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Nonlinear changes in selection on a mating display across a continuous thermal gradient

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Understanding how animal communication varies across time and space is critical to understanding how animal signals have evolved and how they function. Changes in temperature, which occur across both time and space, can alter both the courtship and mate choice behaviour of ectothermic animals. In this study, we examine the effect of daily thermal variation on courtship and mate choice in the wolf spider *Schizocosa floridana*, which produces a complex song with vibrations from three distinct body parts. We test the hypothesis that different components of *S. floridana*'s courtship respond differently to daily changes in temperature and that corresponding mate choice patterns lead to complex, overlapping shifts in selection on the display itself. By manipulating the thermal environment of courting and choosing pairs, we found that several song components increased in production rate with increased temperature, whereas others decreased, or did not respond at all. We also found evidence that selection on courtship shifts with temperature in several ways, with some display components experiencing directional selection at higher temperatures, but not at lower temperatures. Our findings make it clear that understanding the effect of environmental variation on communication is critical to understanding how selection operates on mate choice and how signals, particularly complex signals, evolve.

1. Introduction

Animals experience variation in selection across time and space, often as a result of changing environmental factors [1–5]. Animal communication may be especially sensitive to environmental shifts [2,6], which can dampen the directional effects of selection on signal form [1], maintain genetic variation in signalling traits [7,8] and even drive the evolution of signal complexity [9–11]. The study of these factors is complicated by the fact that signals, especially courtship signals, commonly contain multiple discrete components that may interact to influence receiver behaviour (e.g. [12–15]). Change along even a single environmental axis can lead to varying, uncorrelated changes across separate signal components and equally complex changes in receiver responses (e.g. [10,16]). To understand how animal signals evolve, it is thus critical to understand how environmental variation affects both signaller and receiver behaviours. Together, the interaction of these two factors determines the strength and form of selection that drives the evolution of signals.

Variation in temperature is among the most important environmental factors that animals experience. Because biochemical reaction rates are temperature-dependent, an animal's metabolism is intrinsically tied to its body temperature [17,18]. For ectotherms, whose body temperatures are not internally buffered, changes in environmental temperature can therefore alter the performance of whole-organism activities from locomotion [19,20] to prey capture [21,22] and habitat selection [23,24]. In particular, ectotherm courtship signals commonly increase in production rate at higher temperatures, probably as a result of metabolic rate increases [25–31]. Because mate preferences frequently focus on the energetics of courtship [32], changes in environmental temperature have the potential to drastically alter the attractiveness of a courting individual.

Chooser behaviour can also drive shifts in selection across the thermal range, and there is significant evidence that mate preferences can change with temperature. Choosing individuals in many species exhibit 'temperature-coupled' preferences [27,33,34], increasing their threshold for acceptance, or preferred courtship rate, as temperatures increase. This may be adaptive, ensuring that choosers do not inappropriately accept low-quality mates at higher temperatures or reject high-quality mates at lower temperatures, or it may be an emergent property of shared neuromuscular systems [35]. However, this pattern is far from universal. In some species, chooser preferences are unchanged across temperatures despite changes in courter signal form [30,36]. In others, preferences shift, but not to the same degree as courtship does [37]. These potential signal preference mismatches probably lead to important changes in selection on signal from across temperatures. Yet, while previous studies have examined the effects of temperature on courter and chooser behaviour separately, few studies have tested how these two factors interact to affect mate choice, and thus selection, across a thermal range.

Here, we assess interacting male and female behaviours to determine how the selection landscape varies across a continuous thermal gradient in the wolf spider *Schizocosa floridana*. Male *S. floridana* court females using a multicomponent vibratory song [38] produced by stridulation of the pedipalps, vibration of the abdomen and percussive tapping of the forelegs [38,39]. These songs are transmitted through a leaf litter substrate [39], and females generally prefer males with faster display rates [16,40], though previous work finds that both courtship form [16,38,40] and patterns of female choice [38,40] are variable across environments. By simultaneously assessing male courtship and female choice behaviours, we seek to explore how selection acts on this complex display. Specifically, we test the hypothesis that different components of *S. floridana*'s courtship respond differently to daily changes in temperature, and that corresponding changes in female preferences lead to overlapping shifts in selection regimes on the display itself.

