



# Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae)

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Jumping spiders in the genus *Habronattus* use complex multimodal signals during courtship displays. In the present study, we describe multimodal displays from the *Habronattus coecatus* clade, comprising a diverse group of 23 described species. *Habronattus coecatus* group displays are made up of sex-specific ornamentation and temporally coordinated combinations of motion displays and vibratory songs. Vibratory songs are complex, consisting of up to 20 elements organized in functional groupings (motifs) that change as courtship progresses. This temporal structuring of displays is analogous to a musical composition. Vibratory elements are associated with movement displays involving coloured and patterned ornaments on the male body. We describe general patterns of multimodal displays for 11 species including one, *Habronattus borealis*, which appears to have lost complex display behaviour. *Habronattus coecatus* group courtship is one of the most complex communication systems yet described in arthropods and this group may reveal important factors driving the evolution of complex signals. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **105**, 522–547.

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## INTRODUCTION

Complex sexual displays have long stimulated the imagination of naturalists and been the focus of biological research. Classic examples include the ornate plumage and ‘dances’ of male birds-of-paradise (Frith & Beehler, 1998; Irestedt *et al.*, 2009), the elaborate bowers used by male bowerbirds (Borgia, 1995; Doucet & Montgomerie, 2003; Frith & Frith, 2004; Endler *et al.*, 2005), and the dance ‘struts’, vocalizations, and plumage of sage grouse males (Gibson, 1996; Krakauer *et al.*, 2009). Although arthropod

display behaviour is generally considered to be simple, sexual signalling in some taxa rivals their vertebrate counterparts. In one of the most spectacular examples of complex signalling, mantis shrimp males signal using combinations of colourful, polarized ornaments, and water-borne vibrations (Patek & Caldwell, 2006; Marshall, Cronin & Kleinlogel, 2007; Chiou *et al.*, 2008; Kleinlogel & Marshall, 2009). In the present study, we document elaborate signalling in jumping spiders, rivalling that of bird groups such as the birds-of-paradise.

Numerous adaptive hypotheses for complexity in sexual displays have been proposed, including multiple sources of quality information (‘multiple messages’), compensation for environmental variation, and increased efficacy of signal transmission and

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reception (Guilford & Dawkins, 1993; Rowe, 1999; Hebets & Papaj, 2005; Partan & Marler, 2005). These hypotheses, however, do not adequately address the evolution of highly complex displays because, under most conditions, highly complex signals are predicted not to evolve (Pomiankowski & Iwasa, 1993; Iwasa & Pomiankowski, 1994). For example, as the value of new information in signals reaches an asymptote (in terms of each information bit's contribution to the reduction of uncertainty), the theoretical costs of producing/decoding new information continues to accelerate, leading to the prediction that economically, communication systems have severe constraints (Ay & Polani, 2008). In addition, the physiology of sensory neurones (i.e. habituation, adaptation), as well as the memory capabilities of receivers, may set limits to the amount of information that animals are able to effectively detect and process (Rowe, 1999; Hillis *et al.*, 2002; Mishra, Martinez & Hillyard, 2008). In a recent meta-analysis, it was shown that, across taxa, selection for shorter duration signals was stronger than longer duration signals, suggesting the existence of constraints for evaluating complex signals (Reinhold, 2011). The factors driving the evolution of highly complex displays remain an open question.

Jumping spiders use visual and vibratory signals during courtship. Jumping spiders have visual systems with high spatial acuity (Land, 1985) and well developed colour vision (Forster, 1982a, b; Land, 1985; Koyanagi *et al.*, 2008). Not unexpectedly, jumping spiders use vision as the dominant sense in a variety of contexts (predation: Harland & Jackson, 2002; Nelson & Jackson, 2009; navigation: Hill, 1979; Hoefler & Jakob, 2006; communication: Uhl & Elias, 2011). In some jumping spiders, males use substrate-borne vibration signals (Jackson, 1980; Edwards, 1981; Maddison & Stratton, 1988a, b; Noordam, 2002; Elias *et al.*, 2003, 2006b, 2008) that are crucial to mating success (Elias *et al.*, 2005, 2010; Elias, Hebets & Hoy, 2006a; Sivalingham *et al.*, 2010).

