	t	p
Visual variable				
Sidle rate	-1.01	0.13	-7.69	4.98×10^{-09} *
Percent time sidling	-1.79	0.11	-15.71	$< 2 \times 10^{-16}$ *
Movement bouts/sidle	2.58	0.19	13.92	7.86×10^{-16} *
Movement bout length (s)	-0.30	0.08	-3.97	0.0003*
Vibratory variable				
Scrape duration (s)	-1.63	0.038	-42.63	$< 2 \times 10^{-16}$ *
Thump duration (s)	-1.12	0.039	-28.38	$< 2 \times 10^{-16}$ *
Buzz duration (s)	0.92	0.06	16.22	$< 2 \times 10^{-16}$ *
Scrape rate (scrapes/s)	1.69	0.03	49.84	$< 2 \times 10^{-16}$ *
Scrape peak frequency (Hz)	3.84	0.08	47.89	$< 2 \times 10^{-16}$ *
Thump peak frequency (Hz)	4.31	0.04	97.34	$< 2 \times 10^{-16}$ *
Buzz fundamental frequency (Hz)	4.37	0.04	111.70	$< 2 \times 10^{-16}$ *
Scrape amplitude (RMS)	3.90	0.02	191.90	$< 2 \times 10^{-16}$ *
Thump amplitude (RMS)	3.80	0.03	111.50	$< 2 \times 10^{-16}$ *
Buzz amplitude (RMS)	3.36	0.05	67.00	$< 2 \times 10^{-16}$ *

Table 2 Statistical details for smoothed (non-parametric) portion of GAMM models for male vibratory components. $k = 15$ for all models. * $P < .05$

	Est. df	Ref. df	<i>F</i>	<i>p</i>	<i>R</i> ² (adj.)
Visual variable					
Sidle rate	1.00	1.00	1.67	0.20	0.002*
Percent time sidling	2.38	2.38	6.63	0.002	0.12
Movement bouts/sidle	1.00	1.00	3.07	0.09	0.03*
Movement bout length (s)	1.00	1.00	6.06	0.02	0.09
Vibratory variable					
Scrape duration (s)	3.11	3.11	25.9	4.68×10^{-12}	0.63
Thump duration (s)	2.70	2.70	23.0	5.58×10^{-10}	0.55
Buzz duration (s)	1	1	52.7	3.03×10^{-10}	0.45
Scrape rate (scrapes/s)	2.907	2.907	37.19	6.02×10^{-16}	0.66
Scrape peak frequency (Hz)	1	1	14.36	0.0004	0.15
Thump peak frequency (Hz)	2.80	2.80	24.71	8.26×10^{-11}	0.50
Buzz fundamental frequency (Hz)	2.13	2.13	31.87	3.04×10^{-11}	0.55
Scrape amplitude (RMS)	1	1	16.36	0.0002	0.21
Thump amplitude (RMS)	1	1	8.88	0.004	0.11
Buzz amplitude (RMS)	1	1	3.90	0.05	0.05

threshold at which males are no longer able to increase their performance. These peaks occur at about the same temperature (~40 °C) across different signal features. In other studies of signals, the relationships with traits and temperature tended to be linear although the temperatures used in these other studies were much narrower than those described here (Gerhardt 1978; Pires and Hoy 1992; Ritchie et al. 2001; Michaelidis et al. 2006). The presence of a threshold and the overall shape is consistent with what we might expect from a typical ectotherm thermal performance curve (Huey and Kingsolver 1989). In thermal performance curves, the peak or plateau is considered the “thermal optimum” or the temperature at which a given behavior is performed at its best. Although we do not yet know what aspects of male signals are most attractive to females, it is interesting that mating success is higher nearer this presumptive thermal optimum point for most signal components.

These thermal curves also have interesting implications for changing climate. If temperatures increase beyond peak threshold, signal aspects will increase more slowly, stop changing, or even decrease. This scenario could lead to further breakdowns in courter–chooser relationships. We suggest the possibility that breakdowns such as these may occur in other animal systems. While past studies have not shown this pattern, those experiments did not examine the ranges of temperatures explored in this study. It will be interesting to examine other species, particularly ones that have wide thermal ranges to see if and to what extent these patterns may be broadly applicable to other ectotherm groups.