2. Material and methods

(a) Collection and housing

We collected subadult *S. floridana* ($n \sim 700$) from 2–4 February 2017 in Alachua County, Florida. Spiders were transported to UC Berkeley, where they were housed individually in the laboratory in 6 cm × 6 cm × 8 cm clear plastic containers (Amac Plastic Products, Petaluma, CA, USA). Spiders were maintained on a 12 L : 12 D schedule, at an ambient laboratory temperature of 24°C. All spiders were fed one cricket matched to their body size twice per week and were provided with *ad libitum* water. All spider containers were checked daily for the presence of a moult, which indicated that the spider had matured.

(b) Courtship trials

To assess mate choice, we ran courtship trials in which one male and one female (determined by adult genital dimorphism, which is highly correlated with gamete production type) were allowed to interact freely, and measured male courtship behaviours and mating success. Female *S. floridana* do not produce visual or vibratory displays of receptivity and do not respond to playbacks of recorded courtship. To assess mate choice, it is therefore necessary to allow females the opportunity to assess and potentially choose to mate with a live courting male.

Trials were run inside of a temperature-controlled incubator (Panasonic MIR-154-PA Compact Microbiological Incubator). Two batches of six trials were run per day, and all trials within a batch were run at the same temperature. Trials were run with the incubator set at every degree between 12°C and 38°C, though the order of the temperature was randomized. Temperatures at the collection site range from a recorded low of −2.8°C to a recorded high of 35°C during *S. floridana*'s breeding season (March and April) with a daily mean low of 11°C and a daily mean high of 26°C (NOAA Local Climatological Data for Gainesville, FL, 2005–2015), but preliminary trials determined that males do not court at temperatures of 11°C or below. We thus chose a temperature range that began above 11°C and extended to 38°C, just beyond the maximum recorded field temperature.

Trials were run in an 18 cm circular arena floored with filter paper (Whatman no. 1 filter paper; 18.5 cm diameter; Schleicher and Schuell, Keene, NH, USA), surrounded by a three-inch-high acetate wall. Prior to the trial, we placed a female in an arena and a male in a plastic vial inside the incubator, where both spiders acclimated to their experimental temperature for 30 min. After acclimation, we deposited the male into the arena and allowed the pair to interact for 25 min. We consider 25 min sufficient duration to determine whether copulation is likely to occur. Successful males mated quickly. Of the pairs that did copulate, 73% did so in the first 10 min, and only 6% did so in the last 10 min. Only one copulation occurred later than 20 min. During the trial, the incubator was turned off to facilitate laser vibrometer recordings (see below). This resulted in temperature changes of a degree or less during most trials, but was a necessary step in order to reduce fan noise that disrupted both spider behaviour and the clarity of vibratory recordings. We recorded the temperature inside the arena using an Omega Type K thermocouple, recording temperature measurements once per second onto a Reed SD-947 data logger.

We recorded substrate-borne vibrations using a laser vibrometer (Polytec PDV100) set for a peak velocity measurement range of ±20 mm s^{-1} with a low pass filter at 22 kHz. Using a mirror positioned under the arena, the vibrometer laser was focused on a square of retroreflective tape (Polytec, 3 mm × 3 mm) placed in the centre of the underside of the filter paper. Output from the vibrometer was recorded as a 24-bit WAV file using Audacity (audacity.sourceforge.net). At the end of the 25 min trial, we ceased recording both temperature and vibrations and removed the arena from the incubator. *S. floridana* copulation continues for more than 2 h, so copulation success for each pair was scored visually as the pair was removed from the incubator. Copulation is also an acoustically distinct event, and its time was confirmed on the audio recordings. The incubator was then turned back on and allowed to run for 5 min to re-equilibrate to the experimental temperature before beginning the next trial. Out of 162 potential trials, 6 were aborted before recording due to the escape of one or both spiders and 5 had to be discarded due to poor recording quality or faulty temperature measurements. We also discarded all trials in which the male failed to begin courting within the first 15 min of the trial ($n = 37$). This left 115 trials that were used in all analyses.