Among the best studied jumping spiders are those of the genus *Habronattus*. These small (body length 5–8 mm) jumping spiders live on sticks, rocks, and dry leaves on exposed open ground. *Habronattus* is one of the most diverse genera in jumping spiders (approximately 100 described species) and includes species with some of the most elaborate visual ornamentation described (Peckham & Peckham, 1889, 1890; Griswold, 1987; Maddison & McMahon, 2000; Maddison & Hedin, 2003). Sexual selection on male secondary characteristics has been implicated as an important driver of diversification throughout the group (Maddison & McMahon, 2000; Masta, 2000; Masta & Maddison, 2002; Hebets & Maddison, 2005; Elias *et al.*, 2006a; Hedin & Lowder, 2009). Males in

one species, *Habronattus dossenus*, produce complex multicomponent substrate-borne signals (Elias *et al.*, 2003). In addition, unique, independently produced visual signals are precisely coordinated with distinct substrate-borne signals (Elias *et al.*, 2006d). Displays in *H. dossenus* follow sets of stereotyped patterns that change and progress through time. Courtship initially starts several body lengths away as males produce visual motion displays. As males approach females, they begin to perform multimodal displays (visual plus vibration) and males gradually add new multimodal display elements, ramping up the complexity (i.e. number of different elements used) and intensity (i.e. rate at which different elements are presented) of the display (Elias *et al.*, 2003).

Phylogenetic analyses have resolved *Habronattus* into a series of discrete species groups (Griswold, 1987; Hedin & Maddison, 2001; Maddison & Hedin, 2003; Hedin & Lowder, 2009). One of the major supported phylogenetic clades is the *Habronattus coecatus* group, consisting of at least 23 described taxa (Griswold, 1987; Maddison & Hedin, 2003). Monophyly of this group is strongly supported and males of this group include the most elaborate ornamentation of all *Habronattus* species groups, as well as the highest number of nominal species (Griswold, 1987; Maddison & Hedin, 2003). Previous studies of courtship signals indicated the presence of substrate-borne vibrations in one *H. coecatus* group species, *Habronattus schlingerii* (Elias *et al.*, 2005) and in another species, *Habronattus borealis*, distinct populations differed in the number of stereotyped displays used (Richman & Cutler, 1998).

In the present study, we characterized in detail the multimodal courtship displays of 11 species in the *H. coecatus* group (male substrate-borne vibrations and accompanying motion displays). We observed that the majority of species had multiple elaborate visual ornaments, complex multicomponent vibratory songs, and coordinated multimodal displays. Courtship signals in the *H. coecatus* group are quintessential examples of terrestrial arthropod sexual displays and are among the most highly complex displays found in the entire animal kingdom. The present study sets the stage for future work on signal evolution and behaviour in the group.

## MATERIAL AND METHODS

### SPECIES SAMPLING

*Habronattus coecatus* group members were sampled throughout North America (see Supporting information, Doc. S1). In total, we report on complete courtship displays from 11 different species representing the majority of fauna found in the USA. We measured

displays from two to seven individuals per species and each individual was sampled once. Additionally, we report visual displays for four other species (see Supporting information, Table S1). Voucher specimens are currently housed in the personal collection of D.O.E. and will ultimately be deposited at the California Academy of Sciences.

#### COURTSHIP RECORDING AND ANALYSIS

All courtship behaviour was videotaped 'face on' (30 frames/s; Navitar Zoom 7000 lens, JAI CV-S3200 CCD camera) and substrate-borne vibrations recorded using a Laser Doppler Vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head). Video and substrate-borne vibrations were recorded on a digital VCR (Sony DVCAM DSR-20 digital VCR; sampling rate of 48 100 kHz).

Mating recordings were conducted on a custom-made arena consisting of a piece of nylon fabric stretched on a circular wooden needlepoint frame (diameter 27 cm). The arena was positioned firmly at the center of a larger circular (diameter 35 cm) rotating platform on wooden dowels (height 7.5 cm). Glued to the top of the larger platform was a belt-pulley system with one drum attached at the center of the platform. On top of the centrally placed drum, we attached a small piece of cork to which female models could be attached (see below). At the outermost part of the larger platform, we placed the second drum of the belt-pulley system and, by rotating the outermost drum, we were able to turn the innermost drum. Small pieces of reflective tape (1 mm<sup>2</sup>) were placed at the center of the arena to serve as measurement points for the LDV. Nylon fabric passes all relevant frequencies with no significant distortion (Elias *et al.*, 2006e). Arenas were cleaned with 75% ethanol between trials.

