2021. Journal of Arachnology 48:221–232

Complex courtship in the *Habronattus clypeatus* group (Araneae: Salticidae)

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Abstract. It is not uncommon to find courtship displays that incorporate numerous components across different sensory modalities. We studied displays in male jumping spiders of the genus *Habronattus* F.O. Pickard-Cambridge, 1901, which court females using a combination of ornament and motion (dance) displays coordinated with vibrational songs. To explore the diversity in *Habronattus* courtship complexity, we focused on quantifying the dance and vibratory displays in nine members of the *Habronattus clypeatus* species group, with preliminary observations on two additional species from this group. Additionally, we looked at display variation across populations in two widespread species from this group. We document three main courtship types: "stilting", "buzzing", and "spinning", each identifiable by the presence or emphasis on particular display types. We found that for the widespread species *H. clypeatus* (Banks, 1895), different populations differed significantly and could be classified as either stilting or buzzing types. We discuss these results in relation to broader patterns of signal evolution and diversification in *Habronattus*.

Keywords: substrate-borne vibration, jumping spiders, vibratory courtship, multimodal signals, biotremology.

https://doi.org/10.1636/JoA-S-18-045

Courtship complexity abounds throughout the animal kingdom, with stunning variation in displays across taxa (Partan & Marler 1999, 2005; Higham & Hebets 2013). While many examples exist in vertebrates, there is an equally astounding diversity of displays in other taxa, particularly in animals that use signals that humans cannot perceive without specialized equipment. The butterfly *Heliconius cydna*, for example, has been shown to use polarized visual signals in mate recognition, while female *Bicyclus anynana* butterflies choose mates based on the brightness of their UV-reflective color patches (Sweeney et al. 2003; Robertson & Monteiro 2005). Male tettigoniid katydids attract females by rubbing their wings together to produce ultrasonic songs (Montealegre-Z et al. 2006; Sarria et al. 2014). Many species of plant hoppers use substrate-borne vibrations in male and female duets which are exchanged during courtship (Cocroft & Rodriguez 2005). This hidden diversity has led to the realization that many animal groups are more complex and varied than once believed (Jones 1997; Henry et al. 1999; Sullivan et al. 2002; Bickford et al. 2007).

Spiders have emerged as key examples of the importance of these hidden signaling characters (chemicals, substrate-borne vibrations, UV coloration; Uhl & Elias 2011). For example, work on wolf spiders has provided classic examples of multimodal signaling (visual and vibratory; reviewed in Uetz et al. 2009; Uhl & Elias 2011; Hebets et al. 2013) even though it is only in the past few decades that acoustic signals have been recognized as a component in spider courtship behavior (Rovner 1967). Similarly, it has recently become evident that in jumping spiders, mating interactions often involve the aforementioned traits imperceptible to humans. For example, *Cosmophasis umbratica* Simon, 1903 and *Phintella vittata* (C.L. Koch, 1846) use UV ornaments in mating interactions (Li et al. 2008; Lim et al. 2008; Painting et al. 2016). Jumping spiders have also been shown to use substrate-borne signals extensively (Jackson 1980; Gwynne & Dadour 1985; Maddison & Stratton 1988a; Sivalinghem et al. 2010; Girard et al. 2011, 2015; Elias et al. 2012) and in many instances, substrate-borne signals clearly predict mating or competitive success (Elias et al. 2004, 2005, 2006a, 2008, 2010; Sivalinghem et al. 2010). These examples demonstrate how crucial it is to understand the totality of courtship signals, including features not necessarily obvious to humans (e.g., UV, substrate-borne vibrations, and chemicals).

Habronattus F.O. Pickard-Cambridge, 1901, is a genus of approximately 100 described species (Griswold 1987; Leduc-Robert & Maddison 2018), most from North America, whose courtship ornaments and behaviors are diverse and complex (Peckham & Peckham 1889, 1890; Maddison & Stratton 1988b; Richman & Cutler 1998; Maddison & McMahon 2000; Elias et al. 2003, 2006b, 2012;). Some species in this genus show extensive geographical variation with populations showing morphological differentiation, especially in male sexual characters such as visual ornaments, stereotyped movement patterns (dance), and substrate-borne vibratory displays (Richman & Cutler 1998; Maddison & McMahon 2000; Masta & Maddison 2002; Elias et al. 2006b, 2012; Hedin & Lowder 2009; Blackburn & Maddison 2014; Brandt et al. 2018; Hedin et al. 2020). Genetic, behavioral, and morphological evidence supports the hypothesis that strong sexual selection is driving signal diversification in this group (Masta 2000; Masta & Maddison 2002; Maddison & Leduc-Robert 2013) even in the face of gene flow (Blackburn & Maddison 2014).

One feature that is evident in many *Habronattus* species is the complexity of their courtship displays. Many male *Habronattus* perform elaborately coordinated vibratory song and visual dance displays which emphasize colored appendages (Elias et al. 2003, 2005, 2006a,b,c, 2012). Displays among *Habronattus* species vary along many axes including: the presence, number and position of visual ornaments; the color of visual ornaments; the presence of vibratory signal components; the spectral and temporal properties of vibratory signals; the coordination between visual and vibratory signals; and the sequence of presentation (Elias et al. 2006b, 2012).

The goal of this study was to characterize multimodal displays in the *Habronattus clypeatus* species group, one of the most diverse groups in the genus with 10 described species (Maddison & Maddison 2016). Males in this group have ornaments on various body parts that are displayed to the female (figs. 2 & 8, Maddison & Maddison 2016). The first legs have lateral fringes of setae (hairs and flattened spines), and in some species are bright green. The third legs of most species have unusual swellings or spurs on the femur and/or patella, and have various fringes and bands of color (Maddison & Maddison 2016). The face in most species is vertically striped. Maddison (2017) has even suggested that a pattern near the retina within the anterior median eye may be a courtship ornament. Given this complexity of ornamentation, we expected that the motions and vibrations of courtship might also be complex. We recorded multimodal displays from nine species and quantified properties of vibratory signals and the overall structure of displays. We also characterized display variation across populations in two widespread species from this group. We discuss these multimodal displays in the context of signal evolution and species diversification.

METHODS

Spider collection.—We collected *Habronattus* males from nine species of the *clypeatus* group, including *H. arcalorus* Maddison & Maddison, 2016*, H. aztecanus* (Banks, 1898)*, H. californicus* (Banks, 1904)*, H. clypeatus* (Banks, 1895)*, H. dossenus* Griswold, 1987*, H. formosus* (Banks, 1906)*, H. forticulus* (Gertsch & Mulaik, 1936)*, H. gilaensis* Maddison & Maddison, 2016, and an undescribed species informally called *H.* "rio grande". We collected spiders between 2002–2019, from multiple sites during the spring and summer breeding season for each collection year. After collection, we housed spiders individually in the lab on a 12:12 hour light:dark cycle, with weekly feeding on a mixed diet of *Drosophilia melanogaster* and pinhead crickets. Voucher specimens are housed in the personal collection of CR and DOE and will ultimately be deposited at the California Academy of Sciences and the Essig Museum of Entomology. Supplementary Table S1 (online at https://doi.org/10.1636/JoA-S-18-045.s1) reports all the locations, elevation, and sample sizes for the displays evaluated in this study.

