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RESEARCH ARTICLE

The potential for the evolution of thermally sensitive courtship behaviours in the treehopper, *Enchenopa binotata*

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Abstract

The ability of animals to adapt to warming will depend on the evolutionary potential of thermally sensitive traits. The number of studies measuring the quantitative genetics of a wide variety of thermally sensitive traits has steadily increased; however, no study has yet investigated the quantitative genetics of thermal sensitivity for courtship traits. Since courtship often precedes mating, the ability of these traits to respond to warming may impact reproduction and therefore population persistence. Here, we use classic quantitative genetics breeding design to estimate heritability of various aspects of the thermal sensitivity of courtship behaviours in the treehopper *Enchenopa binotata*. We generated individual-level thermal courtship activity curves for males and females and measured levels of genetic variation in the thermal sensitivity of courtship activity. We found low heritability with 95% credible intervals that did not approach zero for most traits. Levels of genetic variation were highest in traits describing thermal tolerance. We also found some evidence for genetic correlations between traits within but not across sexes. Together, our results suggest that the range of temperatures over which these treehoppers actively court can evolve, although it remains unclear whether adaptation can happen quickly enough to match the speed of warming.

KEYWORDS
courtship, quantitative genetics, reproduction, thermal sensitivity, treehoppers, warming

1 | INTRODUCTION

Understanding organismal responses to changing thermal environments has become one of the most pressing questions in modern biology. Although plasticity (changes in phenotype across environments) can buffer the detrimental effects of shifts in local thermal conditions (Catullo et al., 2019; McGaughran et al., 2021; Merila & Hendry, 2014; Sunday et al., 2012), plasticity alone might not be sufficient to deal with long-term thermal trends (Kellermann & van Heerwaarden, 2019; Radchuk et al., 2019). Thus, genetic adaptation may be key for organisms to respond to temperature change (González-Tokman et al., 2020; Hoffmann & Sgro, 2011; Sinervo et al., 2010). A growing body of research has found significant genetic variation—a prerequisite to adaptive genetic responses—in the thermal sensitivity of a range of ecologically relevant traits, including those that affect life history (Garant et al., 2008; Møller, 2001; Pulido et al., 2001; Van Der Jeugd & McCleery, 2002), physiology (Diamond et al., 2017; Doyle et al., 2011; Kelly et al., 2012; Ketola et al., 2012; Leal & Gunderson, 2012; Mattila & Hanski, 2014; Meffe et al., 1995; Munday et al., 2017; Muñoz et al., 2015), and performance (Gilchrist, 1996; Latimer et al., 2011; Logan et al., 2020). However, adaptation to novel climatic regimes ultimately requires adjustments in traits related to reproduction in addition to those related to survival (García-Roa et al., 2020; Moore et al., 2021; Leith et al., 2020; Leith et al., 2022). Little attention has been directed to understanding genetic variation in mating-related traits despite their prevalent sensitivity to temperature (reviewed in Leith et al., 2021).

For many animals—particularly ectotherms—mating occurs within limited thermal windows (Heidinger et al., 2014; Leith et al., 2020; Macchiano et al., 2019). Rising global temperatures and increased thermal fluctuations (Easterling et al., 2000; Rohr & Raffel, 2010, including heat waves: Oliver et al., 2018) can reduce the total time and predictability of when temperatures that are appropriate for coordinating mating occur (Leith et al., 2021; Macchiano et al., 2019; Martín & López, 2013; Olsson et al., 2011). Understanding the genetic architecture underlying the thermal sensitivity of reproductive behaviours is therefore critical for predicting the ability of organisms to respond to changes in environmental temperatures. Patterns of genetic variation in thermally sensitive traits can provide not only important insight into how organisms have adapted to past thermal conditions but also the potential for adaptation to novel thermal conditions. Absent or low genetic variation can indicate recent strong selection and a low potential for a population to adapt to future climate change; high genetic variation may indicate a lack of recent selection with strong potential to adapt to future changes in selection. Additionally, genetic correlations across traits and across sexes can constrain the evolution of different traits and/or the sexes in response to global warming.

Here, we investigate heritability and genetic correlations in various traits describing the thermal sensitivity of courtship behaviour. Courtship is paramount for mating success in many animals and thus can affect population viability (Leith et al., 2021). However, one challenge to investigating how temperature affects courtship is the function-valued nature of the behaviour (Kingsolver et al., 2001); function-value traits are best described using a curve rather than a single value for the trait (Meyer & Kirkpatrick, 2005). Thus, we implement a function-valued approach to quantifying genetic variation in how courtship behaviour changes with temperature (e.g., Meyer & Kirkpatrick, 2005; Stinchcombe et al., 2012). The thermal courtship activity curves we measure depict how the likelihood of engaging in courtship changes with temperature (Macchiano et al., 2019; Leith et al., 2020; Figure 1) and are similar to thermal performance curves that depict, for example, how running speed changes with temperature (e.g., Artacho et al., 2013; Careau et al., 2014). All aspects of thermal courtship activity curves may respond to selection (Stinchcombe et al., 2012): the entire curve itself can vary across genotypes or individuals and be a target of selection, but also specific aspects of these curves (e.g., the upper or lower thermal limits of courtship) could themselves be targets of selection (e.g., Kingsolver et al., 2001; Stinchcombe et al., 2012). For instance, increased mean environmental temperatures may favour shifts to a higher temperature at which reproductive activity is maximal (i.e., increased thermal activity peak), whereas increased variability in environmental temperatures may favour a broader range of temperatures at which courtship occurs (e.g., a wider thermal activity window; Angilletta et al., 2002; Logan et al., 2018; Logan et al., 2020; but see Clusella-Trullas et al., 2011).