Female models were used to entice males to court. Conspecific female models were first prepared by taking freshly dead females and waxing them to an insect pin ventrally on the cephalothorax. The insect pin was inserted into the cork glued to the central drum of the belt-pulley system. This arrangement allowed us to move female models in a 'lifelike' manner, which helped to entice males to court. Males were dropped into the arena and allowed to freely wander. Females were rotated until males noticed them and began to approach. When males began to approach, we positioned the female as if she was observing the courting male. Using the larger rotating platform, we rotated the arena to provide a 'female's eye view' of the male to the regular speed camera. If males stopped courting for 30 s, females were rotated slightly to draw the male's attention once again. At the end of each day, female models

were placed in the freezer. Female models were typically used for a maximum of 3 days (Girard *et al.*, 2011).

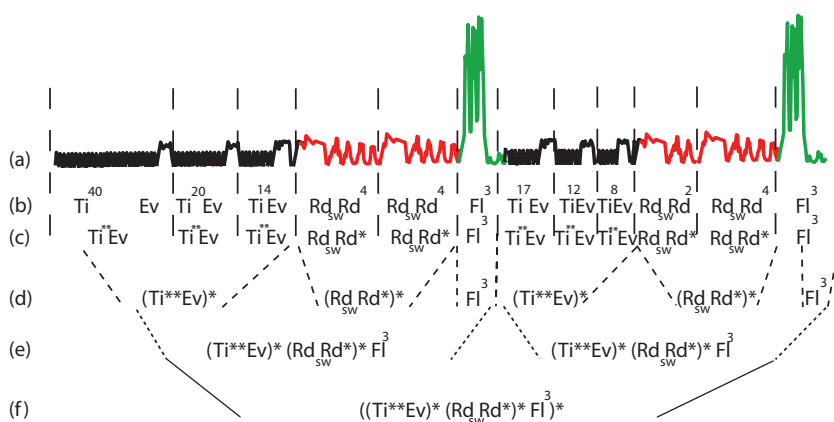
The general progression of courtship in the *H. coecatus* group is highly stereotyped, with individual variation mainly occurring in the number of repeated elements, motifs, and movements (see below). The main variation across species occurs in the types of elements used. The present study aimed to describe courtship in the entire *H. coecatus* group and we report on idealized 'typical' courtship and focus on between species differences in signal elements and not on individual variation in displays within species.

Only displays that progressed to the male mounting the female model were analyzed. Male displays were scored first by qualitatively assigning all distinct behaviours to signal element categories and recording the order of all courtship elements (timeline) for each individual male. Next, each individual timeline was condensed by coding repeated elements to produce an annotated description for each individual (see below). The reported descriptions describe 'typical' displays produced by the majority of individuals. Finally, each qualitative signal element was quantified. For quantification of vibratory displays, five to ten signals for every individual were averaged and the average signal properties are reported for individuals. All signal analyses were performed using custom written scripts in MATLAB, version 7 (Mathworks Inc.) and SOUNDFORGE (Sony). Vibratory traces are presented as RMS waveforms (2.1 kHz sampling) for clarity. Vibratory display measurements are reported in the Supporting information (Table S2–S8).

Our experimental set-up made recording early portions of courtship display challenging and several of our recordings had shortened or missing Intro portions (see below). In the field, males approach females from longer distances and likely always include introductory portions. The close proximity at which displays began may be the reason that many of the courtship displays began with Introductory Bursts (In; see below) or Ticks (Ti; see below). We report any Intro elements observed, even if the majority of males did not produce this behaviour.