(c) Quantification of courtship behaviour

Following a modified version of measurements from [16] and [38], we measured 11 acoustic display components from the first 2 min of courtship produced by each male (figure 1). We measured the total number of (i) stridulatory thumps, (ii) percussive taps and (iii) abdominal chirps produced during the 2 min time frame.

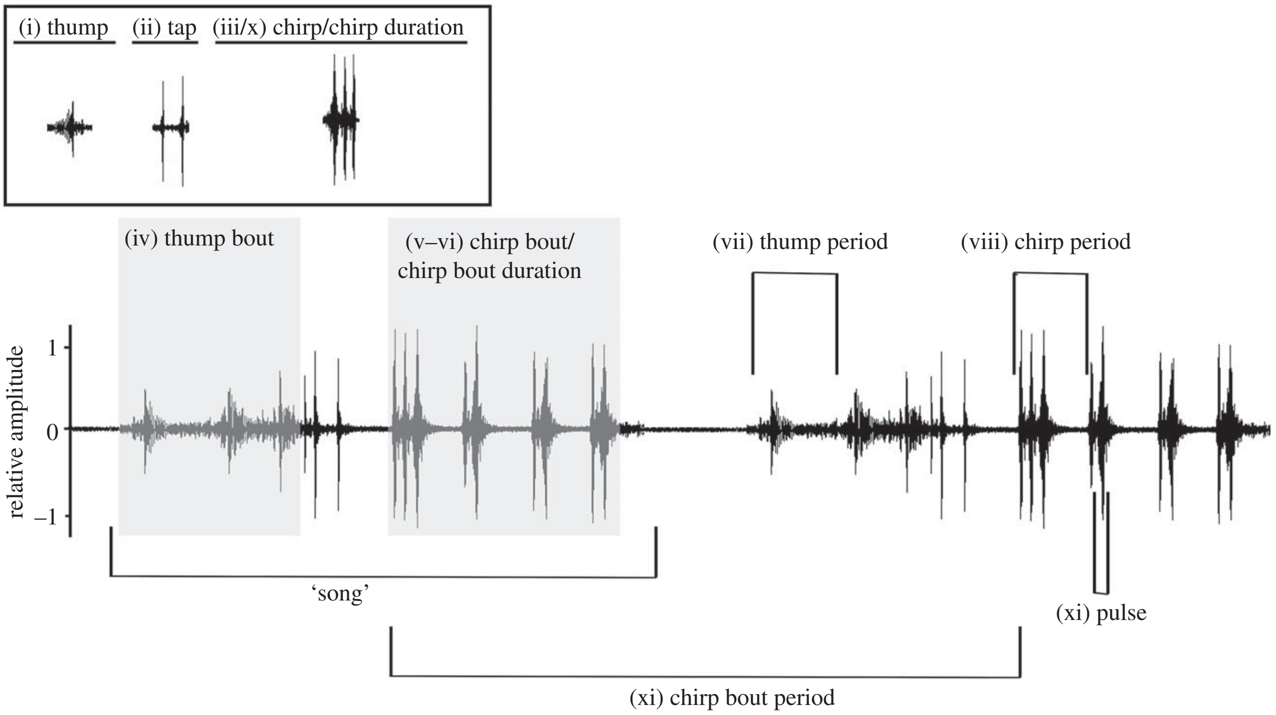

Figure 1. Diagram of a single *Schizocosa floridana* song, demonstrating the stridulatory, percussive and chirp display components. Vibratory components pictured are as follows: (i) stridulatory thumps, (ii) percussive taps, (iii) tremulatory chirps, (iv) thump bout, (v) chirp bout, (vi) chirp bout duration, (vii) thump period, (viii) chirp period, (ix) pulses per chirp, (x) chirp duration and (xi) period between chirp bouts.

