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Authors

Yan, Lin

Sabaria, Athena

Elias, Damian O

et al.

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Unraveling female mate choice in *Schizocosa mccooki*: The interplay of male mass and vibratory courtship

Lin Yan[1] | Athena Sabaria[1] | Damian O. Elias[1] | Malcolm F. Rosenthal[1,2]

[1]Department of Environmental Sciences, Policy, and Management, University of California, Berkeley, Berkeley, California, USA

[2]Columbia University, New York, New York, USA

Correspondence
Lin Yan, Department of Environmental Sciences, Policy, and Management, University of California, Berkeley, Berkeley, CA, USA.
Email: linyan@berkeley.edu

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Abstract

Sexual selection is an important evolutionary force and despite extensive research, understanding mate choice on naturally occurring trait variation remains an intriguing area of study. The correlation between mass, a trait associated with courter viability and common target for mate choice, and signals is particularly noteworthy. This study focuses on *Schizocosa mccooki*, the largest member of a wolf spider genus renowned for its diverse complex male courtship. Our objective was to understand the relationship of male mass and other courtship signals on female choice within this species. We conducted lab experiments involving random pairings of field caught males and females, recording vibratory courtship and its outcomes. Our findings revealed that *S. mccooki* courtship consisted of vibratory signals with two major components, thumps and raps. Male mass, overall courtship vigor, and thump duration were found to predict mating success. Interestingly, we found no correlation between temporal traits and mass suggesting independent information and an absence of trade-offs between mass, courtship vigor, and signal component rates/durations. Instead, we found that heavier males tend to produce thumps with lower frequencies. The finding that male mass predicts mating success contrasts with patterns observed in other species in this well-studied genus. By uncovering the mate choice patterns of *S. mccooki*, this study underscores the importance of comparative studies to understand the ways in which sexual selection drives diversification, even among closely related taxa.

KEYWORDS
biotremology, mate choice, multiple messages, redundant signals, *Schizocosa*, spectral properties, temporal properties, vibratory signal

1 | INTRODUCTION

Sexual selection is a key evolutionary process that has given rise to enormous biodiversity particularly in the form of signals (Andersson, 1994; Endler, 1992; Janicke et al., 2018). Sexual selection acts on traits (e.g. courter signals and chooser preferences) that increase an individual's fitness in reproductive contexts through intrasexual (competition) and/or intersexual (mate choice) selection (Andersson, 1994; Hunt et al., 2009; Rosenthal, 2017; Wiens & Tuschhoff, 2020). In both scenarios, signals have repeatedly been demonstrated to directly or indirectly convey information on identity, status, quality, etc. to other individuals (Gibson et al., 2010; Hughes, 1996; Sangiamo et al., 2020; Tuni & Berger-Tal, 2012; Zahavi, 1975), although this may not always be the case (Castellano & Cermelli, 2010; Ord & Stamps, 2008; Rodd et al., 2002; Wilkinson & Reillo, 1994). Understanding why choosers prefer some traits and how patterns of mate choice vary across species is important to understanding patterns of biodiversity (Andersson, 1994;

Rosenthal, 2017). A large body of literature has attempted to understand the process of mate choice, and while these works have brought to light many of its mechanisms, patterns, and nuances (Andersson & Simmons, 2006; Jennions & Petrie, 1997; Rosenthal, 2017), many aspects require further investigation. In particular, understanding mate choice on naturally occurring signal variation and signals that consist of multiple components from one or more sensory modalities is of interest.

Previous research has shown that mate choice based on complex signals can be complicated, nuanced, and plastic (Coleman et al., 2004; Secondi et al., 2015; Stange et al., 2017). Hypotheses of complex signal function (Bro-Jørgensen, 2010; Candolin, 2003; Hebets & Papaj, 2005; Mitoyen et al., 2019; Patricelli & Hebets, 2016) include scenarios where different signal components can serve as backups (Hebets & Papaj, 2005), independent forms of information (Doucet & Montgomerie, 2003), and/or amplifiers (Hebets, 2005; Preininger et al., 2013) to one another. Multiple signal components may act synergistically to provide new sources of information to choosers (Koren & Geffen, 2009; Uy & Safran, 2013) or target different receivers (Coleman et al., 2004). Choosers may also simultaneously select on traits such as size and mass that can be assessed directly or through correlated signaling traits (Charlton et al., 2007; de Luca & Morris, 1998).