Another challenge to understanding how function-valued traits—like thermal courtship activity curves—evolve is the potential for genetic covariance among different aspects of the curves to constrain evolutionary responses (Stinchcombe et al., 2012). It is well-established that thermal performance traits are often phenotypically correlated. In fact, much of the theory of the evolution of thermal performance curves has been built around phenotypic correlations. For instance, the “hotter is better” hypothesis predicts that the thermal optimum should positively correlate with maximal performance, that is, the hotter the temperature at which an organism peaks in performance, the higher the actual performance peak is (Angilletta et al., 2010; Huey & Kingsolver, 1989; Kingsolver & Huey, 2008). The specialist/generalist trade-off hypothesis posits that organisms can either perform well at a small range of temperatures or less well but at a broader range of temperatures (Angilletta et al., 2002; Huey & Hertz, 1984; Huey & Kingsolver, 1989, 1993). However, it remains unclear whether phenotypic correlations result from underlying genetic correlations (Logan et al., 2020). Only a few studies have quantified genetic correlations between thermally sensitive traits in animals, and these studies have found few significant genetic correlations (Logan et al., 2020; Martins et al., 2019). Additionally, cross-sex genetic correlations may also limit the ability of one or both sexes to evolve in response to changing thermal conditions. For example, if males and females differ in optimal temperatures for activity, which is not uncommon in arthropods (e.g., Brandt et al., 2018; Grossi & Canals, 2015; Leith et al., 2020; Macchiano et al., 2019; Stillwell et al., 2010), and this trait is genetically correlated across sexes, then selection cannot maximize performance in both sexes (although the correlation itself can also evolve). Thus, quantifying genetic variation and genetic correlations (cross trait and cross-sex) can provide key insight into evolutionary responses to changing thermal conditions.

We implement classic quantitative genetics breeding design to test for broad-sense heritability in traits that describe

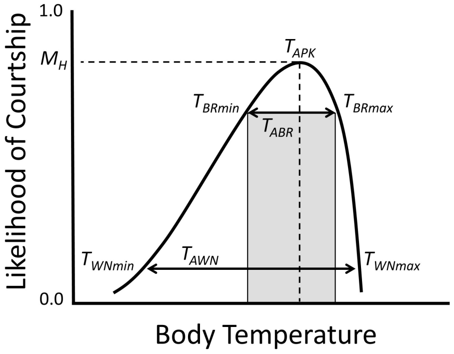

FIGURE 1 A typical thermal activity curve with extracted traits measured in this study. Descriptions of traits can be found in the main text. M_H, maximal activity height; T_{ABR}, thermal activity breadth; T_{APK}, thermal activity peak; T_{AWN}, thermal activity window; T_{BRmin} and T_{BRmax}, thermal breadth min and max; T_{WNmin}, thermal window min. Shaded area represents the range of thermal activity breadth

thermal courtship activity curves, as well as cross-trait and cross-sex correlations, in the treehopper *Enchenopa binotata* (Hemiptera: Membracidae). These small, sap-feeding insects use substrate-borne vibrational communication to initiate mating interactions: males produce advertisement signals that travel through the stems and leaves of their host plant and interested females respond with their own vibrational signal to initiate a duet that precedes pair formation (Cocroft & Rodríguez, 2005; Hunt, 1994). The ease of assaying courtship activity in controlled laboratory settings (e.g., Fowler-Finn et al., 2018; Leith et al., 2020) and the importance of temperature on courtship behaviours (Jocson et al., 2019; Leith et al., 2020; Macchiano et al., 2019) make these treehoppers a tractable system in which to measure the quantitative genetics of the thermal sensitivity of courtship. Furthermore, the sexes differ both in the temperature at which their courtship activity is highest and in the range of temperatures over which they signal (Leith et al., 2020, Macchiano et al., 2019).

Previous work on the heritability of thermally sensitive traits has focused primarily on performance or physiological traits (e.g., Kingsolver et al., 2004; Latimer et al., 2011; Logan et al., 2018; Martins et al., 2019). Here we focus on behaviour, as behaviour mediates how organisms interact with their world. We specifically tested the hypothesis that the thermal sensitivity of behavioural traits (in this case, courtship activity) is heritable. We also tested the hypothesis that heritability of thermal courtship activity curves is sex-specific. This second hypothesis stems from differences between the sexes in the thermal sensitivity of their courtship behaviour (i.e., Jocson et al., 2019; Leith et al., 2020; Macchiano et al., 2019), suggesting that selection may act differently on the two sexes.

2 | METHODS

2.1 | Rearing design

To measure the quantitative genetics of thermal activity traits related to courtship behavior, we implemented a classic full-sibling split-family quantitative genetics rearing design. We collected adult female *E. binotata* from Medford, Massachusetts (42.4248069, −71.1458345) in the late summers of 2016, 2017, and 2018 and brought them to the Saint Louis University greenhouse in St. Louis, Missouri. Each female was individually housed on an exemplar *Ptelea trifoliata* hostplant covered in a mesh netting to prevent the female from escaping. Females remained and laid eggs in the stems of their individual hostplant exemplars until their death. Since females only mate once (Sullivan-Beckers & Cocroft, 2010; Wood, 1993), all offspring from each female are full siblings. We hereafter refer to each sibling group as a "family."

Eggs hatch and offspring emerge in the spring once phloem begins flowing through the plant (Wood et al., 1990), which typically occurs in May. After the offspring moulted to their second instar (of five), we evenly split siblings from each family into two to three replicate host plant exemplars (depending on the number of offspring produced by a female), with up to 30 individuals on a replicate hostplant exemplar (following Fowler-Finn et al., 2018). The offspring remained on these replicate hostplants until they reached adulthood, at which point we transferred males and females to netted sex-specific host plant exemplars. Males do not start signalling until 1–2 weeks post-adult moult, so splitting adults prior to this point allowed us to control for sexual experience (e.g., Fowler-Finn & Rodríguez, 2013). This design resulted in at least two replicate host plants per family per sex.