These three vibratory components are produced in an ordered format, organized into repeating 'songs' consisting of a bout of thumping, followed by a leg tap, followed by a bout of chirping (figure 1). We also measured (iv) the total number of thump bouts in the 2 min time frame, (v) the total number of chirp bouts in the 2 min time frame and (vi) the average duration of a chirp bout. Within bouts of thumping and chirping, we measured (vii) the mean period between thumps and (viii) the mean period between chirps. Chirps consist of multiple repeated pulses. We measured (ix) the average number of pulses within a chirp and (x) the mean duration of a chirp. Finally, we measured (xi) the mean period between bouts of chirping as a measure of the mean period between songs.

(d) Analysis of courtship form across temperatures

To assess the effect of temperature on courtship behaviour, we first performed a principal components analysis on the correlation matrix of the original 11 acoustic variables. Three principal components had eigenvalues over 1 and cumulatively explained 80% of the variance in the dataset (table 1). Thump, tap and chirp number (i–iii), as well as the number of chirp and thump bouts (iv and v), load positively onto PC1, indicating increased production rate at higher values of PC1. The periods between chirps or thumps within a bout (vii and viii), the period between bouts of chirps (xi) and the duration of chirp bouts and of individual chirps (vi and x) all load negatively onto PC1, indicating shorter periods between signalling components and shorter signal component durations at higher values of PC1. Both positive and negative loadings likely represent more energetic signalling at high values of PC1 (with the possible exception of component (x), which we discuss below), as more energetic signalling should increase the number of components produced, and decrease the periods between components. Two signal components, chirp bout duration (vi) and pulses per chirp (ix) load weakly onto PC1 and are likely better explained by other principal components (PC2 and PC3).

PC2 most strongly reflects chirp duration and pulses within a chirp (ix and x), both of which load positively on PC2. Conversely, chirp bout duration (vi) loads negatively onto PC2. Few other traits load strongly onto PC2, though thump number (i), thump bout number (iv), thump period (vii) and chirp period (viii) all load positively on PC2, but weakly relative to PC1. In summary, PC2 primarily reflects chirp duration and the number of pulses within a chirp, as well as chirp bout duration. Like PC1, higher values of PC2 indicate more energetic courtship, with chirp length

Table 1. Factor loadings for the principal components analysis. The proportion of variance explained by each factor is given parenthetically next to each factor name.

		PC1 (0.51)	PC2 (0.20)	PC3 (0.08)
(i)	thump number	0.840	0.357	−0.011
(ii)	tap number	0.890	0.278	0.053
(iii)	chirp number	0.774	−0.253	0.456
(iv)	thump bout number	0.885	0.388	0.095
(v)	chirp bout number	0.902	0.282	0.192
(vi)	chirp bout duration	−0.390	−0.606	0.638
(vii)	thump period	−0.621	0.397	0.058
(viii)	chirp period	−0.692	0.341	0.433
(ix)	pulses per chirp	−0.345	0.732	0.156
(x)	chirp duration	−0.648	0.690	0.157
(xi)	chirp bout period	−0.592	−0.007	−0.121