Recording procedures.—We recorded courtship displays on a custom-built arena, constructed using thin nylon fabric stretched tightly 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). To stimulate courtship behavior, we presented males with a female model prepared by taking freshly dead females and affixing them to the blunt end of an insect pin by a drop of dental/bees wax on their ventral cephalothorax. The pin was attached to a belt-pulley system we used to control rotation of the female model (Girard et al. 2011), simulating a female that visually tracked the male throughout his display (receptive females track males during displays; Elias et al. 2006a; Li et al. 2008; Painting et al. 2016). When possible, we used conspecific female models (73/107) although in many instances this was not possible (34/107). In the field, male *Habronattus* will routinely court heterospecifics (Taylor et al. 2017) thus we hypothesize that male displays were minimally affected. Arenas were cleaned between trials using 75% ethanol.

We videotaped courtship behavior (30 frames/second; JAI CV-S3200 CCD camera; Sony Lumix) and recorded vibratory songs using a Laser Doppler Vibrometer (Polytec OFV 3001 controller and OFV 511 sensor head –*H. arcalorus, H. californicus, H. clypeatus, H. dossenus, H. formosus,* and *H. forticulus*; PSV-I-400 LR, USA and an OFV-505 scan head - *H. aztecanus* and *H. gilaensis*; sampling rate 48 100 kHz, PDV 100 – *H. arcalorus, H. clypeatus, H. dossenus, H. formosus,* and *H.* "*rio grande*"). For recordings conducted in 2019, temperature was standardized to 40°C using reptile heating lamps, as temperature has dramatic effects on courtship (Brandt et al. 2018, 2020). Video "vouchers" of displays for each species were archived at the Macaulay Library of Natural Sounds, Cornell Lab of Ornithology, Cornell University, Ithaca NY (online at https://www.macaulaylibrary.org/) (See Supplementary Table S2, online at https://doi.org/10.1636/JoA-S-18-045.s2 for voucher numbers).

Nomenclature.—Courtship in the *clypeatus* group is stereotyped, with individual variation mainly occurring in the types of elements, number of repeated elements and progression through the display. In this study, our goal was to describe courtship in the entire *clypeatus* group, hence we report on idealized courtship on most species. We build on the naming conventions described in detail in a previous study (Elias et al. 2012). Briefly, display notations should be read as algebraic equations. Complete courtship displays are referred to as display compositions. Display compositions are made up of movements comprised of stereotyped motifs that repeat within each movement. Motifs are made up of signal element "notes." Signal elements are defined by unique combinations of substrate-borne vibrations and/or visual motions. Superscripts in display compositions denote how often signal elements occur, for example an integral number (x) describes the typical repetition of the signal element, a single asterisk* denotes a small variable repetition number (typically from 2–8 repetitions), a double asterisk** denotes a large variable repetition number typically from 10–30 repetitions. If an integral superscript (x) contains a comma, this denotes a gap between signal element repetitions, for example the superscript ^{2,1} would denote 2 elements in rapid succession followed by a pause (silence of more than 500ms), followed by 1 element. Subscripts denote signal elements which are distinct but variations on a theme.

Population differences.—For two species (*H. clypeatus* and *H. formosus*), we conducted further analyses on individuals collected from different populations. For *H. clypeatus*, we recorded courtship from 10 populations in Arizona, Utah, and New Mexico (Fig. 6). For *H. formosus*, we recorded courtship from five populations in Utah, Arizona, Nevada, and California (Fig. 7). For each individual, we quantified the proportion of time each male spent performing different motifs. For each species, we next performed a principal

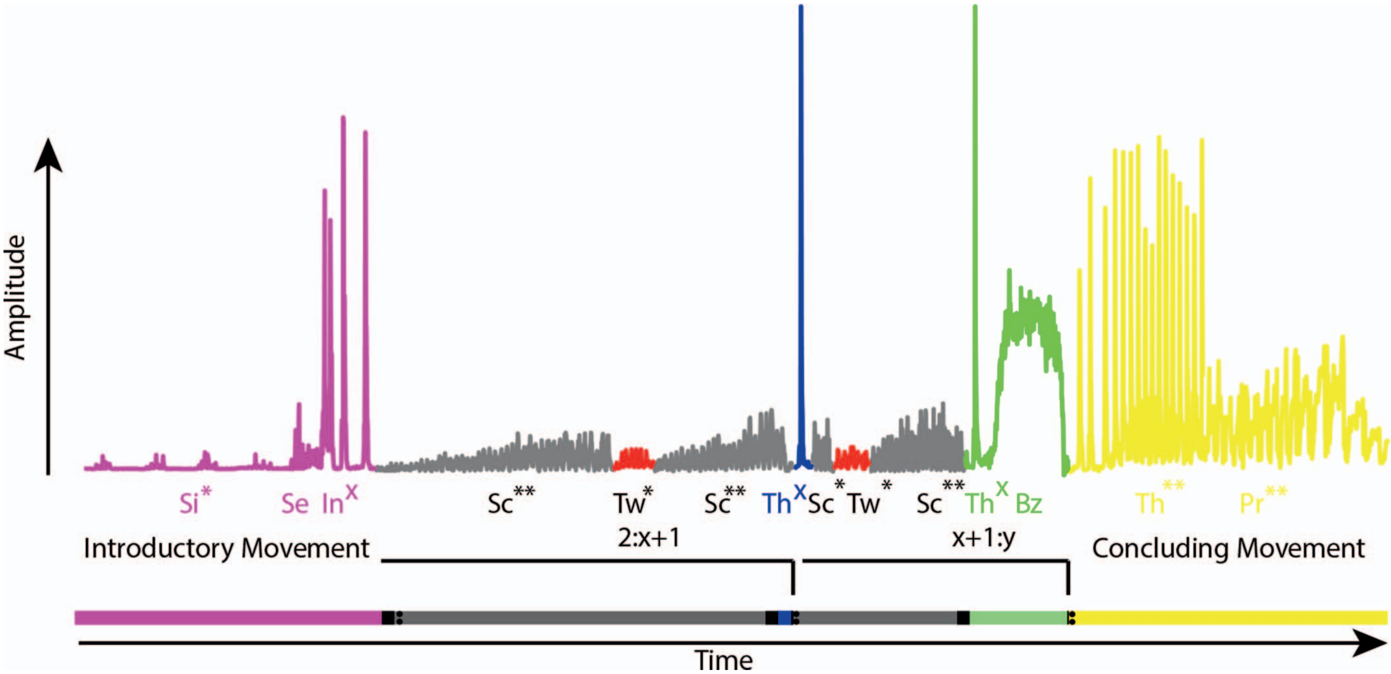

Figure 1.—Idealized courtship display of *H. clypeatus* group. Displays consist of several movements, each made up of several motifs. The upper row shows the RMS amplitude of vibrational song motifs; the lower row shows the song 'score' of the display composition, with notations indicating number of repeated movements. This example shows four movements: an Introductory movement (indicated by pink bar in the lower row), two Scrape movements (indicated by gray bar in lower row) ending in a thump bridge (indicated by blue bar) and a buzz bridge (indicated by a green bar), and a Concluding movement (yellow bar). Repeat sign notation is used to indicate the beginning (dots on the right of a black line) and end of a movement (dots on left of the black line). The number of times each movement is repeated varies across individuals and species. If a display composition is made up of 1 to z movements (in this example, $Z = 4$), then the 1st movement is always the Introductory movement, here including a sidle (Si), settle (Se) and a series of introductory thumps (It). This is followed by a number of movements (movement 2 to movement $x + 1$) comprised of Scrape Motifs—consisting of Scrapes (Sc, gray) and Twists (Tw, red)—punctuated by a Thump Bridge (Th, blue). For buzzing species, these sets of movements would then be followed by an additional number of movements made of Scrape Motifs (movement $x + 1$ to movement y) punctuated by a Buzz Bridge (Bz, green). The Concluding movement is always the Pre-Mount Motif (yellow) consisting of Thumps (Th) and Purrs (Pr). Superscripts indicate how often signal elements occur; for example, an integral number (x) describes the typical repetition of the signal element, a single asterisk* denotes a small variable repetition number (typically from 2–8 repetitions), a double asterisk** denotes a large variable repetition number typically from 10–30 repetitions. An integral superscript (x) that contains several numbers separated by commas denotes a gap between signal element repetitions; for example, the superscript ^{2,1} would denote 2 elements in rapid succession followed by a pause (silence of more than 500ms), followed by 1 element. Subscripts denote signal elements which are distinct but variations on a theme.