2.2 | Assessing courtship activity across temperatures

We tested individuals for courtship activity starting at sexual maturity, which begins 2 weeks after the moult to adulthood for males and 6 weeks after the moult to adulthood for females. We tested whether each individual treehopper courted at each of seven ecologically relevant temperatures (18, 21, 24, 27, 30, 33, and 36°C; Jocson et al., 2019). Not all individuals survived long enough to be tested at all seven temperatures (Table S1), so we included individuals that were tested at a majority of temperatures for the analyses (see inclusion criteria below). To assay courtship activity, we took advantage of the duetting system and used vibrational playbacks of sex-specific stimuli, to which individuals can respond or not. Both male and female *E. binotata* readily respond to vibrational playbacks like they would to signals from live animals (Jocson et al., 2019; Rodríguez et al., 2012; Rodríguez & Cocroft, 2006). Responses of live animals to stimuli correspond to reproductive receptivity and mating rates (Leith et al., 2020). We tested each individual at three or four temperatures on each of two consecutive days in order to test each at all seven temperatures. The order of the testing temperature did not significantly affect the likelihood to respond ($p = 0.22$ for males, $p = 0.70$ for females). The temperature in the testing incubator at the time of the trial was generally within +1°C of the target temperature (mean absolute difference between target and actual temperature = 0.5°C ± 0.45 *SD*). We individually marked all treehoppers with non-toxic paint applied to their pronota. Between trials on a given testing day, we placed individuals in a vial with a leaf from which they could feed at room temperature. We placed individuals back on their home host plant in the greenhouse overnight between testing days.

Prior to a trial, we acclimated individuals to the testing temperature by keeping them alone in a vial with a leaf and stem from which they could feed and placing them in an incubator for at least 20–40 min, following protocols established by Jocson et al. (2019). We then transferred the individual onto an exemplar hostplant within a testing incubator and waited 2 min for the individual to settle before starting the trial. Next, we played sex-specific primers (see details below) and recorded whether the treehopper responded with a vibrational signal of their own (following Jocson et al., 2019; Macchiano et al., 2019; Leith et al., 2020). Using sex-specific primers maximizes the likelihood of individuals to signal, which allows for the accurate assessment of the willingness for males and females to court. Male and female courtship responses are easy to discern from other activity as they are highly stereotyped (Rodríguez et al., 2004, Figure S1) and correlate strongly with copulation likelihood in both sexes (Leith et al., 2020). Although most responses occur within a second of the primer being played, responses at any point indicate active courtship, which was the trait we were interested in assaying.

For males, primers consisted of a duet of a male signalling and female responding recorded at 25°C. Previous work has shown that this playback elicits a response from males regardless of testing temperature (Jocson et al., 2019; Leith et al., 2020; Macchiano et al., 2019). We played the duet twice and then repeated the playback every 2 min for 10 min. Males that responded to the duet recording by signalling to any one of the playbacks were marked as actively courting at that temperature. For females, primers consisted of recordings of male signalling. However, individual females differ in their preferred signal frequency (Fowler-Finn & Rodríguez, 2013; Rodríguez et al., 2013) and male signal frequency varies across ambient temperature (Jocson et al., 2019). Thus, in order to assess female receptivity and mitigating inter- and intra-individual variation in preference (following Jocson et al., 2019; Macchiano et al., 2019), we provided each female with three stimuli that covered a range of frequencies. Each stimulus consisted of a bout comprising six signals (corresponding to the population mean number of signals/bout; Rodríguez & Cocroft, 2006) recorded from a male signalling at (1) the testing temperature (due to difficulties in obtaining recordings from males at extreme temperatures, we used male signals recorded at 21°C for testing females at 18°C and a male call recorded at 33°C for testing females at 36°C; following Macchiano et al., 2019), (2) 25°C (approximately the mean temperature at which this species is most likely to signal; Jocson et al., 2019), and (3) either 21°C for testing temperatures below 27°C or 33°C for testing temperatures equal to or above 27°C. So, for example, when testing a female at 27°C, we played primers consisting of a male recorded at 27°C, a male recorded at 25°C, and a male recorded at 33°C. We played all three stimuli in a randomized order, waited 2 min, and then repeated this process until a female responded or each stimulus had been played three times. Females that responded at any time during a trial were marked as actively courting at that temperature. To play the vibrational stimuli from WAV files, we used the programs Audacity v2.1.1 (males) and Matlab 2017 v9.3 (females). The primers passed first from the computer to an amplifier (Tascam US20x20 attached to a Behringer Powerplay) and then through a linear resonant actuator (LRA coin type Z-axis Model G0832012) attached with bee's wax to the plant stem. Playbacks were adjusted to be at a volume of ~0.5 mm/s. We monitored responses of focal individuals using accelerometers (Vibra Metrics Model No. 9002A accelerometer attached to signal conditioner and power supply Model P5000, and PCB Peizotronics MODEL accelerometer attached to signal condition model 480E09) attached to a Behringer U-phoria 404HD audio interface. This audio interface was connected to a computer that recorded the signals from the accelerometer using Audacity v2.1.1.