Besides courtship signals, the role of mass on mate choice has been studied repeatedly and has been shown to be a common target for mate choice due to its direct links to fitness (Rosenthal & Evans, 1998) and constraints on deceit (Kotiaho et al., 1998). Interestingly, there are examples where this is not the case (De Nardo et al., 2021; Kotiaho et al., 1996; Passos et al., 2014). The role of mass in mate choice, its correlations (if any) with signaling, and its relationship with other sexually selected traits continue to be an intriguing question. In some cases, male sexual signals and mass/size are separate targets of female choice and potential interactions and/or trade-offs exist (Kotiaho et al., 1998). In other cases, male size is the direct target of female choice but sexual displays have evolved to exaggerate size (Rosenthal & Evans, 1998).

Spiders are an ideal system for studying mate choice on complex signals. Many spider species use and process visual, vibratory, and chemical cues (Uhl & Elias, 2011). While some web-building spiders generally use chemical and simple vibratory signals during courtship (Gaskett et al., 2004; Wignall & Herberstein, 2013), courtship signals in cursorial spiders can be quite complex (Elias et al., 2012, Elias, Hebets, & Hoy, 2006; Elias, Lee, et al., 2006; Elias & Mason, 2011; Hebets et al., 2013), involving signal parameters such as degree of ornamentation (Hebets & Uetz, 2000; Lietzenmayer et al., 2019; Stratton, 2005; Wilgers & Hebets, 2012) and rate, frequency and duration of vibratory components (Gibson & Uetz, 2008; Girard et al., 2015; Rosenthal & Elias, 2019). *Schizocosa* wolf spiders are a well-established system in the study of sexual selection. Species in the genus exhibit different levels of complexity in courtship, from multicomponent unimodal vibratory courtship to multimodal signals consisting of both visual and vibratory signals (Hebets et al., 2013). The vast majority of research on the *Schizocosa* genus has focused

on the *Ocreata* clade which includes species with relatively complex courtship (Hebets et al., 2013; Starrett et al., 2022). Across the species that have been studied, traits such as overall courtship rate/intensity (Rosenthal et al., 2018; Rosenthal & Elias, 2019; Shamble et al., 2009), complexity (Choi et al., 2022), body condition (Gibson & Uetz, 2012), and static signal properties (e.g. coloration and pigmentation) (Gibson & Uetz, 2008) have been shown to predict mate choice. In these studies, temporal properties of vibratory signals have been shown to be particularly important (Rosenthal et al., 2018; Rosenthal & Elias, 2019; Shamble et al., 2009). Size and mass has also been studied across multiple species, and studies have shown that male mass generally does not predict mating success especially in studies using naturally occurring variation (Choi et al., 2022; McGinley et al., 2023; Persons & Uetz, 2005; Rosenthal & Hebets, 2015).

In this study, we examined mate choice in *Schizocosa mccooki*. *Schizocosa mccooki* is widely distributed from southern Canada to central Mexico and is not closely related to species in the *Ocreata* clade, the focus of nearly all mating behavior and mate choice work in *Schizocosa* (Hebets, 2003; Meyer & Uetz, 2018; Stoffer & Uetz, 2015). Despite its wide distribution, its courtship display seems consistent (Stratton & Lowrie, 1984). *Schizocosa mccooki* generally have simpler visual and vibratory signals than those of the *Ocreata* clade and have the least pigmented forelegs in the *Schizocosa* genus (Starrett et al., 2022). Additionally, *S. mccooki* males vary more widely in size/mass (Starrett et al., 2021), with the largest/heaviest being the western group of *S. mccooki*, the subject of this study. Phylogenetic studies have suggested that geographic isolation is driving the evolution of *S. mccooki* in contrast with the *Ocreata* clade, in which most groups occur in sympatry and thus geographic isolation is thought to not play a major role in courtship trait evolution (Starrett et al., 2021). This underlines the importance of studying *S. mccooki* to more broadly understand signal evolution across the *Schizocosa* genus. Here we aimed to (1) describe signaling behavior of male *S. mccooki*, (2) test for correlations between mass and vibratory signaling parameters, and (3) examine female mate choice patterns particularly how mass and/or vibratory signaling predict mating patterns. We hypothesize that females prefer to mate with heavier males that court more and that courtship signals (temporal and spectral properties) are correlated with male mass (Hebets & Uetz, 1999; Kotiaho et al., 1996).