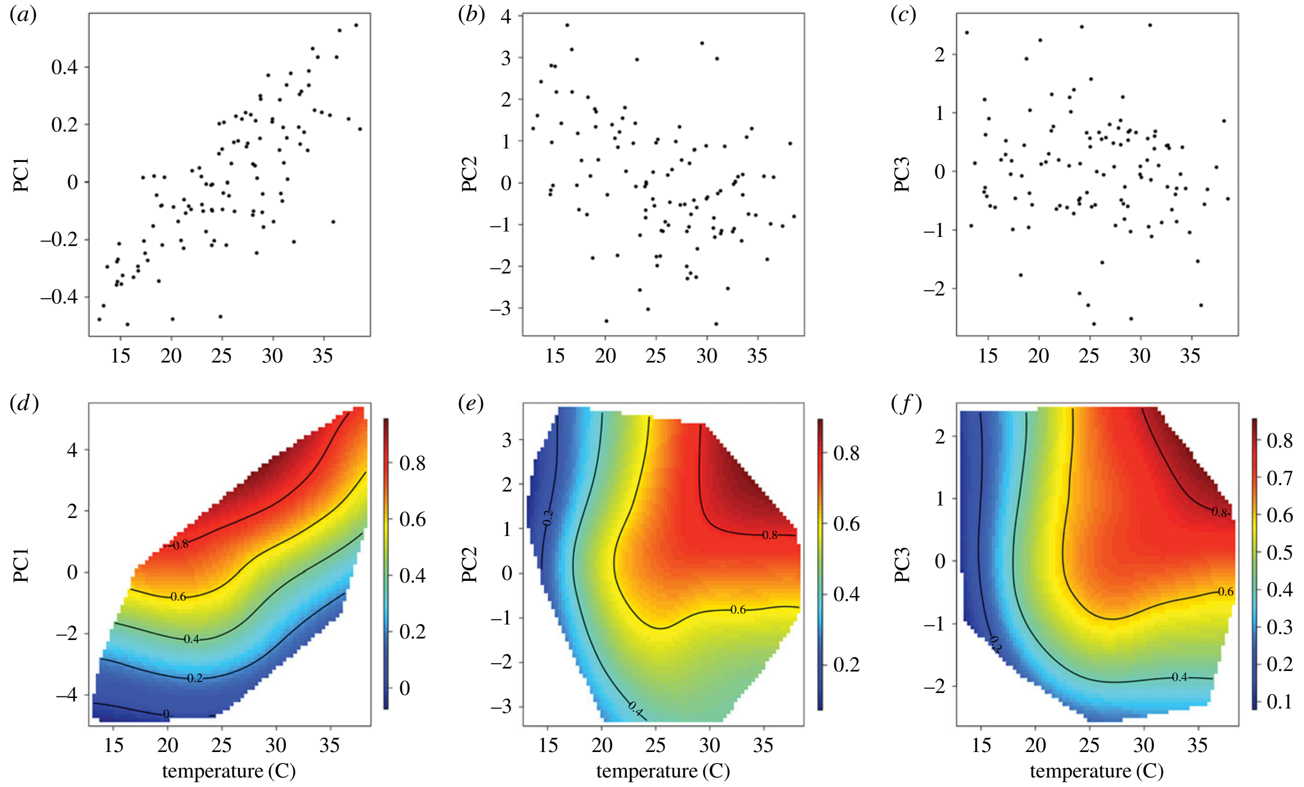

Figure 2. Relationship between temperature and (*a*) PC1, (*b*) PC2 and (*c*) PC3. Thin-plate spline visualizations of the interacting effects of temperature and (*d*) PC1, (*e*) PC2 and (*f*) PC3 on copulation success. The colours represent the probability of copulation, with low to high rates illustrated as blue to red.

increasing, probably as a result of increased pulses per chirp, and chirp bout length decreasing as a result of shorter chirp periods.

PC3 primarily reflects the average duration of chirp bouts (vi), which load positively, indicating longer bouts of chirping at higher values of PC3. This is the only principal component onto which chirp bout duration loads positively. Other traits, such as chirp number (iii) and chirp period (viii), load positively onto PC3, but weakly relative to other principal components.

To test the effect of temperature on these principal components, we ran a MANOVA with the three principal components as dependent variables and temperature as the independent variable. Temperature in this analysis (and all following analyses) was a continuous variable, calculated as the mean temperature recorded during each courtship trial.