Although males performed visual sidling bouts at a similar rate across temperature treatments (Fig. 4a), they spent more time sidling in warmer temperatures (Fig. 4b). At first glance, this may seem to be a counterintuitive result, as one would

expect the lengths of signal components to decrease with temperature (as they do in vibratory displays). However, in ectotherms, it is generally recognized that “performance” increases with increasing temperature. In many spiders, short, high-frequency signal components have been shown to be more attractive (Kotiaho et al. 1996, 1999; Gibson and Uetz 2008; Girard et al. 2015), but a long sidling bout might also be more attractive than a short one if it represents an increase in stamina or time investment in courtship. Long sidling bouts may also maintain female attention as jumping spiders are particularly sensitive to movement (Zurek and Nelson 2012a, b; Menda et al. 2014).

In general, we find that shorter, faster, higher-frequency signals are correlated with higher mating rates across our three temperature treatments. This agrees with other studies that suggest that higher-frequency, faster, and louder signals are often more attractive in spiders. However, we also found that the amplitude (RMS) of vibratory elements decreased with increasing temperature and that this relationship was more linear than other signal element properties (Fig. 5d–f) although this pattern was not significant for buzzes. This suggests that there might be a tradeoff between rate/frequency and amplitude. In other systems, it has been suggested that such tradeoffs are important for the maintenance of honesty in acoustic signals, so this may be at play here (Podos 1997; Manica et al. 2017). Alternatively, females may weigh amplitude less than other components when considering whether to mate with a given male. This result is particularly interesting given that amplitude is rarely addressed in studies of thermally variable courtship. The sole example we found other than our own study suggested that the amplitude of electric signals increases with increasing temperature in a weakly-electric fish (Dunlap et al. 2000). Additional work is needed to explore

how amplitude relates to attractiveness of signals and what potential tradeoffs may exist.

The differential patterns between signaling types lend credence to the idea that early and late display phases serve different functions. One hypothesis for the existence of the initial sidling bout is that it allows males to gauge the level of interest and aggression in females (Uhl and Elias 2011). By showing increased willingness and stamina to perform long sidling bouts, males may be increasing their chances of being allowed to move onto later phases of courtship. If different information can be conveyed by different parts of a display, this may drive the evolution and maintenance of complex signals (van Doorn and Weissing 2004; Partan and Marler 2005; Bro-Jørgensen 2010; Wilson et al. 2013). Also, if abiotic factors influence these different signal aspects in different ways, there could be complex and unpredictable changes to the information conveyed. If, on the other hand, similar information is conveyed with different signal aspects, those that are less affected by temperature may buffer those that are more temperature-dependent. Although we did not statistically compare the relationships between specific signal aspects and temperature, there seem to be differences in the shape of these relationships. Future work will address what specific aspects of the display are important for females and how the higher-order structure of the displays changes across temperature.

Our results emphasize that sexual communication is dependent on temperature, but many questions about their thermal ecology are still unanswered. Our lab experiments greatly simplify the variation inherent in thermal environments. First, we only measured environmental temperatures across a subset of time in the breeding season. Therefore, our lab experiments did not encompass the total variation of temperatures, which are likely to be much hotter in the early summer months. Second, our field temperature measurements were limited to surface temperature and did not incorporate the many other ways that spiders can exchange heat with their environment, particularly direct solar radiation which is likely important in desert environments (Clusella-Trullas et al. 2007). Because of this, our field measurements may underestimate the temperatures that spiders may be experiencing. Third, within time points, there may be large differences in adjacent patches of substrates. Animals may shuttle between temperatures, thereby buffering some of these differences. Regardless, our study demonstrates that mate choice and by extension sexual selection may be dramatically different across the day and even within a few steps.

Conclusions

Temperature has large, wide-ranging impacts on intersexual behavior in *Habronattus clypeatus*. These impacts can be dramatic and complex. Changes in temperature likely have large

impacts on the ability for females to discriminate among males and for males to produce signals that will secure mates. The long-term effects of this interaction are complicated and difficult to predict, particularly when we consider that two parties are involved and that both of those parties' behaviors may be temperature-dependent in different ways. These complexities are compounded by the fact that male signals are multimodal, and different aspects of the signals can be affected differently by changing temperatures. Our data suggest that profound differences in mating behavior can result from ecological conditions that vary and that differences between the sexes could potentially amplify these effects. This work underscores the importance of obtaining fine-grained ecological knowledge that is relevant to the size and biology of the organism in question. Understanding how changing climatic regimes will affect the selective landscapes of all animals is one of the greatest challenges facing biologists today and one that must be ultimately tackled in different organisms and at different biological scales.

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