2 | METHOD

2.1 | Study organism

Penultimate female and male *S. mccooki* were collected at the Angelo Coast Range Reserve, CA in early June 2018 (39.706510, −123.645493). Spiders were brought back to UC Berkeley and individually housed in clear plastic containers (6 cm × 6 cm × 8 cm). The containers were wrapped in brown paper to isolate each container. Spiders were fed twice weekly with one body-size matched cricket,

and water was provided ad libitum through a 1.5-mL centrifuge tube. Spiders were checked three times a week for maturity, and the date of maturation was recorded.

2.2 | Courtship description

In order to describe courtship behavior in *S. mccooki*, we used detailed observations on three courting males as the basis of our courtship descriptions. Male display behaviors were highly similar to male courtship with live females (see below). Recording arenas consisted of thin nylon fabric stretched over a circular embroidery hoop (27 cm in diameter). The arena was positioned at the center of a circular ~35 cm diameter rotating platform on wooden dowels (~7.5 cm in height). Nylon fabrics pass relevant frequencies contained in vibratory displays with little distortion and minimal background noise (Elias & Mason, 2014). We videotaped courtship behavior (JAI CV-S3200 CCD camera; Sony Lumix) and recorded vibratory songs using a Laser Doppler Vibrometer (PDV-100). Males were induced to court by arenas via the presence of female silk by placing females in the arena for 30 min and then removed, prior to placing the males in the arena (Kaston, 1936; Roberts & Uetz, 2005; Rovner, 1968).

2.3 | Courtship measurements

We conducted 63 courtship trials. All trials were conducted during the summer of 2018, in 25°C ambient temperature and full spectrum light. Mature male and female *S. mccooki* that were 10–18 days past

maturation were paired randomly and weighed before trials (OHAUS analytical plus RS232). All male and female individuals were used once except for one male who was used twice. The experimental arena, which has a diameter of 16 cm, was constructed from filter paper. The filter paper was replaced after each trial. Each female was allowed in the experimental arena for a minimum of 1 h for acclimation and silk deposition. Next, a random male was dropped into the arena and all vibratory signals were recorded using a laser Doppler vibrometer (Polytec-PDV100). Pairs were allowed to interact freely for 25 min, and the outcome (copulation/no copulation) was recorded. Vibratory signals were recorded for the 25 min period, and all thumps and raps were identified for each individual and measured using Audacity (ver. 2.2.2). Variables measured were duration and number of thumps and raps, as well as the number of pulses within each rap (see below; Figure 1). For each individual trial, all signals were identified and temporal properties averaged across each trial for use in subsequent data analyses. Recordings of vibratory signals were measured twice by two independent scorers (L.Y. and A.S.). Four trials were excluded as outliers from the analysis (2.5–5 SDs), yielding a total sample size of 59 trials for analyses. To assess the reliability of measurements from the two observers, an intraclass correlation analysis was conducted using the R package *irr* (Gamer et al., 2012; Shrout & Fleiss, 1979). The intraclass correlation coefficients for the five variables measured ranged from .73 to .94, indicating high agreement between the measurements from the two scorers for all variables (Koo & Li, 2016). The mean of measurements from two scorers was used in subsequent analyses. To quantify spectral properties of thumps and raps, we randomly selected 20 raps and 20 thumps from each trial, ending up with 1231 raps from 56 recordings and 918 thumps from 54 recordings (Araya-Salas, 2017).
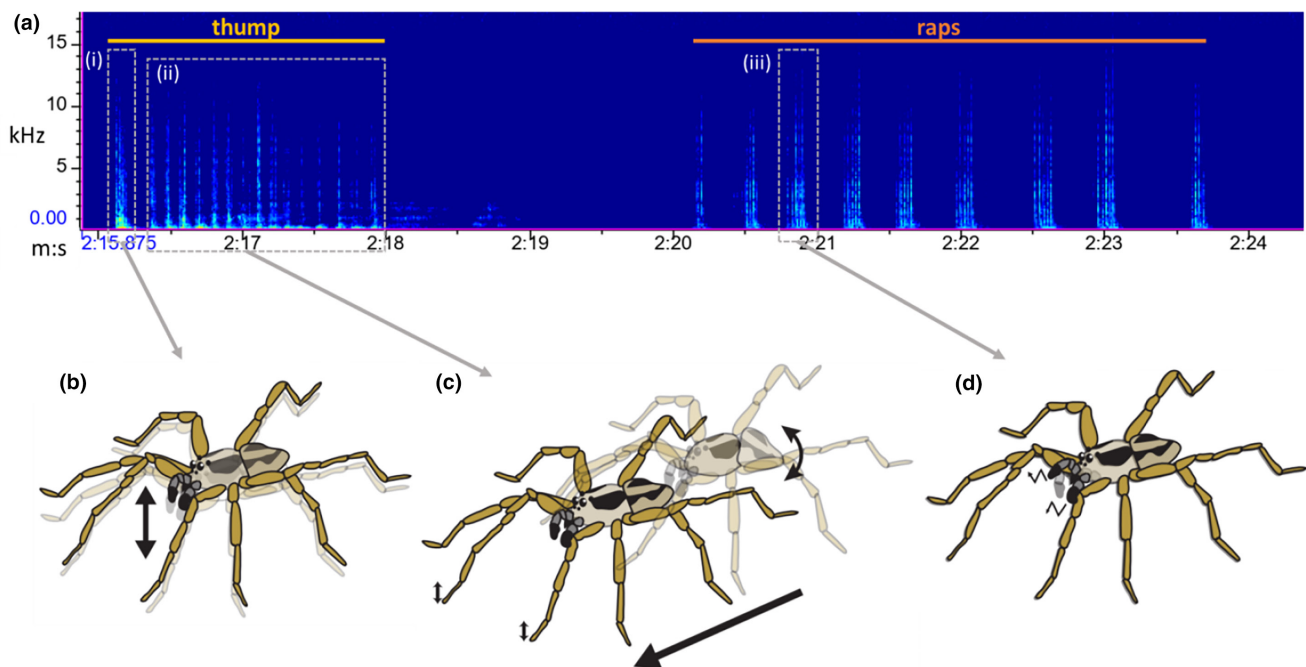