components (PC) analysis on these signaling data. Next, we performed a Normal Mixtures analysis to identify potential data clustering in the PC variables. The optimal number of data clusters were identified using the model with the lowest AICc score. If any of the species showed more than one data cluster, we next performed a Discriminant Function (DF) analysis on the original signaling dataset to test whether the identified clusters represented "true" distinct courtship displays. All statistical analyses were conducted using JMP (online at https://www.jmp.com).

RESULTS

Habronattus clypeatus group males perform multimodal displays consisting of visual dance displays using both visual ornaments and substrate-borne vibratory songs. A detailed ethogram of signaling elements is presented in Supplementary Table S3 (available online at https://doi.org/10.1636/JoA-S-18-045.s3). Below we describe dance and vibratory displays.

Overall display progression (movements).—In general, *clypeatus* group display compositions have 3–7 movements. Introductory Movements (In) start the entire display composition. Pre-mount (Pr) movements are the finale of the display, just prior to a copulation attempt. In general, there are 4 motifs that comprise displays, one of which serves as a bridge. The four motifs, in order, are *Introductory Motif*, *Scrape Motif*, *Thump Bridge*, and *Pre-mount Motif* (Fig. 1). *Introductory Motifs* occur only in the introductory movement of the composition. Pre-mount motifs only occur in the concluding movement of the composition. The *Scrape Motif* (Sc) is the main *clypeatus* group motif. *Thump bridges* bridge Sc motifs with other Sc motifs and have two variations, the simple thump bridge and the buzz bridge. As the movements progress, the male slowly moves forward so that by the end of the display composition, he is touching the female. Below we describe typical motifs in display compositions.

Introductory motif.—Introductory motifs are made up of three display elements, Sidles (Si), Settles (Se), and Introductory thumps (It) (Supplementary Table S3). *Habronattus forticulus*

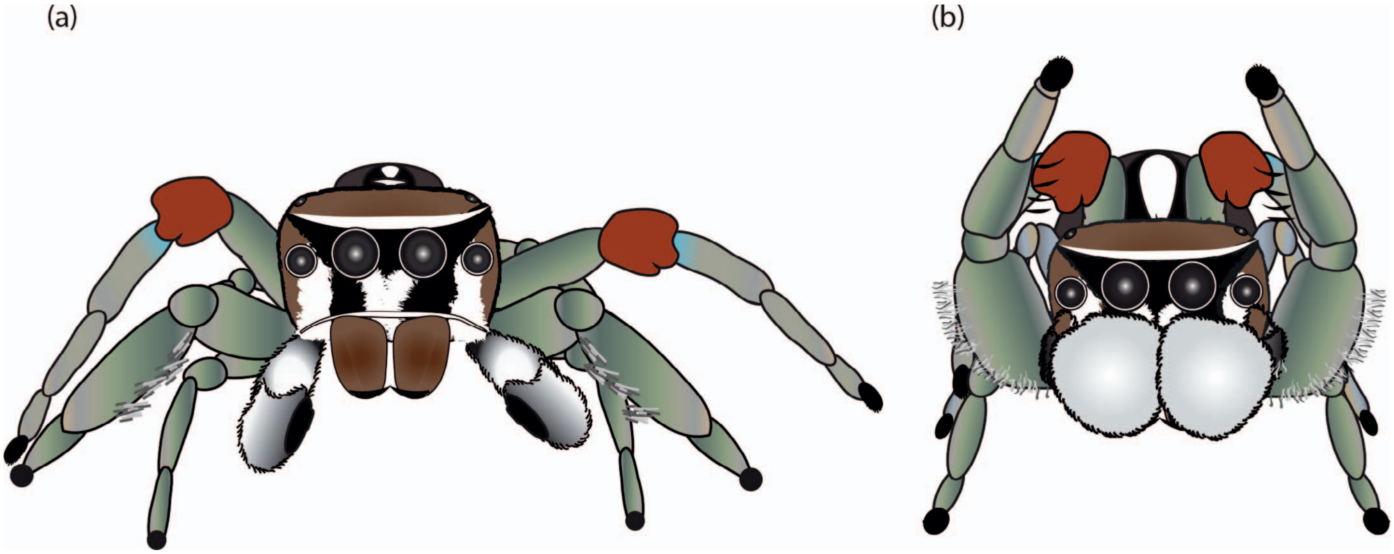

Figure 2.—Idealized displays, including two distinct postures. (a) Sidling (Si) visual display. Sidling postures occur only during the Intro movement when the male is relatively far from the female. During Si posture, males expose ornaments on the face, palps, and forelegs to females and approach in a zig-zag manner. (b) Main courtship posture (Ma posture) Ma posture is the courtship posture for most movements, with the exception of the intro movement. During Ma posture, males expose ornaments on the forelegs, palps, and third legs to females.

replaces the typical introductory motif with a unique display element, Spins (Sp) (Supplementary Table S3).

Introductory Motif: Si** Se It^x (where x is an integer)

The first signal element is a Sidle (Si). Si's begin at a relatively long distance as soon as the male orients to a female. Si's consist of stereotyped movements and no associated substrate-borne vibrations. As a male approaches the female, he spreads his forelegs and palps laterally, exposing the face and the underside of the forelegs (Fig. 2a). The male then approaches the female in an arching zig-zag pattern. The arcs of the zig-zags diminish as the male gets closer to the female. Si's appear to keep the female attentive to his display. Si's are repeated until the male reaches about 2–3 body lengths from the female, after which he performs a Settle (Se) display. Se's serve to transition from Si posture (Fig. 2a) to main courtship (Ma) posture (Fig. 2b). Main courtship posture is the courtship posture for most movements, with the exception of the introductory movement. During Ma posture, males expose ornaments on the forelegs, palps, and third legs to females.

Se elements are usually followed by an introductory thump display (It). During this movement, males produce a loud broad-band substrate-borne vibration that is coordinated with movements of the forelegs but slightly advanced relative to the foreleg movements.

Introductory Motif forticulus variation: Si**Sp**

Habronattus forticulus produces an introductory movement that is substantially different from those of its relatives (but see below for description of *H. velivolus*). In addition to the typical intro motif elements, *H. forticulus* males approach females using Spin (Sp) elements. Sp's consist of stereotyped movements and vibratory displays. During this behavior, males elevate the third legs and orient the legs so that the patellae are nearly touching and the tibial and tarsal leg segments are orientated parallel to the ground. As the male approaches the female, the third legs are moved outward, then inward. Simultaneously the tips of the forelegs are moved in a circular manner. During this approach, males produce a unique substrate-borne signal. Once a male reaches 2–3 body lengths from the female, he transitions to a Scrape Motif (see below).