(e) Analysis of mating success across temperatures

We were primarily interested in the interaction of temperature and courtship on copulation success. For that reason, we chose to run three separate mixed-effects logistic regressions to test for significant interactions between temperature and courtship. Each analysis contained copulation success as the dependent variable, temperature, one principal component and the interaction of that principal component and temperature as fixed effects, and latency to begin courting as a random effect. Latency to begin courting was included as a random effect in order to control variation in the time females had to assess courtship that resulted from variation in when males began courting. However, most individuals began courting quickly (the median time to initiate courtship was 112 s).

In order to assess the nature of the interaction of two continuous variables (courtship and temperature) on copulation success, we visualized the fitness surface using thin-plate splines (*Fields* R package [41]). Splines were fitted using the value of the smoothing parameter (λ) that minimized the generalized cross-validation score. This visualization allows for the assessment of nonlinear interaction effects of temperature and courtship rate on copulation success. It is comparable to the fitness surface visualizations used in [42] but differs in that it compares one phenotypic and one environmental axis, instead of two phenotypic axes.

Table 2. Results of MANOVA examining the effect of temperature on the three principal components.

full model	$F_{3,114} = 120.93$	$p < 0.0001$
PC1	$F_{1,114} = 166.26$	$p < 0.0001$
PC2	$F_{1,114} = 19.82$	$p < 0.0001$
PC3	$F_{1,114} = 2.44$	$p = 0.121$

3. Results

(a) Courtship form across temperatures

The MANOVA testing the effect of temperature on the three principal components was significant (table 2). PC1 increased with increasing temperature, whereas PC2 decreased with increasing temperature, and PC3 was unaffected by increasing temperature (figure 2*a*–*c*). The individual display traits which load onto these principal components responded similarly (electronic supplementary material, figure S1). Thus, it appears that PC1 reflects those aspects of the display that increase energetically with increasing temperatures. At hotter temperatures, traits that load onto PC1 increase in rate or decrease in period. Traits that load onto PC2, however, appear to decrease in energetic investment at higher temperatures. Chirps at higher temperatures have fewer pulse components and are therefore shorter. Finally, PC3 reflects those aspects of the display that are temperature-independent. The duration of chirp bouts

Table 3. Results of mixed-effects logistic regressions examining the interacting effects of each principal component and temperature on copulation success.

PC1	$z = -2.363$	$p = 0.004$
temperature	$z = 2.317$	$p = 0.065$
PC1 × temperature	$z = 2.542$	$p = 0.027$
PC2	$z = -2.363$	$p = 0.018$
temperature	$z = 2.317$	$p = 0.021$
PC2 × temperature	$z = 2.542$	$p = 0.011$
PC3	$z = -1.719$	$p = 0.086$
temperature	$z = 2.820$	$p = 0.005$
PC3 × temperature	$z = 2.016$	$p = 0.044$

remains constant across temperatures, potentially as a result of the balancing effect of increasing chirp rates and decreasing chirp duration as temperature increases.

(b) Selection on courtship across the thermal range

In all three cases, the nominal logistic regression models testing the effects of the principal components and temperature on copulation success were significant, with copulation success being predicted by an interaction of temperature and each principal component (table 3). The probability of copulating increases with higher values of PC1, but the probability of copulating at a given value of PC1 decreases with rising temperature (figure 2*d*). At higher temperatures, the probability of copulating increases with higher values of PC2, but there is no relationship between PC2 and copulation likelihood at lower temperatures. The same pattern is found with PC3 (figure 2*e,f*).