FIGURE 1 Male *Schizocosa mccooki* vibratory display. (a) Spectrogram of a typical song, consisting of a thump (i + ii) followed by a group of raps (iii). (b–d) Illustrations of male movements while producing each signal, respectively.

25 spectral measurements for each sound component were then acquired using the specan() function in warbleR. Each spectral measurement of each signal was averaged across each individual recording. The abbreviations are shown in the figures but one can find the full list of measurements at https://www.rdocumentation.org/packages/warbleR/versions/1.1.25/topics/specan.

2.4 | Statistical analysis

To determine whether temporal properties of vibratory elements covary, or whether they covary with male mass, we conducted a pairwise Pearson's correlation test of the five vibratory signal measurements as well as male mass. Bonferroni corrections were applied to all correlation tests here and after to account for multiple comparisons (Armstrong, 2014). Due to the high correlation between most signal measurements, we used a principal component analysis to understand the relationship between variables and calculate new variables for use in subsequent analyses. For spectral properties, we conducted a pairwise Pearson's correlation test of male mass and measurements of thumps and raps to explore correlations between mass and spectral properties.

To test what predicts female mate choice, a generalized linear model (GLM) with logistic regression was used. The first four PCs (94% of overall variance) and female mass were used as candidate predictors. We chose PCs 1–4 because they represented most of the total variance, and copulation was used as a binary dependent variable. All models were compared with a null model, and stepwise model selection was performed based on the lowest AIC. Starting from a saturated model, if each exclusion of a candidate variable led to a decrease of >2 in AIC, the exclusion was performed, otherwise rejected. Variables included in the final model were tested for their partition of variance using the likelihood ratio chi-square.

3 | RESULTS

3.1 | Description of male courtship

Male vibratory courtship consisted of two major components: a multicomponent "thump" sometimes followed by a "rap" (Figure 1a). The thump is produced when a male suddenly "jumps" (quick upward movement producing an initial high amplitude percussive pulse, Figure 1b) followed by a broad band rumble associated with abdominal movements and foreleg taps as the male moves forward (Figure 1c). The initial impulse is produced by the sudden up and down movement of the body, while subsequent sounds are produced by a combination of limb movements including the abdomen and forelegs (Figure 1d). Thumps have a mean duration of 2.05 s (SD=0.98, N=59). Raps are produced by the drumming of the palps against the substrate. A single percussive pulse is produced by every impact of the palp against the surface, and a rap consists of many of these pulses produced consecutively with alternating palps. Raps

are made up of a mean of seven pulses (SD=2.95, N=59) with a mean total duration of 2.74 s (SD=1.20, N=59). Raps occur while the male is stationary.

3.2 | Courtship and male mass

Most temporal measurements of *S. mccooki* vibratory courtship are highly correlated with each other (Figure 2). Average duration of each rap is positively correlated with the number of pulses within each rap (r=.97); more pulses within each rap make the rap longer. The number of raps is also significantly positively correlated with the number of thumps and the average duration of each thump. However, male mass is not significantly correlated with any temporal attributes of courtship measured (Figure 2). On the other hand, median/mean frequency of thumps and raps correlate with male mass (r=.42 and .4, respectively), with heavier males producing lower frequency signals (Table 1).