Scrape motif.—Scrape motifs are the most common display type in *clypeatus* group displays and are a major part of most displays. Scrape motifs consist of two elements, Scrapes (Sc) and Twists (Tw). The order of a typical Scrape Motif is:

Scrape Motif: Sc** $Tw_{a\text{ or }s}$* Sc**

Scrape signal elements consist of stereotyped movements and associated substrate-borne vibrations. In short scrape bouts (*), the male moves his forelegs up and down followed by up and down movements of the abdomen, creating a rocking motion. In long scrape bouts (**), the forelegs pivot outward and then inward while they are being moved up and down (Fig. 3a). Scrapes are relatively broad band and are produced in rapid bouts (Fig. 3b) using a stridulatory file found on the back of the cephalothorax (Elias et al. 2003, 2005). After a series of scrapes, males often follow with a series of twist displays. Twist elements consist of stereotyped movements of the third pair of legs along with low amplitude substrate-borne vibrations (Fig. 4). There are two variations of twist displays, alternating twists (Tw_a, Fig. 4a) and stilting twists (Tw_s, Fig. 4b). Tw_a occur when the male, while in Ma posture, proceeds to move the third legs upward and outward so that they move in small circular motions (Fig. 4a). The third leg movements occur out of phase with each other so that legs rapidly alternate. Tw_s occur when the male, while in Ma posture, moves the third legs upward and outward so that they move in alternating circular motions (Fig. 4b). During this behavior the male also extends the standing legs (2nd and 4th pair) while pivoting the abdomen upward. This creates a "stilting" posture that is repeated. Tw bouts are usually followed by another Sc bout (Fig. 4c). During twists, a stereotyped low amplitude "whirring" vibration is produced

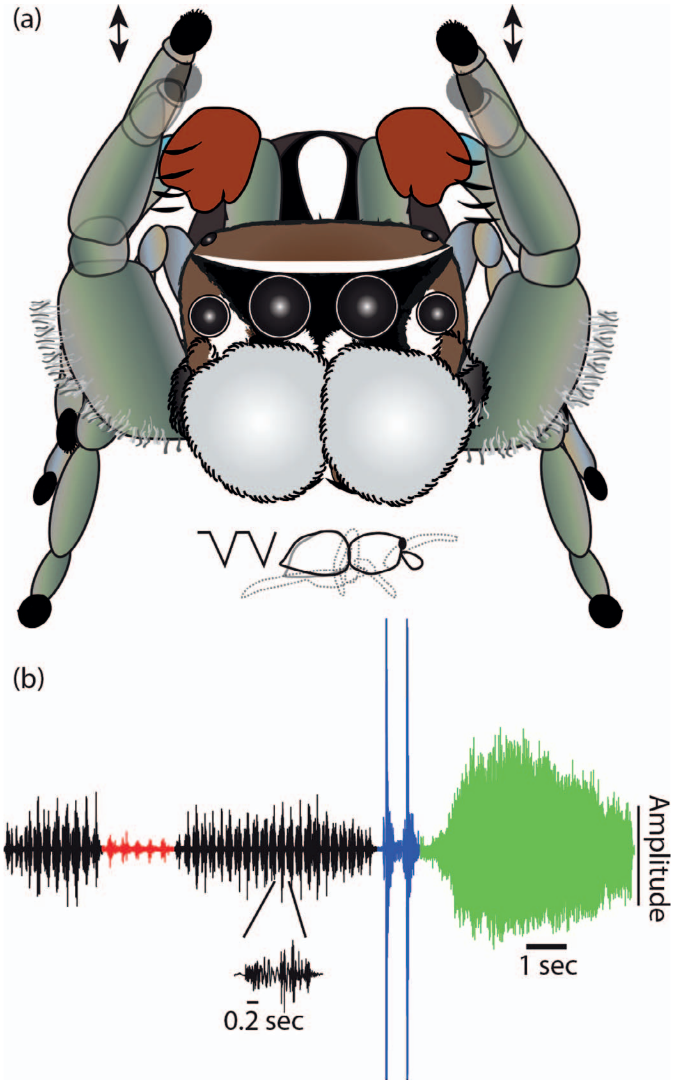

Figure 3.—Scrape displays. (a) Illustration of idealized Scrape (Sc) visual display. While in Main courtship posture (Ma posture), the male moves the forelegs up and down accentuating ornaments on the forelegs. (Inset) Side view of Sc display showing abdominal movements. Male moves the abdomen up and down during the display. Abdominal movements correspond to the production of a vibratory display. (b) Oscillogram of vibratory display. Sc elements are in black, Twist (Tw) elements are in red, Thump (Th) elements are in blue, and Buzz (Bz) elements are in green. (Inset) Detail of a single Sc element.

(Fig. 4c). The height of the stilting posture and the degree of pivoting of the abdomen varies among species.

Thump bridge.—Thump bridges occur after Scrape Motifs and serve to bridge movements. There are two variations in thump bridges: thump bridges and buzz bridges. Thump bridges are made up of individual thumps (Th). Buzz bridges are made up of thumps (Th) and buzzes (Bz). In many species/populations, the number of Th's gradually increases through the display compositions until the finale of the display composition.

Thump Bridge: Th^{x} (where x is an integer from 1 to 4)

Th's are associated with stereotyped motions and substrate-borne vibrations. The display element begins when the male, in Ma posture (Fig. 5a), arches his forelegs downward and then rapidly flicks them upward so that the tips are oriented vertically with the tips pointing upward (Fig. 5b). The amplitude of the downward deflections varies from slight deflections to large deflections bringing the foreleg tips in contact with the ground. While the forelegs are flicked upward, males bend their abdomen forward and then release it producing a loud broad-band vibration (Fig. 5b inset, Fig. 5d). Abdominal movements are delayed from foreleg movements and the delay varies (range: 4 – 400 ms). Substrate-borne vibrations are produced using a stridulatory file on the back of the cephalothorax (Elias et al. 2003). If a male contacts the substrate with his forelegs, the contact produces a percussive impulse which although substantial, is often softer in amplitude than the vibrations produced by abdominal movements (Elias et al. 2003).

Thump Bridge Variation: Buzz Bridge: Th^{x} Bz (where x is an integer from 1 to 6)

Buzz bridges occur after Scrape motifs and serve to bridge movements. Buzz bridges occur in later movements of the display composition while thump bridges occur in early movements. Buzz bridges are made up of thumps (Th) and buzzes (Bz).

Buzz bridges always begin with Th's (see above). After the final Th in the series, while the legs are elevated with the tips pointing upwards, the male produces a Bz element (Fig. 5c). During Bz's, the male slowly curls his legs forward so that the tips of the legs are eventually pointing forward (Fig. 5c), and during this foreleg movement he produces a tonal substrate-borne sound (Fig. 5d). Bz's are produced by rapid oscillations of the abdomen (tremulation; Elias et al. 2003) .

Pre-mount motif.—Pre-mount motifs are the concluding movement of a display composition and occur just prior to an attempted copulation. For the recordings, we did not use live females, hence courtship recordings were terminated as soon as males attempted to copulate with female models. Pre-mount motifs consist of thumps (Th) and Purrs (Pr) and follow the general pattern outlined below:

Pre-mount Motif: **Th*Pr***

Pre-mount motifs begin when, in Ma posture, males produce a rapid series of Th's. As the series progresses, the male gradually extends his forelegs forward so that they are just above the female. After the series of thumps, males produce a Pr display which consists of the male contacting the female and producing short bursts of vibrations that are likely tactile signals as well. Pr's have similar spectral properties to Bz's and are produced by rapid tremulations. In our scoring of components, Pr motifs are the concluding movement.