4. Discussion

Male *S. floridana* produce a complex song with some components that respond dynamically to changes in temperature and others that do not. Considering mating success as a proxy for male fitness, we also find evidence that the relationship between courtship form and fitness shifts continuously across temperatures in several ways. First, the odds of mating at a given value of PC1 decrease as temperature increases. Second, increasing values of PC2 and PC3 predict copulation success at temperatures above roughly 22°C but do not at lower temperatures. If variation in mating success is driven by female mate choice behaviour (which we discuss below), then these fitness surfaces represent shifting selection landscapes. In this context, our results suggest that temperature may drive piecemeal selection on complex displays, as not all display components correlate with mating success across all thermal regimes. Given that the average daily temperatures during the breeding season range from 11°C to 26°C, these shifts in selection potentially occur over the course of a single day.

(a) Temperature and courtship

For most ectotherms, the effect of increasing temperature is an increase in the production rate of courtship (e.g. [26–31]). We find this is true for *S. floridana* courtship as well, with almost all measured display components increasing in production rate or intensity at higher temperatures. However, there are several display components that decrease in intensity at higher temperatures or that do not respond to temperature. Thus, we are among the first to show a complex response to temperature by a multicomponent signal (but see [29]), providing novel evidence that environmental changes exert multifaceted effects on the form of complex signals.

The simplest explanation for most of the observed changes in courtship is that they are driven directly by the effect of temperature on *S. floridana*'s metabolism. It is likely that courtship represents a form of maximal exertion, given that females prefer more energetic displays (e.g. [16,38,40]), and at higher temperatures, higher metabolic rates will enable spiders to court more energetically. Increases in courtship rate could also represent a plastic response by the courter to the changing environment or to changing chooser behaviour. For example, choosers may become more receptive at higher temperatures. If courters signal more vigorously to more receptive choosers, then changes in courtship behaviour could be driven by the effect of temperature on chooser receptivity.

A general increase in courtship rate at higher temperatures might also force tradeoffs in production between components. For example, the negative relationship between temperature and PC2 could be the result of changes in the energetic or temporal tradeoffs of producing one type of display component or another. Males may be sacrificing the number of pulses within a chirp in favour of producing more chirps per minute, or they may be incapable of producing a large number of pulses so closely together when chirps are faster. Such tradeoffs may also be responsible for the 'stabilizing' of PC3 across temperatures, possibly the durations of chirp bouts are stabilized by the balance of increased chirp production and reduced chirp duration and period.

Regardless of the cause, changes to the structure of courtship affect the nature of the information that courtship is able to transmit. For example, traits that increase in production rate as temperatures rise also increase in variance (electronic supplementary material, figure S1). Courtship components with greater between-individual variance may transmit information more effectively, as discrimination is easier when the differences between signallers are greater. If courtship production rate is associated with male quality or attractiveness (which may be the case—as we discuss in the next section), then these changes will affect the ability of choosers to effectively express their preferences. Thus, the temperature may directly affect the ability of choosers to make optimal mating decisions, which may in turn lead to selection for reduced overall receptivity in some environments, or reduced receptivity to those components that become less reliable in certain environments.

(b) Temperature and selection

We document continuous variation in the relationship between male fitness (i.e. mating success) and courtship phenotype across temperatures. This strongly suggests that different aspects of *S. floridana*'s complex song are under selection at different times throughout a single day. Local variation in environmental factors has been shown to lead to fluctuations in the form, strength and direction of both natural and sexual selection (e.g. [7,11,43,44]). But to our knowledge, this is the first study to suggest that these fluctuations may happen over such a short time span (i.e. daily). Our findings also suggest that several display components may be degenerate (i.e. different structures, shared function [45]) at higher temperatures, but not at lower ones. Changing temperatures therefore have the potential to alter the functional relationships between display components.