2.3 | Generating thermal courtship activity curves

The sex-specific vibrational playbacks allowed us to assay the same behaviour for males and females: the willingness to participate in courtship across a range of temperatures. The raw data consisted of courtship activity as a binary response (yes/no) across 7 target temperatures for each individual. From this data, we generated individual-level thermal courtship activity curves using cubic spline regressions in the program PFunc (Kilmer et al., 2017) implemented in R v3.5.1, with a standardized smoothing value of 0.01. Cubic splines describe variation in raw data as functions without making assumptions about the shape of the curve aside from that the curve is smooth (Schluter, 1988). From each of the individual-level courtship activity curves, we measured several traits that correspond to thermal preferences, tolerances, and the shape of the curve (Figure 1; described in Macchiano et al., 2019). Thermal activity peak describes the preferred courtship temperature of the individual. Thermal activity breadth describes the size of the range of temperatures over which the likelihood of activity is ≥90% of the maximum activity level for an individual, whereas thermal activity window describes the size of the range of temperatures over which the likelihood of courtship activity is at least 10%. Thermal preference strength provides a quantitative measure of how quickly courtship activity levels decrease as temperatures deviate from the temperature of peak activity and is calculated as the square of the coefficient of variation in the individual responses to stimuli across the range of temperatures (adapted from Fowler-Finn & Rodríguez, 2013). Maximal activity height measures the highest likelihood of courtship activity and ranged from 0–1.0. We also extracted activity breadth min, activity breadth max, activity window min and activity window max, which are the specific temperatures that bracket the range limits of activity breadth and activity window. We excluded activity window max in our analyses as that temperature often corresponded to the highest temperature at which an individual was tested, and so most variation present was due to random variation in maximum testing temperature rather than underlying biological variation. Finally, we measured mean courtship activity across all temperatures. When assaying female mate preferences, this term is often referred to as responsiveness (i.e., levels of sexual receptivity, Kilmer et al., 2017), but we use the term mean courtship activity here to avoid confusing it with the responsiveness of individuals to changes in temperature. For example, an individual that did not court at any temperature has a mean courtship activity of 0.0, whereas an individual that courted at every temperature has a mean courtship activity of 1.0. This metric significantly correlates with female mating activity (Leith et al., 2020). Thermal breadth, window, height, strength, and mean courtship activity all contribute to the shape of the curve, which can be used to infer the degree to which an individual specializes in the range of temperatures over which they court (i.e., the degree to which an individual is a thermal specialist or generalist).

2.4 | Sample sizes and inclusion criteria

We tested 145 males from 23 families for a total of 718 male tests of courtship activity and 275 females from 25 families for a total 1493 female tests of courtship activity. For all analyses, we included only those families for which at least two replicates had two or more individuals that were tested at five target temperatures (females) or four target temperatures (males). Our inclusion criteria for males were more lenient due to the more limited male sample size resulting from a naturally shorter adult lifespan for males. These criteria resulted in a sample size of 73 males in 10 families and 164 females in 25 families (see Table S1). Three males and three females courted at every temperature, which meant we could not calculate thermal courtship activity peak for these individuals. For these same individuals, activity breadth equals activity window for individuals that courted at every temperature. Thus, we ran two sets of analyses for thermal activity breadth: one that included only individuals that did not respond at every temperature and one that included individuals that responded at every temperature. Thirty females did not respond at any temperature. We included these 30 females only in the analysis of mean courtship activity and repeated the analysis of mean courtship activity without the 30 unresponsive females. We indicate the number of families and individuals included in each analysis as presented in Table 1.

2.5 | Estimating heritabilities and coefficients of variation

We used an animal model approach to estimate broad-sense heritability (H^2) with 95% credible intervals (CIs) and the genetic coefficient of variation ($CV_{genetic}$) for each trait. We derived estimates for males and females separately. H^2 includes additive and non-additive genetic effects and thus provides an upper limit to narrow sense heritability (Roff, 2012). We assigned one mother and one father to each family to create a pedigree that represented the full sib, split brood design within the model. We used the MCMCglmm package in R (de Villemereuil, 2012; Hadfield, 2010; Wilson et al., 2010) to run the models with the animal term and replicate as random effects. Each model was run with 1 000 000 iterations, sampling every 100 iterations, and a burn-in time of 500 000 iterations. The models used evenly weighted priors with low weight given to the priors. Heritability estimates for each model were calculated by dividing the mode of the posterior distribution generated for the animal term by the sum of the modes of the posterior distributions for animal, replicate, and residual terms. For each model, we calculated the $CV_{genetic}$ using the formula: $100 \times \sqrt{(\text{trait variance} / \text{trait mean})}$. We use the term $CV_{genetic}$ rather than CV_A (Houle, 1992) to indicate that our estimate of the genetic coefficient of variation includes maternal effects and non-additive genetic effects (Fowler-Finn et al., 2018). We tested for model convergence using the gelman.diag function in R (Brooks & Gelman, 1998).

TABLE 1 Samples size for heritability and genetic correlation analyses. "Mean activity (signalled)" analysis excluded individuals that did not signal at any temperature

	Males (families, individuals)	Females (families, individuals)
Activity Peak	(10, 70)	(22, 131)
Activity Breadth	(10, 70)	(22, 131)
Activity Breadth all responded	(10, 73)	(22, 134)
Activity Window	(10, 70)	(22, 131)
Strength	(10, 70)	(22, 131)
Mean Activity	(10, 76)	(25, 164)
Mean Activity (signalled)	(10, 7)	(22, 131)
Cross-sex correlations	(10, 70)	(10, 66)

2.6 | Estimating phenotypic and genetic correlations between traits and sexes

Phenotypic and genetic correlations were calculated separately for each sex. We estimated phenotypic correlations and their 95% confidence intervals by running pairwise correlational comparisons between all thermal courtship activity curve traits.