Variation between populations.—For two species, *H. clypeatus* and *H. formosus*, we tested for potential differences between allopatric populations based solely on the time devoted to scrape motifs, thump bridges, and buzz bridges. For *H. clypeatus*, the first two PC components explained 96.5% of the variance (Supplementary Table S4, available online at https://doi.org/10.1636/JoA-S-18-045.s4). The Normal Mixtures analysis suggested that the display data could be divided into two distinct clusters (Supplementary Table S4). Based on these clusters, we categorized the ten populations of *H. clypeatus* into "montane" (Fig. 6b: Mule, n = 2, Sierra Nacimiento, n = 4; Abajo, n = 4; Chiricahua, n = 1; Villanueva, n = 2; Raton Mesa, n = 3) and "desert" (Willcox Playa, n =1;

Baboquivari, $n = 1$; Santa Rita, $n = 5$, Galiuro, $n = 3$) forms, broadly matching habitat transitions going from east to west and by changes in elevation (1955 m ± 249.5 SD, 1286 m ± 85.34 SD; Supplementary Table 1) . The discriminant function analysis based on the original variables and our two categories resulted in a 96.2% positive classification rate (Entropy $R^2 = 0.79890$). Only one individual from the Galiuro Mountain populations was misclassified as a "montane" form. All other individuals ($n = 25$) were classified correctly. For *H. formosus*, the first two PC components explained 97.7% of the variance (Supplementary Table 4). The Normal Mixtures analysis could not identify more than one distinct cluster in the data (Supplementary Table 4) from our five sampled populations (Fig. 7b: Lake Berryessa, $n = 6$; Moapa, $n = 2$; Pine Valley, $n = 3$; Superstition, $n = 3$; Death Valley, $n = 3$).

Species comparisons.—*Display composition:* Within the overall *clypeatus* display structure, we can distinguish three major groups based on the motifs used and the time spent performing certain motifs (Supplementary Table 2). One group ("stilters": *H. arcalorus*, *H. aztecanus, H. californicus,* montane *H. clypeatus*, *H. formosus, H.* "rio grande") emphasizes scrape motifs, has minimal buzzing elements in their thump bridges, performs stilting twists during scrape motifs, and has relatively elaborate third leg ornamentation (Fig. 8b, c, d). A second group ("buzzers": desert *H. clypeatus, H. dossenus, H. gilaensis*) includes species that use buzz bridges, do not use stilting twists in their scrape motifs, and have relatively simpler third leg ornamentation (Fig. 8e, f). *Habronattus gilaensis* is unique in that it has no twist display and lacks obvious third leg ornamentation (Maddison & Maddison 2016). The third group is represented only by *H. forticulus* ("spinner"), which appears to have a unique introductory movement and no stilting or buzzing elements (Fig. 8a).

Additional preliminary observations.—We also examined video-only recordings of the remaining described *clypeatus* group species (*H. divaricatus* and *H. velivolus*). Although we did not record vibratory displays, our video recordings suggest that *H. divaricatus* is a buzzing species. In addition, we hypothesize that *H. velivolus* is a stilting species based on visual displays and third leg ornaments. This species however appears to have an intermediate Introductory display between "typical" stilting species (*H. aztecanus*, *H. formosus*) and *H. forticulus*. After a typical Si display, males switch to a direct approach where the male flicks his third legs upwards and outwards while making circular motions with his forelegs. This direct display is similar to the *H. forticulus* Introductory display.

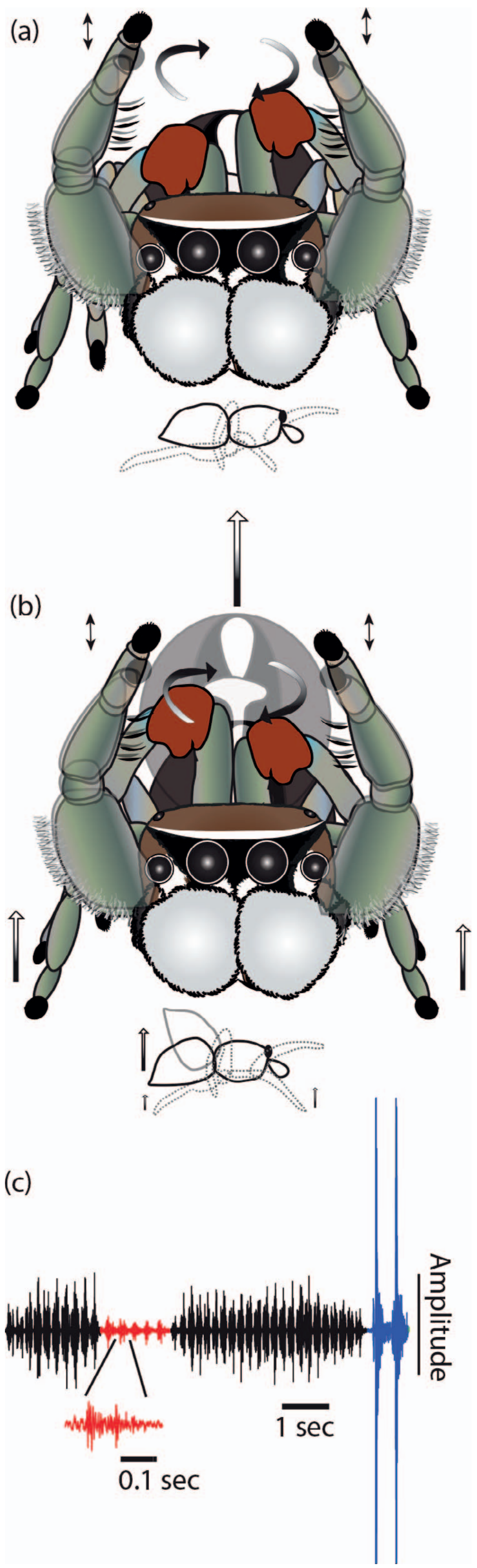

Figure 4.—Twist displays. (a) Drawing of idealized visual alternating Twist display (Tw_a). Starting at a typical Ma posture, males alternate in lifting each third leg, up and then out, emphasizing third legs' patella ornaments. (Inset) Side view of display showing abdominal movements. (b) Drawing of idealized visual stilting Twist

←

display (Tw_s). Starting at a typical Ma posture, males alternate in lifting each third leg, up and then out, emphasizing ornaments on the patellas of the third legs. (Inset) Side view of display showing abdominal movements. During stilting displays males lift the abdomen and extend their 2nd and 4th pair of legs. (c) Oscillogram of vibratory display. Sc elements are in black, Tw elements are in red, Thump (Th) elements are in blue, and Buzz (Bz) elements are in green. (Inset) Detail of a single Tw element.