#### NOMENCLATURE

To describe complex displays, we have adopted aspects of mathematical and musical nomenclature in our descriptions. Displays should be read as algebraic equations. We refer to complete courtship displays as display compositions. Display compositions are made up of movements comprising stereotyped motifs that repeat in each movement. Motifs are made up of signal element 'notes'. Signal elements are produced



**Figure 1.** Nomenclature of spider displays. Example of notation of a jumping spider vibratory display. Row A, vibration waveform (RMS amplitude versus time) of a ‘typical’ 2nd movement. The sequence of vibrational display elements can be transcribed as a list of element identifiers (letter codes) with superscripts representing the number of repetitions for each element. Rows B–F, repeating patterns are iteratively reduced until a simplified overall description of the entire sequence is constructed (F). Low numbers of repetitions (2–9) are indicated by a single asterisk (\*); higher numbers of repetitions (10–30) are indicated by a double asterisk (\*\*). Numerals represent stereotyped number of repetitions. Display summaries should be read as algebraic equations.

by males in the context of courtship behaviour and are defined by unique combinations of vibrational energy 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 in the range 2–9; and a double asterisk (\*\*) denotes a large variable repetition number typically in the range 10–30. For example, the notation:  $((A^{**}B)(CD^{*})^{**}E^3)^*$  should be read as a display motif where the  $A$  element is first repeated many times (10–30) [ $A^{**}$ ] followed by a single  $B$  element [ $B$ ]. This set of  $A$  and  $B$  elements is repeated two to eight times [ $(A^{**}B)^*$ ] and is then followed by a single  $C$  element followed by two to nine repetitions of the  $D$  element [ $D^*$ ]. This set of  $C$  and  $D$  elements is then repeated two to nine times [ $(CD^*)^*$ ] and is followed by the  $E$  element which is repeated three times [ $E^3$ ]. The entire set of elements is then repeated again two to nine times [ $((A^{**}B)(CD^*)^*E^{3or4})^*$ ]. An example of this process is provided in Figure 1.

If an integral superscript ( $x$ ) contains a comma, this denotes a gap between signal element repetitions; for example, the superscript  $^{2,1}$  would denote two elements in rapid succession followed by a pause, followed by one element repetition. Subscripts denote signal elements which are distinct but variations on a theme; for example, both  $Wa_{lo}$  and  $Wa_{hi}$  denote a multimodal behaviour where the male extends its forelegs forward, waving them rapidly at the same time as producing a sustained vibratory signal.  $Wa_{lo}$  displays are low in frequency and typically have a relatively tonal structure, whereas  $Wa_{hi}$  displays are

higher in frequency and typically have a broadband structure (see below).