To calculate genetic correlations (r_g) and 95% CIs between each pairwise combination of traits, we used the MCMCglmm package in R (de Villemereuil, 2012; Hadfield, 2010; Wilson et al., 2010). Each model was run with 1 000 000 iterations, sampling every 100 iterations, with a burn-in of 500 000 iterations. We could only calculate genetic correlations between mean courtship activity and other traits using the subset of individuals that called at least once because individuals that never called did not have values for other traits.

We estimated the cross-sex genetic covariance for thermal courtship activity traits by estimating r_{MF} and its 95% CIs using the MCMCglmm package in R (de Villemereuil, 2012; Hadfield, 2010; Wilson et al., 2010).

3 | RESULTS

3.1 | Estimates of heritabilities and coefficients of variation

We found generally low heritability estimates with 95% CIs that did not overlap zero for most thermal courtship activity traits in both males and females (Table 2, Figure 2, Figures S2 and S3). For both sexes, levels of genetic variation were generally higher for traits describing the overall shape of the curve (i.e., activity breadth, activity

TABLE 2 The heritability (with 95% CIs) and genetic variation of thermal sensitivity and thermal tolerances of courtship activity of the treehopper *Enchenopa binotata*

Males	H^2	$CV_{genetic}$	Females	H^2	$CV_{genetic}$
Activity Peak	0.11 (0.04, 0.79)	9.9	Activity Peak	0.09 (0.03, 0.39)	7.1
Peak height	0.14 (0.03, 0.62)	16.2	Peak height	0.06 (0.02, 0.39)	11.4
Activity Breadth (without all called)	0.12 (0.03, 0.66)	32.9	Activity Breadth (without all called)	0.09 (0.02, 0.39)	35.1
Activity Breadth Min Temp	0.17 (0.05, 0.83)	11.4	Activity Breadth Min Temp	0.10 (0.03, 0.40)	8.1
Activity Breadth Max Temp	0.12 (0.03, 0.78)	7.4	Activity Breadth Max Temp	0.07 (0.03, 0.35)	5.5
Activity Breadth (all called)	0.08 (0.03, 0.65)	35.8	Activity Breadth (all called)	0.13 (0.03, 0.49)	40.4
Activity Window	0.10 (0.02, 0.58)	46.2	Activity Window	0.10 (0.02, 0.42)	46.2
Activity Window Min Temp	0.11 (0.03, 0.63)	7.1	Activity Window Min Temp	0.15 (0.03, 0.53)	8.2
Strength	0.09 (0.02, 0.57)	53.3	Strength	0.11 (0.03, 0.44)	55.1
Mean Activity	0.08 (0.02, 0.63)	22.9	Mean Activity	0.28 (0.05, 0.66)	34.2
Mean Activity (signalled)	0.08 (0.03, 0.61)	19.6	Mean Activity (signalled)	0.09 (0.02, 0.37)	18.9

Note: "Mean activity (signalled)" excluded individuals that did not signal at any temperature.

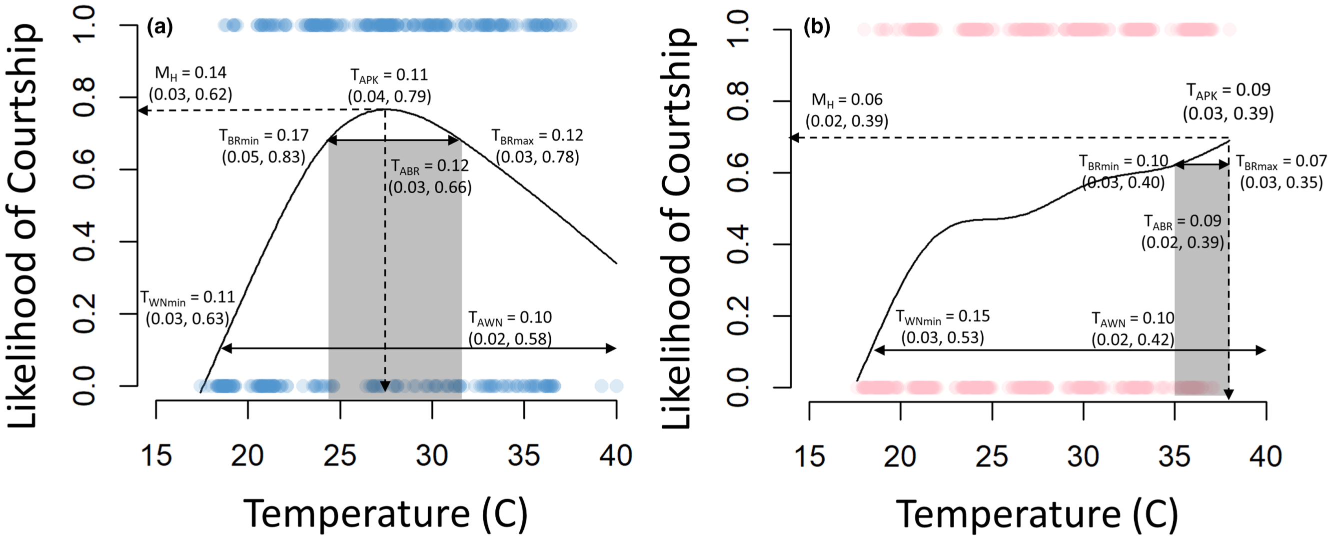

FIGURE 2 Overall activity curves for all males (a) and females (b) used in the analyses with heritabilities and 95% CI for each curve trait. Blue and pink points at 1.0 and 0.0 indicate trials in which individuals did or did not call, respectively. T_{APK}, thermal activity peak. M_H, maximal activity height; T_{ABR}, thermal activity breadth; T_{AWN}, thermal activity window; T_{BRmin} and T_{BRmax}, thermal breadth min and max; T_{WNmin}, thermal window min

window, preference strength, and mean courtship activity) than traits measured by a single temperature (i.e., activity peak, activity breadth min and max, and activity window min, Table 2).