Shifting female preferences may account for changes in selection. For example, it appears that female *S. floridana* are expressing temperature-coupled preferences (e.g. [28]), for those courtship components that increase in production rate with rising temperatures. The value of PC1 at which pairs have, for example, a 60% chance of copulating increases with rising temperatures at the same rate as the average values of PC1 do (figure 2*a*,*d*). This could represent an adaptive shift in female preferences intended to prevent inappropriate mating decisions as temperatures change. Similarly, females may be altogether forgoing assessment of some aspects of courtship in some thermal regimes. For example, longer chirps (e.g. PC2) may only be meaningful when they are maintained in the face of temporal or energetic tradeoffs with other components. Whereas many spiders have higher values of PC2 at lower temperatures, it is possible that only high-quality courters are able to sustain longer chirp durations at higher temperatures. Alternatively, shifting selection on the display components in PC2 and PC3 may be due to changes in their relationships with other display components. Previous work with *S. floridana* has documented variation in selection strength on some signal traits as a result of changes in their correlation with other traits that were continuously under selection [16].

Classical approaches to the study of complex signals emphasize a reductionist approach that seeks to characterize the discrete interactions between all measured signal components and the discrete nature of chooser preferences for those components [12–15]. Recent work has highlighted the important possibility that these interactions may change across environments (e.g. [16,45]). Here, we find that a complex trait is subject to multiple overlapping nonlinear selection regimes. Rather than considering complex displays as necessarily the result of selection on the display as a whole, we therefore suggest that complex displays may be the result of inconsistent selection and that not all display components function together. Instead, complex displays may evolve in response to a selection process that varies rapidly across environments.

A critical missing piece is understanding how these animals interact with their varying thermal environments. When, and how, *S. floridana* searches for mates and chooses to court will determine the effects of environmental temperature. For example, male *Drosophila montana* courtship is temperature-dependent, but female preferences are not. However, this mismatch may not lead to shifts in the selection, as females restrict mate searching for a brief period of the day [30]. Likewise, behavioural thermoregulation gives individuals the ability to determine their temperature to some degree, and behaviours in some systems suggest that animals may use this to their advantage, treating warm spots as valuable resources to be sought out, and potentially, defended [46,47].

Finally, we consider the association of phenotype with mating success to be a strong proxy for selection given what is known about this study system. However, it is worth mentioning that it may be influenced by other processes. For example, if male courtship rate is purely a response to perceived female mating receptivity, then the relationship between mating success and phenotype might not reflect selection on courtship, since the direction of causation is reversed (i.e. likelihood to mate determines courtship rate, rather than courtship rate determining likelihood to mate). This uncertainty is inherent in the study's design, which includes the free interaction of males and females. However, this design also makes it possible to ask these questions in systems where males require exposure to female stimuli to produce courtship behaviours, and in which females require the presence of live males to express preferences. In sum, we consider the benefits of a combined assessment of male and female behaviours to significantly outweigh the drawbacks.

5. Conclusion

Our results have important implications for mate choice research, particularly for animals that cannot metabolically thermoregulate. We find that selection on complex displays responds nonlinearly to changes in temperature, and we present a useful method for visualizing this nonlinear relationship. Even within a single day, average temperatures during the mating season vary enough to shift courting spiders between two significantly different selective regimes, suggesting that the effect of temperature is fundamental (rather than incidental) to the evolution of these displays. Anthropogenic climate change is likely not only to shift average temperatures [48] but also to increase stochasticity and extreme temperature events [49]. Even small climatic changes may have significant effects by, for example, shifting the proportion of time each day spent in each of the two selection regimes. Our results also serve as a cautionary tale to investigators examining mate choice on complex signals. Understanding how selection on signal form responds to changing environmental dynamics may not be optional. Rather, our ability to measure and understand multivariate selection on traits requires the inclusion of environmental variation in experiments, as environment-dependent selection and plasticity are probably a fundamental component of the evolution of complex signals.

Data accessibility. The primary dataset for this study is available as electronic supplementary material.

Authors' contributions. M.F.R. conceived of the study, carried out the experiments and analysis, and led in the writing of the manuscript. D.O.E. assisted in the experimental design and analysis and co-wrote the manuscript

Competing interests. We declare we have no competing interests.

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