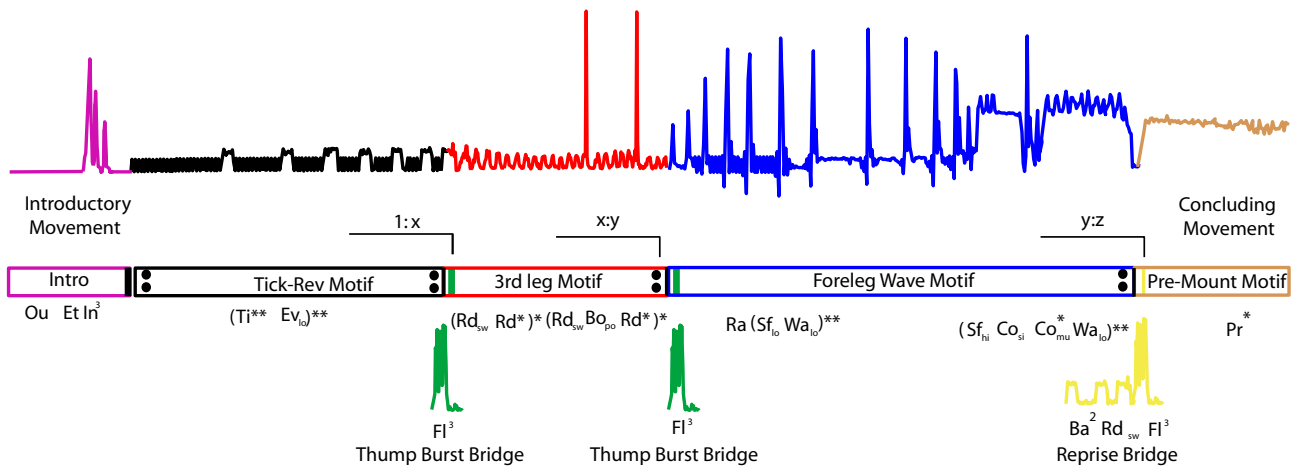
## RESULTS

*Habronattus coecatus* group male multimodal displays consisted of visual ornaments, motion displays, and substrate-borne vibratory songs. Below, we describe motion and vibratory displays; we also describe the ornamentation of one species (*H. coecatus*). Descriptions of vibratory songs include average dominant frequencies ( $\pm$  SD), as well as minimum and maximum frequencies (10 dB below peak amplitude) (Table S2–S8). The majority of spider songs were broadband (i.e. broad frequency spectrum) and the range of frequencies is probably the most salient feature of spider signals. Some signals are relatively tonal in structure and, for those signals, we included average fundamental frequency (see Supporting information Table S2–S8). For edited courtship recordings of select *H. coecatus* group species, see <http://nature.berkeley.edu/eliaslab/coecatusgroup.html>.

### MULTIMODAL DISPLAYS (MOTION DISPLAYS AND SUBSTRATE-BORNE VIBRATIONS)

#### *Overall display progression (movements)*

In general, *H. coecatus* group display compositions occurred in 4–5 movements. Introductory Movements (Intro) started the entire display composition. Post-mount (PM) movements were the finale of the display, just before a copulation attempt. Between the Intro and PM were movements consisting of specific motifs (or sets of motifs). In general, the second



**Figure 2.** Summary of idealized display of a typical *coecatus* group member. Displays consist of several movements punctuated by one of two bridges [Thump Burst (TB) Bridge, Green double bold line; Reprise Bridge (RB), yellow double bold line]. Repeat sign notation (double bar with dots) indicates the beginning (dots on right of double bar, almost always the Tick-Rev Motif) and end of a movement (dots on left of the double bar, always a TB or RB). The number of repeated movements is highly variable between individuals but more motifs are added as courtship progresses. If a display composition is made up of 1 to  $z$  movements, then the 1st movement is always the Intro movement. This is followed by a number of movements made up of Tick-Rev Motifs alone (movement 2 to movement  $x + 1$ ) punctuated by a single TB Bridge. These sets of movements would then be followed by a number of movements made of Tick-Rev Motifs and 3rd Leg Motifs (movement  $x + 1$  to movement  $y$ ) punctuated by a single TB Bridge. These sets of movements would then be followed by a number of movements made up of Tick-Rev Motifs, 3rd Leg Motifs, and Foreleg Wave Motifs (movement  $y + 1$  to movement  $z$ ), punctuated by a single RB Bridge. The concluding movement is always a series of Tick-Rev Motifs, 3rd Leg Motifs, Foreleg Wave Motifs, concluded by a single Pre-Mount Motif. Different colours represent different motifs or bridges. 1st Row, RMS amplitude of vibrational song motifs; 2nd row, song 'score' of display composition with notations.

movement was comprised of one motif and, in each subsequent movement, more motifs were added until the final PM movement. In total, there were seven motifs that comprised display compositions, with two of these motifs serving as bridges. The seven motifs in order were: Introductory Motif (Intro), Tick-Rev Motif (Tick-Rev), 3rd Leg Motif (3rd-Pop, 3rd-Shake), Thump Burst Bridge (TB), Foreleg Wave Motif (S-Wave-Reach), Reprise Bridge (RB), and Post-mount Motif (PM). Introductory Motifs only occurred in the introductory movement of the display composition. PM Motifs only occurred in the finale of the display composition. Tick-Rev Motifs were the most common motif in *H. coecatus* group displays and were included in most of the movements (excluding the Introductory and PM movements). TBs bridged multiple Tick-Rev Motifs with each other and 3rd Leg Motifs with Tick-Rev Motifs. RBs bridged Foreleg Wave Motifs with Tick-Rev Motifs. As a general rule, the repetition of motifs was greater in earlier movements. Within each motif, transitions between signal 'notes' (elements) were not abrupt and, instead, included a short period where properties of both signal elements were evident (typically between two to four notes). For the purposes of the present study, we did not analyze any elements from this

transitional period. Below, we describe typical motifs and signal elements.