3.2 | Estimates of phenotypic and genetic correlations between thermal activity traits

We found strong phenotypic correlations with 95% confidence intervals that did not overlap zero for many courtship activity traits (Table 3). Patterns of phenotypic correlations were similar for males and females.

We found genetic correlations with 95% CIs that did not overlap zero between a few thermal activity traits (Table 4). Activity peak was significantly positively correlated (95% CIs did not overlap zero) with the activity breadth min in both sexes as well as activity breadth max in females (Table 4). In females, activity window was negatively correlated (95% CIs did not overlap zero) with activity window min (Table 4). Finally, mean courtship activity positively correlated with maximal height in males but not in females (Table 4). All other correlations had 95% CIs that overlapped zero.

We found no significant cross-sex genetic correlations (r_{MF}; Table 5).

4 | CONCLUSIONS

Whether organisms will persist when thermal conditions are rapidly changing may depend in part on the ability to adapt evolutionarily (Hoffmann & Sgro, 2011) and thus the presence of genetic variation in

TABLE 3 Phenotypic correlations between thermal courtship activity traits in *Enchenopa binotata* treehoppers

	Peak	Height	Breadth	Breadth min	Breadth max	Window	Window min	Strength	Mean activity
Males									
Peak	1.00	−0.01 (−0.24, 0.23)	**−0.25 (−0.46, −0.01)**	**0.85 (0.76, 0.90)**	**0.72 (0.59, 0.82)**	0.01 (−0.23, 0.24)	**0.37 (0.15, 0.56)**	0.04 (−0.20, 0.27)	0.07 (−0.23, 0.24)
Height		1.00	**0.61 (0.43, 0.74)**	−0.21 (−0.42, 0.03)	**0.25 (0.01, 0.45)**	**0.41 (0.20, 0.59)**	**−0.35 (−0.54, −0.13)**	**−0.50 (−0.66, −0.30)**	**0.91 (0.86, 0.95)**
Breadth			1.00	**−0.52 (−0.67, −0.32)**	0.13 (−0.11, 0.35)	**0.48 (0.28, 0.64)**	**−0.41 (−0.58, −0.19)**	**−0.46 (−0.63, −0.26)**	**0.59 (0.41, 0.72)**
Breadth Min				1.00	**0.77 (0.65, 0.85)**	−0.18 (−0.40, 0.06)	**0.49 (0.29, 0.65)**	0.23 (−0.01, 0.44)	−0.17 (−0.39, 0.07)
Breadth Max					1.00	0.11 (−0.12, 0.34)	**0.26 (0.02, 0.46)**	−0.05 (−0.28, 0.19)	**0.26 (0.03, 0.47)**
Window						1.00	**−0.75 (−0.84, −0.62)**	**−0.71 (−0.81, −0.57)**	**0.46 (0.25, 0.62)**
Window Min							1.00	0.61 (0.44, 0.74)	**−0.41 (−0.59, −0.19)**
Strength								1.00	**−0.69 (−0.79, −0.54)**
Mean Activity									1.00
Females									
Peak	1.00	**0.19 (0.02, 0.35)**	**−0.32 (−0.46, −0.15)**	**0.94 (0.92, 0.96)**	**0.93 (0.90, 0.95)**	−0.01 (−0.18, 0.17)	**0.29 (0.13, 0.44)**	0.13 (−0.05, 0.29)	−0.04 (−0.21, 0.13)
Height		1.00	**0.20 (0.03, 0.36)**	0.09 (−0.09, 0.26)	**0.25 (0.08, 0.41)**	**0.32 (0.16, 0.46)**	−0.11 (−0.28, 0.06)	**−0.24 (−0.40, −0.07)**	**0.76 (0.68, 0.82)**
Breadth			1.00	**−0.57 (−0.67, −0.44)**	−0.02 (−0.19, 0.16)	**0.43 (0.27, 0.56)**	**−0.41 (−0.54, −0.25)**	**−0.40 (−0.53, −0.24)**	**0.59 (0.47, 0.69)**
Breadth Min				1.00	**0.83 (0.76, 0.88)**	−0.15 (−0.31, 0.03)	**0.41 (0.25, 0.54)**	0.24 (0.07, 0.40)	**−0.22 (−0.37, −0.05)**
Breadth Max					1	0.098 (−0.07, 0.27)	**0.23 (0.06, 0.38)**	0.04 (−0.14, 0.21)	**0.13 (−0.04, 0.30)**
Window						1.00	**−0.85 (−0.89, −0.80)**	**−0.83 (−0.88, −0.77)**	**0.67 (0.56, 0.75)**
Window Min							1.00	0.80 (0.73, 0.86)	**−0.52 (−0.64, −0.39)**
Strength								1.00	**−0.67 (−0.75, −0.56)**
Mean Activity									1.00

Note: Mean activity for correlations used a subset of data that excluded individuals that did not signal at any temperature. Bolded values indicate correlations with 95% CIs that did not overlap zero.