3.3 | Mate choice

For our analyses on temporal properties (i.e. #thumps, mean thump duration, #raps, mean rap duration, mean #pulses in each rap), the first four principal components accounted for 94% of the total variation in our data set (Figure 3); hence, all further analyses were conducted on the first four PCs. Some PCs are easier to interpret
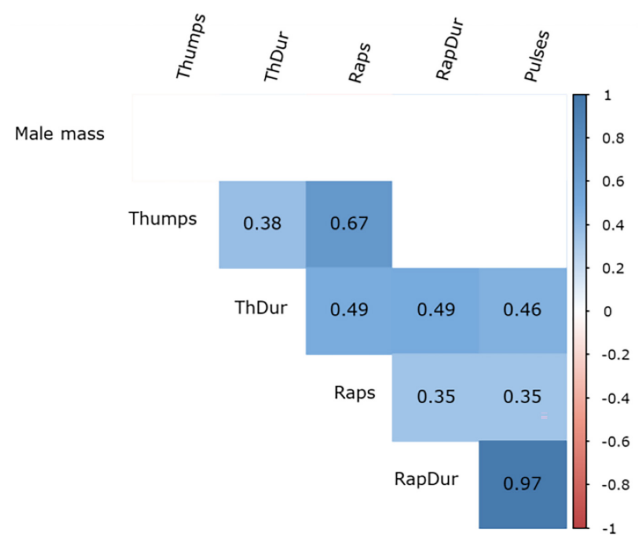

FIGURE 2 Pearson coefficients of correlation with Bonferroni correction for the vibratory signal components and male mass. The number in each grid indicates the coefficient of correlation and colored grids indicate significant correlations after correction (*p* < .05), with blue for positive and red for a negative correlation. The darker the color, the more correlated the two variables are, as indicated by the legend on the right. Thumps: number of thumps; ThDur: average duration of thumps in a given recording; Raps: number of raps; and RapDur: average duration of raps in a given recording.

TABLE 1 Correlation of 25 spectral properties of thumps and raps with male mass.

Measurements	meanfreq	sd	sp. ent	time. ent	freq. median	freq. IQR	modindx	enddom	dfslope	startdom	dfrange	meandom	mindom	maxdom	KURT	sfm	entropy	meanpeakf	skew	time. Q75	time. IQR	time. Q25	freq. Q25	freq. Q75	time. median
Thumps Corr					-.42																				
p-value	.250	1.000	.100	1.000	**.050**	.150	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.125	1.000	.650	1.000	1.000	1.000	1.000	1.000	1.000	.100	1.000
Raps Corr	-.4																								
p-value	**.050**	1.000	.125	.575	1.000	.400	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.225	1.000	.925	1.000	1.000	1.000	1.000	1.000	1.000	.275	1.000

Note: Red indicates negative correlation coefficient. Blank indicates a non-significant correlation ($p > .05$) between the variable and male mass. Bolded p values indicate significant p value ($p \le .05$) after Bonferroni correction.
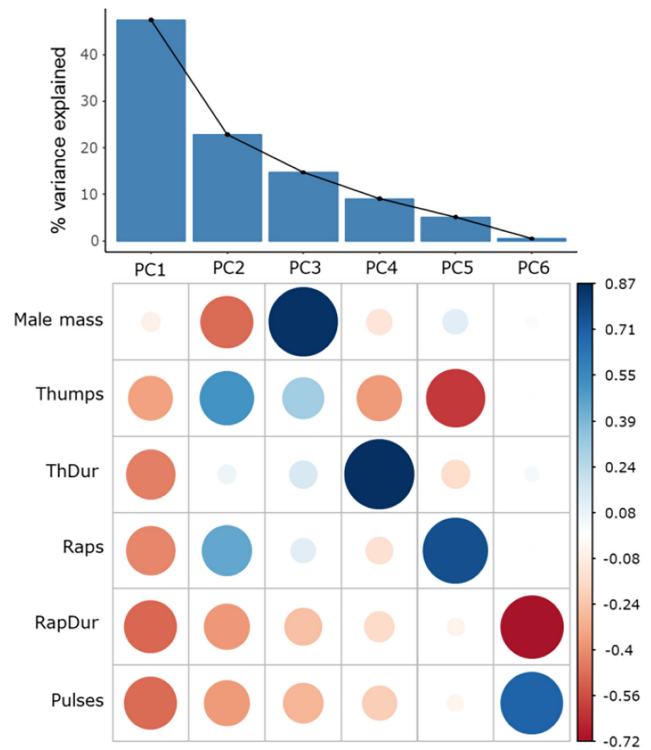