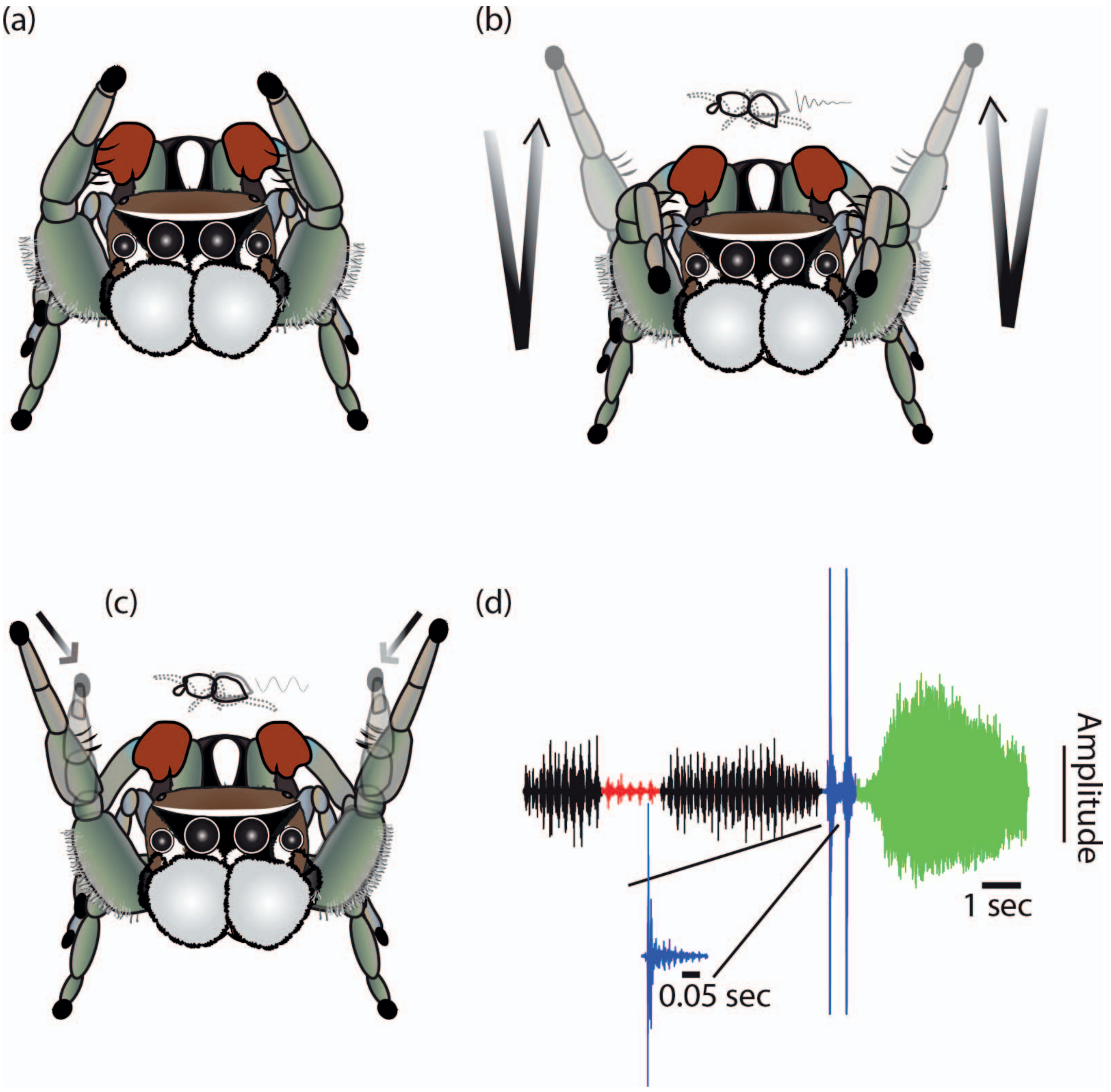

Figure 5.—Thump and Buzz bridge. (a) Typical Main courtship posture (Ma posture). (b) Drawing of idealized Thump visual display (Th). Starting at a typical Ma posture, males rapidly curl their forelegs in and then rapidly flick them up and out. Arrows denote the direction of movement. Transparency corresponds to the drawing. (Inset) Side view of display showing abdominal movements. During Th display, abdomen is pulled forward and the released. Abdominal movements correspond to the production of a vibratory display. (c) Drawing of idealized Buzz visual display (Bz). After a Th element, males slowly bring their forelegs down and in. (Inset) Side view of display showing abdominal movements. During Bz display, abdomen is rapidly oscillated. Abdominal movements correspond to the production of a vibratory display. (d) Oscillogram of vibratory display. Scrape (Sc) elements are in black, Twist (Tw) elements are in red, Th elements are in blue, and Bz elements are in green. (Inset) Detail of a single Th element.

DISCUSSION

In this study, we describe courtship for all known species in the *Habronattus clypeatus* species group, a complex of closely-related taxa where males perform elaborate multimodal displays (Elias et al. 2003; Maddison & Hedin 2003; Brandt et al. 2018, 2020; Leduc-Robert & Maddison 2018). Our examination suggests that across the group, displays are "built" out of similar building block elements (e.g., scrapes, thumps, twists, buzzes) with some species either modifying

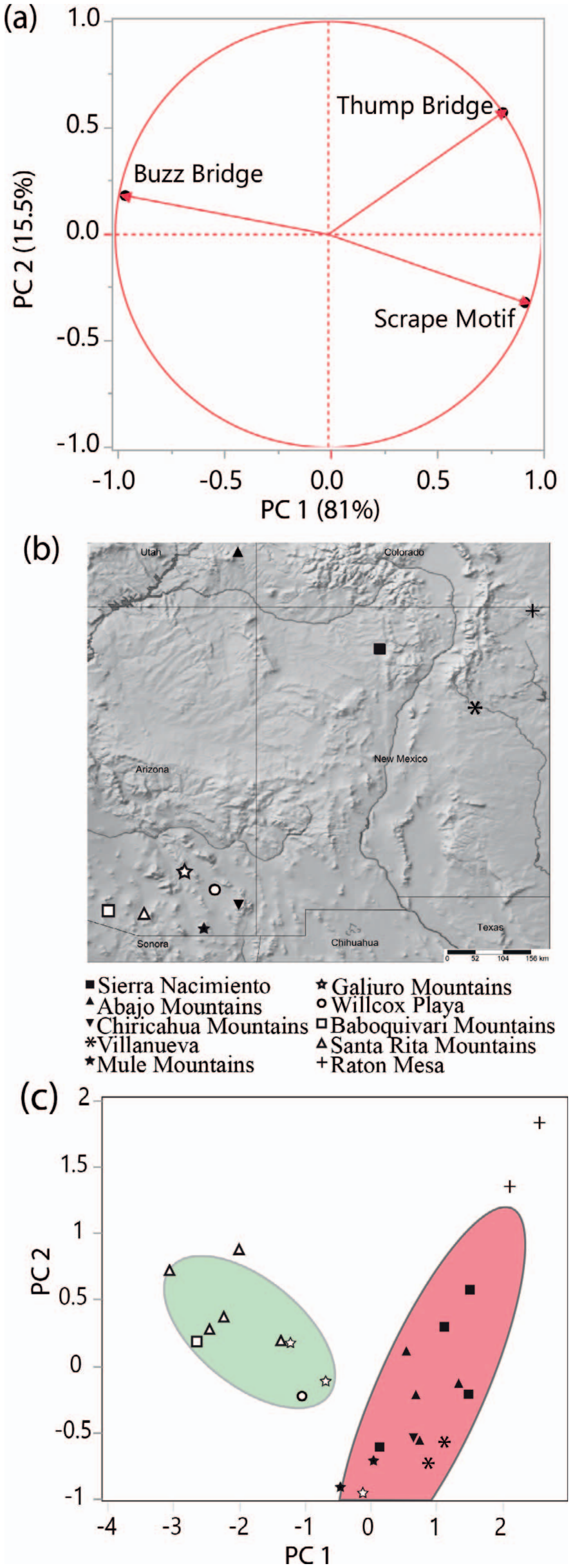

Figure 6.—Variation in vibratory song among *Habronattus clypeatus* populations. (a) Factor loadings for the individual variables used in the Principal Component Analysis. (b) Map of *H. clypeatus* population locations. Solid symbols indicate “montane” forms and open symbols indicate “desert” forms. (c) Scatterplot of PC1 and PC2 of *H. clypeatus* song variables. Shaded ellipses illustrate the two data clusters supported by a Normal Mixtures analysis. Red ellipse indicates “montane” forms and green ellipse indicates “desert” forms.