TABLE 4 Genetic correlations between thermal courtship activity traits for male and female *Enchenopa binotata* treehoppers

	Peak	Height	Breadth	Breadth min	Breadth max	Window	Window min	Strength	Mean activity
Males									
Peak	1.00	−0.67 (−0.92, 0.74)	−0.76 (−0.96, 0.62)	**0.96 (0.42, 0.99)**	**0.95 (0.22, 0.99)**	−0.81 (−0.94, 0.71)	0.85 (−0.58, 0.96)	0.72 (−0.81, 0.89)	−0.49 (−0.86, 0.83)
Height		1.00	0.82 (−0.55, 0.95)	−0.72 (−0.94, 0.66)	−0.66 (−0.89, 0.77)	0.41 (−0.71, 0.92)	−0.82 (−0.96, 0.49)	−0.75 (−0.95, 0.61)	**0.89 (0.09, 98.4)**
Breadth			1.00	−0.84 (−0.96, 0.49)	−0.63 (−0.90, 0.77)	0.84 (−0.63, 0.95)	−0.76 (−0.95, 0.60)	−0.44 (−0.91, 0.71)	0.79 (−0.58, 0.95)
Breadth Min				1.00	0.92 (−0.13, 0.98)	−0.78 (−0.94, 0.70)	0.82 (−0.52, 0.97)	−0.49 (−0.77, 0.92)	−0.73 (−0.89, 0.78)
Breadth Max					1.00	−0.66 (−0.88, 0.79)	0.70 (−0.67, 0.96)	0.51 (−0.83, 0.86)	0.29 (−0.79, 0.89)
Window						1.00	−0.83 (−0.98, 0.41)	−0.87 (−0.97, 0.48)	0.52 (−0.71, 0.91)
Window Min							1.00	0.75 (−0.55, 0.96)	−0.81 (−0.96, 0.46)
Strength								1.00	−0.76 (−0.97, 0.46)
Mean Activity									1.00
Females									
Peak	1.00	0.45 (−0.53, 0.89)	−0.52 (−0.91, 0.48)	**0.88 (0.32, 0.98)**	**0.84 (0.19, 0.97)**	−0.39 (−0.87, 0.61)	0.54 (−0.46, 0.92)	0.33 (−0.64, 0.85)	−0.12 (−0.84, −0.68)
Height		1.00	−0.36 (−0.84, 0.64)	0.53 (−0.55, 0.89)	0.67 (−0.52, 0.89)	0.25 (−0.67, −0.83)	0.10 (−0.74, 0.81)	−0.18 (−0.76, 0.75)	0.50 (−0.36, 0.91)
Breadth			1.00	−0.50 (−0.94, 0.36)	−0.36 (−0.86, 0.60)	0.59 (−0.49, 0.93)	−0.61 (−0.91, 0.48)	−0.52 (−0.92, 0.42)	0.62 (−0.45, 0.93)
Breadth Min				1.00	0.80 (−0.09, 0.96)	−0.55 (−0.90, 0.56)	0.69 (−0.44, 0.91)	0.67 (−0.56, 0.90)	−0.36 (−0.85, 0.65)
Breadth Max					1.00	−0.38 (−0.82, 0.69)	0.30 (−0.55, 0.90)	−0.20 (−0.77, 0.76)	−0.09 (−0.78, 0.71)
Window						1.00	**−0.88 (−0.97, −0.09)**	−0.77 (−0.97, 0.04)	0.73 (−0.28, 0.95)
Window Min							1.00	0.75 (−0.03, 0.97)	−0.60 (−0.93, 0.42)
Strength								1.00	−0.68 (−0.94, 0.31)
Mean Activity									1.00

Note: Mean activity for correlations used a subset of data that excluded individuals that did not call at any temperature. Bolded values indicate correlations with 95% confidence intervals that did not overlap zero.

TABLE 5 Cross-sex correlations with 95% CIs for thermal courtship activity traits in *Enchenopa binotata* treehoppers

	r_{MF}
Peak	0.79 (−0.72, 0.91)
Height	0.31 (−0.72, 0.93)
Breadth	0.39 (−0.79, 0.91)
Breadth Low	0.81 (−0.64, 0.95)
Breadth High	0.70 (−0.79, 0.87)
Window	0.69 (−0.62, 0.94)
Window Low	0.66 (−0.66, 0.95)
Strength	0.24 (−0.73, 0.88)
Mean Activity	−0.45 (−0.88, 0.80)

Note: No cross-sex correlation was statistically significant.

thermally sensitive traits. In this study, we measured genetic variation of traits describing how courtship activity varies with temperature and estimated cross-trait and cross-sex genetic correlations for those traits. We found generally low but present broad-sense heritability for most traits, with the highest heritability estimates—and thus greatest potential for evolutionary responses—in traits that account for tolerance to thermal extremes. Although we found that many traits were phenotypically correlated, only a few were genetically correlated and none were genetically correlated across sexes, suggesting low constraints on traits evolving independently of each other.

Previous studies estimating the genetic variance in thermal performance traits have had mixed results. Some studies have found little genetic variation in thermal optima, breadth, or critical thermal limits (e.g., Logan et al., 2018; Martins et al., 2019); others have found at least some of these traits to be heritable (e.g., Logan et al., 2020). Here, we found that estimates of heritability were highest for traits that describe how specialized or generalized the insects were in the temperatures across which they courted. These included the breadth of temperatures across which the insects court (i.e., activity breadth), how selective the insects were to courting at temperatures deviating from their preferred courtship temperature (i.e., strength), and how likely they were to court on average (i.e., mean courtship activity). This pattern suggests that selection may generate the strongest response in how tolerant the insects are to thermal variation rather than the specific temperatures of the highest courtship activity or thermal limits. With increased climate unpredictability (Canale & Henry, 2010; Easterling et al., 2000; Rohr & Raffel, 2010), genotypes with wider tolerances to thermal deviations from the optimum may have an advantage over those with narrower ranges, despite potential energetic costs to maintaining wide thermal ranges (Verberk et al., 2016). The patterns of the heritability estimates for traits that correspond to specific temperatures, like thermal breadth min and thermal breadth max, were consistent with general trends of lower variation and lower plasticity in thermal maxima than minima that have been seen in other taxa (Alford et al., 2012; Brandt et al., 2020; Hoffmann et al., 2013; Sandblom et al., 2016). However, the propensity for insects in our study to signal at the highest testing temperature (see Figure 2) makes it difficult to discern genetic variation for the thermal upper limits (i.e., breadth and window max).