FIGURE 3 Loading of each variable on the principal components. The upper graph shows the percentage of total variance explained by each PC, and the lower graph shows the partition of variables on each PC. The size and transparency of the circle in each grid indicate the amount of partition, with red indicating negative and blue indicating positive partition. PCs1-4 are included in future analyses due to their high representation of total variance.

than others. PC1 is evenly partitioned by all courtship measures and could be considered as a general measure of courtship vigor. Since all components are negatively partitioned on PC1, more and longer thumps and raps lead to a smaller PC1. PC2 is a balanced partition of all measurements other than thump duration, with the number of thumps and raps positively loaded and the rest negatively loaded. PC3 is dominated by male mass. PC4 consists mainly of thump duration.

For mate choice, the best model included courtship vigor (PC1: $\chi^2 = 3.70$, df $= 1$, $p = .054$), male mass (PC3: $\chi^2 = 7.54$, df $= 1$, $p = .006$), and thump duration (PC4: $\chi^2 = 5.85$, df $= 1$, $p = .002$; Figure 4). Males courting with higher vigor (Figure 4a), larger mass (Figure 4b) and shorter thumps (Figure 4c) were more likely to mate.

4 | DISCUSSION

Schizocosa mccooki courtship displays are multicomponent consisting of two correlated percussive components (raps and thumps) (Figure 1). In addition to the vibratory properties discussed, both elements are inextricably connected to visual movements (putative visual displays) although they are generally subtle compared to leg
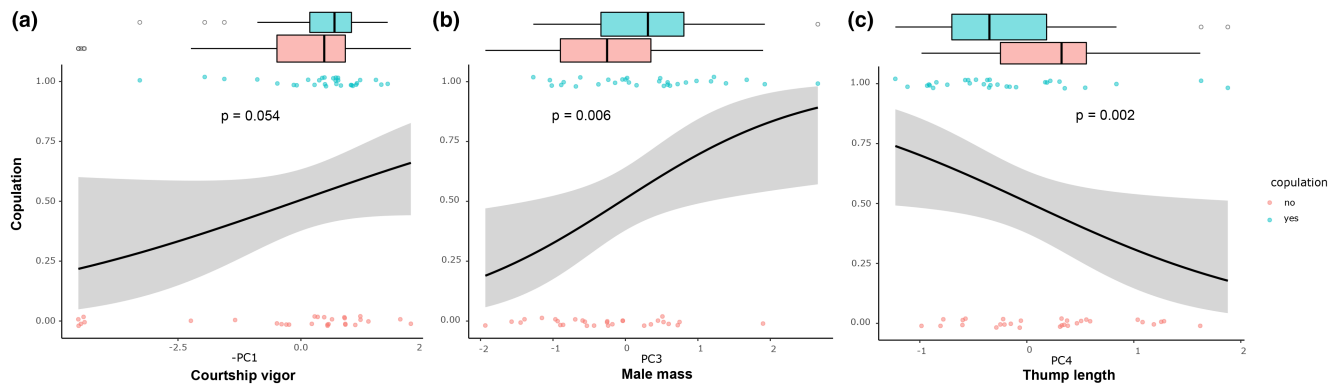
FIGURE 4 Principal components that contribute in predicting copulation. Logistic regression of each PC in the final model is shown. Blue points and boxplot show pairs that copulated, while red ones show the data of pairs that did not copulate. Logistic regression line is shown to indicate whether and how each PC predicts copulation, and the gray area shows the 95% confidence interval. Note that in subplot a, the *x*-axis is minus PC1 for simplification, since PC1 represents negative courtship vigor as shown in Figure 3.

arch displays typically found in species in the *Ocreata* clade (Hebets et al., 2013). Our data show that thump duration, overall courtship vigor, and mass were the variables that most strongly predicted male mating success.