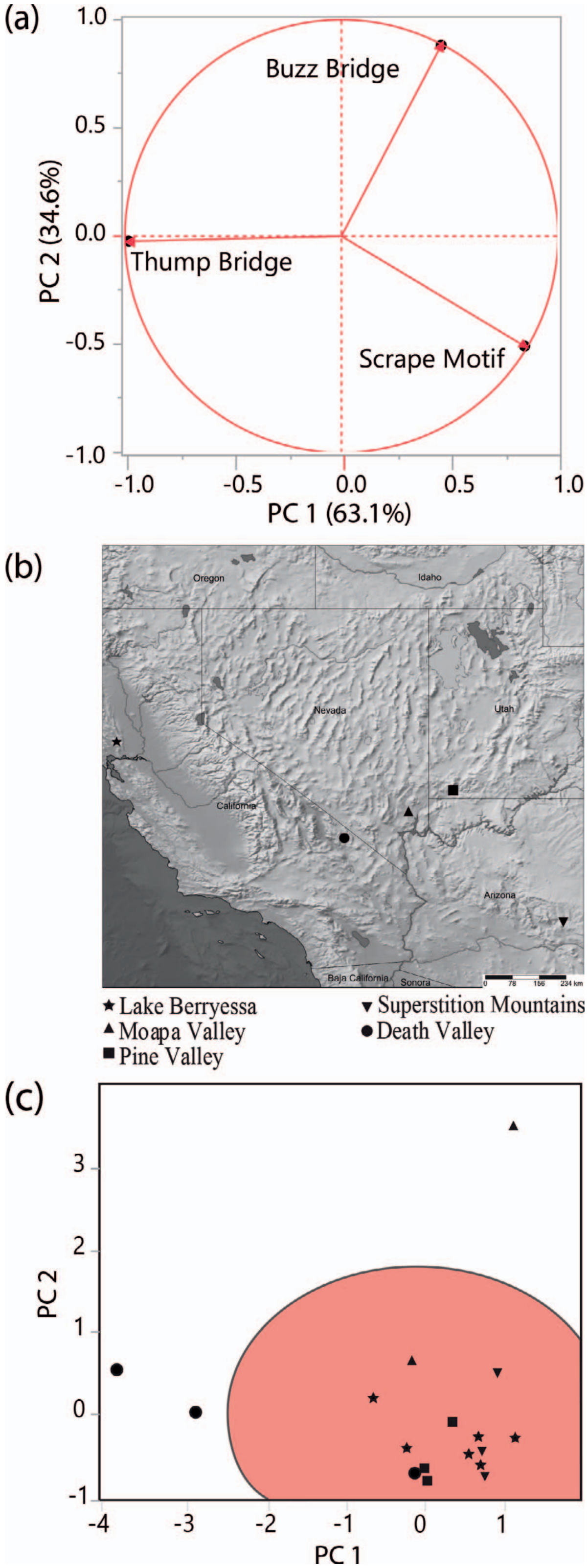

Figure 7.—Variation in vibratory song among *Habronattus formosus* populations. (a) Factor loadings for the individual variables used in the Principal Component Analysis. (b) Map of *H. formosus* population locations. (c) Scatterplot of PC1 and PC2 of *H. formosus* song variables. Shaded ellipse illustrates the data cluster supported by a Normal Mixtures analysis.

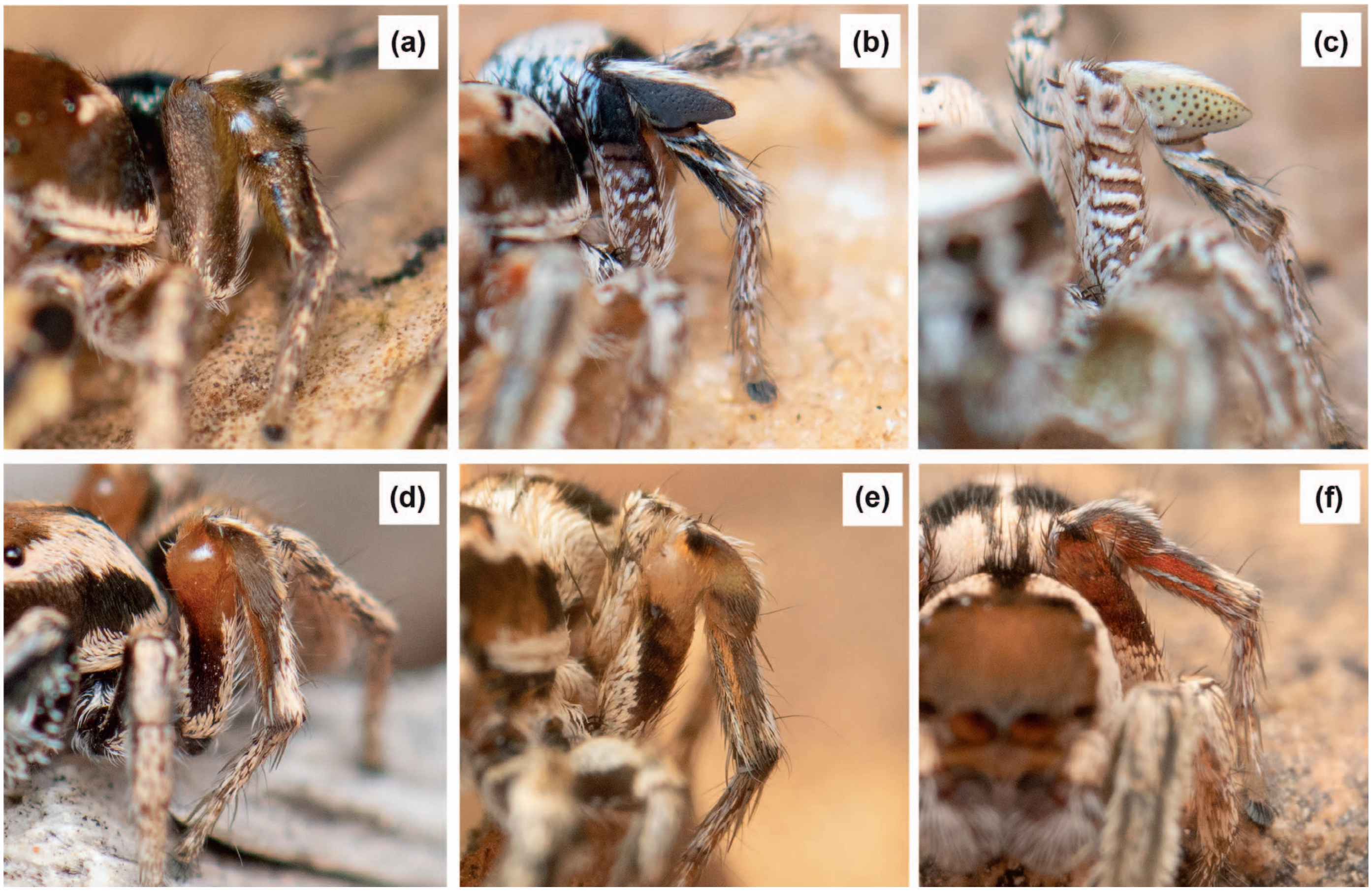

Figure 8.—Third leg modifications of representative *H. clypeatus* group members. (a) *H. forticulus*, MCH 19_021, Bentsen-Rio Grande State Park TX, (b) *H. arcalorus*, MCH 19_049, near Encino NM, (c) *H.* "rio grande", MCH 19_042, Bernalillo NM, (d) montane *H. clypeatus*, MCH 19_039, N of Monticello UT, (e) desert *H. clypeatus*, MCH 19_062, Santa Teresa Wilderness AZ (right leg, imaged flipped horizontally), (f) *H. dossenus*, MCH 19_057, Huachuca Mountains AZ (right leg, imaged flipped horizontally). Photographs by M. Hedin.

some of these elements (e.g., stilting twists), emphasizing certain elements more than others (buzzing species), and some including novel elements (spinning species). We recognize three major types of displays across the species group. For some species, males produced stilting displays, for other species, males produced loud tonal vibratory buzz displays. Finally, one species, *H. forticulus*, appears to have evolved a unique display element.