Heritability estimates of the different thermal courtship activity traits were similar in males and females, despite differences in the overall shape of male and female curves, and thus, the sexes likely have a similar potential to respond to selection. However, females had higher heritability for the mean likelihood to court across all temperatures (i.e., mean courtship activity). The lower heritability and lower $CV_{genetic}$ in male mean courtship activity may be because males generally had higher levels of courtship than females (i.e., more males called at all temperatures than females and more females did not call at any temperature than males; this study, Macchiano et al., 2019, Leith et al., 2020). Lower genetic variation in the thermal sensitivity of courtship behaviour in males may be common in systems where females mate more selectively than males and requires further study in other organisms. These sex-specific patterns suggest that males and females may differ in how they deal with changing environmental conditions: although high genetic variation in courtship rates in females may allow for genetic responses to changes in environmental temperatures, overall high mean courtship activity in males may buffer males from negative impacts of fluctuating environmental conditions. Furthermore, the lack of significant cross-sex genetic correlations suggests that males and females should be able to respond to selection independently of one another. Cross-sex correlations tend to be higher for morphological traits than behavioural or physiological traits (Poissant et al., 2010). However, the limited sample size for the cross-sex correlation analyses ($N = 10$ families) may have reduced our ability to detect significant correlations.

We found that several traits were phenotypically correlated, and these correlations provide mixed support for the specialist/generalist hypothesis (Huey & Kingsolver, 1993). Thermal activity peak and thermal activity breadth were negatively correlated in both males and females and strength was negatively correlated with breadth and window in both sexes. These patterns support the prediction that high thermal optimal temperatures require thermal specialization (Gilchrist, 1996; Martin & Huey, 2008). However, maximal activity height was positively correlated with thermal breadth and negatively correlated with strength, which runs counter to the generalist/specialist hypothesis (Huey & Kingsolver, 1993). We also found limited support for the “hotter is better” hypothesis (Huey & Kingsolver, 1989; Latimer et al., 2011; Logan et al., 2020): in females, but not males, thermal activity peak positively correlated with maximal activity height. However, our thermal activity curves differ from traditional thermal performance curves in that they describe behavioural responses rather than physiological potential (e.g., measured by sprint speed, growth, or metabolism). We also measured binomial responses (i.e., courtship or no courtship) rather than a continuous trait and were bound in the upper limit of testing temperatures due to increased mortality above 36°C (Jocson et al., 2019). These factors may limit our ability to distinguish a drop-off when close to the thermal limits and may make correlations more difficult to detect.

Responses to selection may depend on cross-trait genetic correlations. The detection of few significant genetic correlations is consistent with other studies finding a lack of strong genetic correlations between most thermal traits (Logan et al., 2020; Martins et al., 2019) even when phenotypic correlations exist (Martins et al., 2019). However, we found strong, positive genetic correlations between thermal activity peak and thermal activity breadth min and max for both males and females; thus, selection on the temperature at which a genotype is most active should generate a correlated response in activity breadth limits and vice versa. A lack of a genetic correlation between activity peak and overall breadth suggests that changes to activity peak may shift temperature limits. We also found a positive genetic correlation between maximal height and mean courtship activity in males, suggesting that selection on males to call across a range of temperatures will also increase their likelihood to call at their preferred temperature. Finally, the last significant genetic correlation we found was negative correlation between thermal activity window and window min in females, indicating that increases in activity window may be driven by changes in the lower temperature limit. More generally, all traits with significant genetic correlations also showed strong, significant phenotypic correlations. However, the reverse was not true: we found many phenotypic correlations for traits that were not genetically correlated. The presence of many phenotypic correlations and fewer genetic correlations may suggest that trade-offs between traits may arise more from environmental or developmental factors rather than genetic factors.

Many taxa have thermally sensitive courtship traits (Brandt et al., 2018; Conrad et al., 2017; Donelson et al., 2010; Everman et al., 2018; Macchiano et al., 2019; Ritchie et al., 2001; Souroukis et al., 1992), and measuring the potential of this thermal sensitivity to adapt to warming is essential to understand how and whether species will persist in the face of environmental change. The challenges of generating genetic estimates for function-valued behavioural traits can limit sample sizes and interpretability. However, focusing on the genetics of behaviour, rather than underlying physiology, generates data that are most relevant for how organisms interact with their world. Here, we provided the first quantitative genetic estimates of the thermal sensitivity of courtship behavior, as well as cross-trait and cross-sex phenotypic and genetic correlations. The patterns of genetic and phenotypic variation we found suggest the potential for independent evolutionary responses in multiple traits. We also find evidence that males and females can respond independently to selection and that the sexes may differ in their response to selection from global warming. Further work is necessary to determine if levels of standing genetic variation are sufficient for evolutionary adaptation to keep pace with rapid warming. Any work tackling this question should account for sex-specific selection pressures and patterns of genetic variation to fully understand the potential for traits related to mating to allow organisms to adapt to global warming.

AUTHOR CONTRIBUTIONS

KFF conceived and obtained funding for this project. KFF and DS developed the methods. DS, UA, RB, JH, AH, and AO collected data for this study. DS analysed the data, ran the models (with assistance from JK), and made the figures. DS wrote the initial manuscript and KFF provided substantial revisions to the manuscript. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

Data and code used for the analyses are openly available at Open Science Framework (https://osf.io/qd38p/).

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