Thumps and particularly thump duration (PC4) appear to be particularly important for courtship (Figure 4). Interestingly, the variable with significant rap loadings tended to not predict mating success (i.e. PC2). Generally, males that courted with more vigor and had shorter thumps and larger mass were more likely to mate with females. In contrast to our initial hypothesis, male mass and temporal properties of vibrations (including thumps) were not correlated and instead our data suggest that temporal aspects of vibratory songs and mass are independent traits (Figure 1). Male mass does correlate with some spectral properties of male signals; specifically, heavier males produce thumps and raps with lower frequency. Preliminary analyses (N thumps = 54, N raps = 56) suggest that spectral properties, specifically thump and rap frequency, predicted mating success (data not shown). Overall, our results suggest that temporal and spectral properties are important for mate choice and that temporal and spectral properties reveal independent information about males.

Females have been shown to have preferences for larger males in many species since larger body size is associated with many direct and indirect benefits for females including increased survival, predation success, predator defense, and longevity (reviewed in Hone & Benton, 2005). Our study demonstrates that mass (and indirectly size due to its strong correlation with mass; McGinley et al., 2023; Persons & Uetz, 2005) is an important trait predicting mating success in *S. mccooki* implying that females receive indirect benefits from selecting larger males (there is no paternal care in this species thus there are likely no direct benefits). Alternatively, signals that are produced by larger males are at a frequency that is more detectable. Previous work has shown that many natural substrates, including the ones used by *S. mccooki*, transmit lower frequencies with less attenuation than higher frequencies (Choi et al., 2019; Elias et al., 2004; Hebets, Elias, et al., 2008). For these experiments however, the courting substrate was chosen because it transmits vibrations with

minimal distortion. It is possible that in natural substrates, signal frequency may have larger effects on mate choice because lower frequencies generally propagate with less attenuation. Regardless of the mechanism of the preference, the pattern that larger (or heavier) males are preferred is not observed in most of the *Schizocosa* species studied (Choi et al., 2022; Delaney et al., 2007; Rosenthal, 2015). There are some exceptions; however, *S. ocreata* show size assortative mating suggesting that larger females mate with larger males and smaller females mate with smaller males (Hebets et al., 2008; McGinley et al., 2023). Additionally, in mating trials where diets were manipulated to create high (larger and heavier) and low (smaller and lighter) quality individuals (Uetz et al., 2002), female *S. stridulans* (Rosenthal & Hebets, 2015) and *S. floridana* (Rosenthal & Hebets, 2012) diet was found to alter traits that are potential targets of sexual selection. Mass however did not predict female mate choice in the above examples (Rosenthal & Hebets, 2012, 2015; Uetz et al., 2002). In other cases, diet manipulation did lead to differences in male body indexes, but had no effects in courtship traits or mating success (Rundus et al., 2010; Shamble et al., 2009). For *S. stridulans*, mating trials on field caught individuals with natural variation as opposed to manipulated diet did not show any evidence for females preferring to mate with heavier males (Choi et al., 2022). This contrast between species in the *Ocreata* clade and *S. mccooki*, in which females preferred heavier males (within naturally occurring variation), is intriguing. *Schizocosa mccooki* populations, particularly western populations, are known for being larger/heavier relative to other *Schizocosa* species from the *Ocreata* clade. Additionally, the variance in size/mass in natural populations is high relative to other *Schizocosa* species (Starrett et al., 2021). It is possible that *S. mccooki* females can more reliably assess size/mass differences between individuals whether it be directly or through proxies related to spectral properties of vibratory signals.

Our data suggest that information about male mass is not conveyed to the female through temporal properties of vibratory courtship displays, in contrast to the many studies showing strong relationships between mass and rates/duration of acoustic (airborne or substrate-borne) traits in diverse taxa including katydids

(de Luca & Morris, 1998), crickets, cicadas, frogs, finches, manakins (de Luca & Morris, 1998; Gillooly & Ophir, 2010; James et al., 2021), and spiders (Kotiaho et al., 1998; Watson & Lighton, 1994). There are several potential reasons for this surprising result.