Across all species we suggest that differentiation could occur at the level of temporal patterns of songs. In particular, our study demonstrated a shift in the proportion of time allocated to specific motifs in populations of *H. clypeatus* going from east to west or alternatively from higher to lower elevations (montane forms: 1631 – 2255 meters; desert forms: 1204–1406 meters; see Supplementary Table 1, Figure 6). We suggest that these differences have significant effects on female mate choice and could represent "cryptic" speciation. Alternatively, sexual selection may not be driving differences in vibratory songs (Watts et al. 2019). Future work could examine more precisely the differences in "montane" and "desert" forms of *H. clypeatus*. While divergence appears to be occurring within *H. clypeatus*, this is apparently not the case in *H. formosus,* another species with a similarly broad distribution. Interestingly, *H. formosus* populations show a wide range in the temporal patterns of male songs, for example, males from Death Valley did not produce any Buzz bridges while Lake Berryessa males spent about 4% of their courtship devoted to Buzz bridges.

One of the major differences between stilting and buzzing species is the presence of elaborate ornamentation on the third legs of stilting species. *Habronattus aztecanus, H. arcalorus, H. californicus,* and *H.* "rio grande" all have large colored and patterned protuberances on their third legs (Fig. 8; Maddison & Maddison 2016). *H. formosus* has a rounded protuberance but is similarly ornamented. In buzzing species such as *H. dossenus* (Fig. 8f)*,* there are no elaborate protuberances on the third legs even though they are still colored. Interestingly, for *H. gilaensis*, another buzzing species, minimal ornaments or coloration are found on the third legs (Maddison & Maddison 2016). For *H. clypeatus*, montane and desert forms follow this aforementioned pattern. Montane *H. clypeatus* have relatively swollen third leg ornaments relative to the more subtle desert *H. clypeatus* third legs (Figs. 8d, e). This hypothesized negative relationship between elaborate third leg ornamentation and sustained tonal vibratory displays (e.g., buzzes) may suggest shifts in the targets of female choice and sexual selection from visual to vibratory signals for buzzing species.

Experiments on the buzzing *H. dossenus* demonstrated that vibratory signals are a crucial factor in ensuring mating success when signal production was manipulated (Elias et al. 2005) or when pairs of spiders were placed in environments where vibratory transmission was reduced (Elias et al. 2004). Similar manipulative experiments on *H. pugillis*, which has relatively more simple vibratory signals, showed no effect on mating rates whether vibratory signals were present or not (Elias et al. 2006a). In the sole study examining female choice and variation in male multimodal displays in un-manipulated jumping spiders, Girard et al. (2015) found that in the relatively visual *Maratus volans* (O. Pickard-Cambridge, 1874), variation in visual signals explained more than twice the variance in mating success, even though both visual and vibratory signals significantly predicted mating. These studies suggest that even though signals may be multimodal, some modalities may dominate and be primary targets of female choice (Hebets 2008; Hebets et al. 2013; Girard et al. 2015). Work examining mate choice in manipulated environments and correlative studies in natural conditions is sorely needed to further understand signal function in *Habronattus*.

The differences between stilting and buzzing species could reflect tradeoffs in signal complexity as predicted by models examining multiple signal evolution (Pomiankowski & Iwasa 1993, 1998; Schluter & Price 1993; Johnstone 1996; Fawcett & Johnstone 2003; Bro-Jørgensen 2010; Wilson et al. 2013; Rubi & Stephens 2016). These models predict that multiple signals are unlikely to evolve because of economic limitations in the features females can assess during courtship. According to these theories, females will pay attention to features of signals that provide the most reliable information and over time, females will ignore other aspects of multiple signals due to economic constraints (Pomiankowski & Iwasa 1993, 1998; Schluter & Price 1993; Johnstone 1996; Fawcett & Johnstone 2003; Bro-Jørgensen 2010; Wilson et al. 2013; Rubi & Stephens 2016). We suggest that a similar process may be occurring in the *clypeatus* species group.

In recent years, spiders have served as models to understand different aspects of signal complexity (Herberstein et al. 2014). Even in this context, *Habronattus* displays will provide a particularly interesting test for hypotheses on signal evolution because (1) many female *Habronattus* only mate once (Elias, unpublished observation) and (2) the complexity of displays across the genus varies tremendously. Relative to the closely related *coecatus* species group (Elias et al. 2012), displays of the *clypeatus* group show lower complexity (4 vs. 7 motifs; 10 vs. 20 elements). Other species groups have even simpler displays (Griswold 1987; Maddison & Hedin 2003; Elias et al. 2005). To understand *Habronattus* displays, we must understand the factors that drive the evolution of different signal elements, the features of signal elements (visual and vibratory characteristics, integrated multimodal characteristics), as well as the temporal structure of display elements at different scales (motifs, movements, and overall composition). Similarly, we must investigate which features, if any, females use to assess mates. Understanding patterns in signal evolution in the group will be illuminating in examining the forces that drive signal complexity, multimodal signals, and signal diversification.

ACKNOWLEDGMENTS

We would like to thank M.B. Girard, M.C.B. Andrade, S. Sivilinghem, N. Lee, J. Macias, K. Needham, J. Zhang, M. Bodner, E.A. Hebets, C. Peckmezian, E. Brandt, C-H. Wu, V. Rayno, and K. Silvestre for field and laboratory assistance. This project was funded by a National Science Foundation Grant to DOE (IOS-1021385 and DEB-1754605) and MH (DEB-1354558), Natural Sciences and Engineering Research Council of Canada (NSERC) and grants from the Canadian Foundation for Innovation and Ontario Innovation Trust to ACM.

SUPPLEMENTARY FILES

Table S1.—Specimens, locations, elevations, and sample sizes evaluated across the *Habronattus clypeatus* species group; online at https://doi.org/10.1636/JoA-S-18-045.s1

Table S2.—Display Compositions in the *Habronattus clypeatus* species group summary and video voucher numbers; online at https://doi.org/10.1636/JoA-S-18-045.s2

Table S3.—Ethogram for courtship behaviors in the *Habronattus clypeatus* group; online at https://doi.org/10.1636/JoA-S-18-045.s3

Table S4.—Statistical Analyses for *Habronattus clypeatus* and *H. formosus* populations (Principal Components and Normal Mixtures Analyses); online at https://doi.org/10.1636/JoA-S-18-045.s4

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Manuscript received 23 May 2018, revised 10 March 2019.