First, the assumed relationships between courtship intensity and mass may not hold for *S. mccooki*. Links between courtship rates and mass are often assumed to rely on energetic reserves and/or metabolism (Gillooly & Ophir, 2010). It is possible that the tie between energy/metabolism and vibratory courtship displays in *S. mccooki* is different than expected (Barske et al., 2011; Clark, 2012; Prestwich, 2015; Reinhold et al., 1998) and/or the costs of signaling may not be as high as generally assumed (Chiara et al., 2022; Collier et al., 2022). Relationships between energy/metabolism and sound have primarily been investigated in airborne signalers (Francis & Wilkins, 2021; Gillooly & Ophir, 2010), while research on substrate-borne signalers has severely lagged (Kuhelj & Virant-Doberlet, 2022). In fact, substrate-borne signalers have been specifically excluded from meta-analyses exploring the links between energetics, mass, and signaling (Gillooly & Ophir, 2010). Complicating this is the observation that spiders use several mechanisms to produce their signals (Elias & Mason, 2011; Rosenthal et al., 2021) in contrast to vertebrates that primarily signal using vocalizations produced by either a syrinx (birds) or larynx (Ladich & Winkler, 2017). Signals produced by different mechanisms (e.g. percussion, stridulation, and tremulation) vary in the energetic/metabolic costs of production (Elias et al., 2006). Second, males may not signal with maximal effort because the benefits of high signaling activity may be low due to a high level of mating opportunity. This would be expected in situations where there is a high density of females (like in this system) or where females mate multiply (unknown in *S. mccooki*). In this scenario, males may conserve their energy in any one interaction and instead maximize their energy across the reproductive season. Future work is necessary to explore the links between energy/metabolism and mass/size in substrate borne signals.

While our data suggest that thumps are particularly important, there is a significant correlation between the temporal and spectral properties of the two major vibratory signals, thumps, and raps. This suggests that thumps and raps do not convey independent messages and instead that thumps and raps are redundant and can act as backups for each other. While PC data are difficult to interpret, we suggest that our analyses show that the thump temporal properties is more salient for females (thus loading on multiple PC scores that predict mate choice) but that raps could provide redundant information in case of assessment errors. Alternatively, raps may provide unreliable information to senders but due to the marginal costs of choice, may persist as a multicomponent signal due to the benefits courters may receive (Candolin, 2003; Moller & Pomiankowski, 1993; Smith & Evans, 2013).

Although a major predictor for mating success, male mass was found to be independent from temporal properties of thumps and raps, but was found to correlate with spectral properties of thumps and raps. Spectral properties of thumps and raps potentially represent redundant information on mass. Taken together, this implies that temporal and spectral properties of signals have independent information about the male but that the thump and rap signal themselves have redundant information. In summary, different components of the vibratory courtship of *S. mccooki* might have evolved under different selective forces but ultimately, the multiple components in vibratory displays may act as redundancies to each other. Future experiments that manipulate each signal component will be necessary to understand signal interactions and how they influence mate choice.

In our study, we chose to explore mate choice patterns on naturally occurring variation in one Western population of *S. mccooki*. In contrast to the predominant patterns found in the well-studied *Schizocosa ocreata* clade, we found clear evidence for male mass predicting female mate choice independently from temporal aspects of vibratory signals, while correlating with some spectral properties. We observed that vibratory signals are multicomponent with signals acting as redundant backups but with different properties of the signals (spectral and temporal), putatively encoding independent information. The wide distribution of *S. mccooki* (from the US west coast to the central great lakes region) and the associated variation in climate, prey types, vegetation, and courting substrate types pose challenges for effective communication and signal evolution, and we suggest that signals evolved in response to this variation. This is in contrast to the *Ocreata* clade where most species are narrowly distributed and found in a relatively narrower set of habitats with specialized habitat specific multimodal signaling strategies (Elias et al., 2010; Hebets, Elias, et al., 2008; Rosenthal et al., 2019; Starrett et al., 2022). Additionally, while few studies have included spectral properties of male signal in mate choice context (but see Choi et al., 2024 and Rosenthal et al., 2021), our study suggests an exciting but less-explored avenue of research of comparing temporal and spectral properties across the *Schizocosa* genus. Our results highlight the importance of examining comparative mate choice studies as well as the importance of examining naturally occurring variation to elucidate the complexities inherent with mate choice on complex signals.

AUTHOR CONTRIBUTIONS

Lin Yan: Investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation. **Athena Sabaria:** Investigation; writing – review and editing. **Damian O. Elias:** Funding acquisition; conceptualization; writing – original draft; validation; visualization; methodology; writing – review and editing; project administration; supervision; resources. **Malcolm F. Rosenthal:** Resources; supervision; writing – review and editing; visualization; validation; methodology; conceptualization; investigation; writing – original draft.

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Coast Yuki of the Round Valley Indian Tribes. Experiments and data analysis took place on the UC Berkeley campus, the unceded lands of the Chochenyo speaking Ohlone people.

CONFLICT OF INTEREST STATEMENT

The authors do not declare any conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data are available at: https://github.com/linnyan/Schizocosa-mccooki-mate-choice.

ORCID

Lin Yan https://orcid.org/0000-0001-7355-8994

Malcolm F. Rosenthal https://orcid.org/0000-0003-1291-1728

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