Figure 2 shows an example of an idealized complete display, demonstrating several movements with their associated motifs. The number of movements in each display composition was variable between males of the same species. It is highly likely that this would have been even more variable if females were alive and allowed to interact with males. Regardless, as a general rule, motif and movement order was stereotyped (Fig. 2) (with the exception of *H. borealis*; see below) and more variation occurred in the length and number of movements, as well as the repetition rate of signal elements within motifs, than in the overall order and make-up of motifs. In our scoring of display compositions, we found that early movements had fewer motifs.

#### INTRODUCTORY MOTIF (FIG. 3)

Intro Motifs were made up of three display elements, Bounces (Ou), Settles (Et), and Introductory Flicks (IF). The order of a typical complete introductory motif was:

**Introductory Motif:**  $Ou^* Et IF^x$  (where  $x$  is an integral number)

The first signal element was a Bounce (Ou). Ous begin at a long distance when the male first detected the presence of a female and consisted of stereotyped combinations of 'dance' motions and no associated substrate-borne vibrations. As the male approached the female, he moved (bounced) his body up and down repeatedly, at the same time as alternately waving his palps diagonally (as they were held above the femora of the first legs), his forelegs up and down and his 3rd legs back and forth in synchrony (Fig. 3.1a). Ous were repeated until the male got within two body lengths of the female, after which he performed the Settle (Et) display. Et displays occurred when the male moved his entire body upwards, 'standing' at its highest point. Next, the male folded his 3rd legs towards his body until the patellas were almost touching each other and, at the same time, extended his pedipalps upwards (Fig. 3.2a). Several species performed a variation of this Et display, the 'subtle' Et<sub>o</sub> display. Et<sub>o</sub> display elements differed in that the body of the male was not held at its highest point but, instead, was a simple transition from Ous to IFs with no exaggerated movements. Et displays were always followed by Introductory Flick (IF) displays. IF display elements were made up of several foreleg flicks. The first flick of an IF display consisted of the entire body of the male moving down into regular courtship posture when his pedipalps were moved into forward position (the typical position during most of the display composition), and his legs were arched upwards so that the tips of his forelegs were pointing towards the female (with the femurs almost completely vertical) (Fig. 3.3a). During this movement, males produced a high intensity broadband 'thump' that was coordinated with movements of the forelegs but slightly advanced relative to his foreleg movements (Fig. 3.3a; see also Supporting information, Table S2). In subsequent flicks, the male arched his forelegs up and then down (Fig. 3.3b, c). During this period, the 3rd legs were slightly lowered so that they were positioned closer to his body (Fig. 3.3c). Less intense substrate-borne thumps were also coordinated with these leg flicks. Vibrations and leg motions were coordinated but substrate-borne vibrations were produced by abdominal movements, similar to other *Habronattus* species (Elias *et al.*, 2003). Flick numbers in IF displays appeared to be species specific (Table 1). We did not record Ous or Ets for all species, potentially as a result of differences in the starting position of male displays. When males started displaying close to females, they often proceeded directly to Et or IF displays.

#### TICK-REV MOTIF (FIG. 4)

Tick-Rev Motifs were the most common motif in *H. coecatus* group displays (all species examined used

Tick-Rev Motifs) and were a major part of all movements, with the exception of introductory and PM movements. Tick-Rev Motifs consisted of two signal element types, Ticks (Ti) and Revs (Ev). The order of a typical Tick-Rev Motif was:

**Tick-Rev Motif:** (Ti\*\* Ev)\*\*

The first signal type was a Tick (Ti; Fig. 4). Ti displays had no associated motions and consisted of short, broadband vibrations (see Supporting information, Table S3). Ti displays were produced repeatedly for long periods of time. At the end of a long bout of Ti displays, males produced a Rev (Ev) display element. Ev displays had both vibratory and visual components (Fig. 4). Associated Ev vibrations were longer than Ti vibrations (see Supporting information, Table S3, Fig. 4). Coordinated with these vibrations, a male flicked the tips of his forelegs downwards and slightly vertically (Fig. 4). Three variations of Ev displays occurred (Table 2), Ev<sub>lo</sub>, Ev<sub>hi</sub>, and Ev<sub>o</sub>: Ev<sub>lo</sub> foreleg movements were subtle, Ev<sub>hi</sub> foreleg movements were much stronger and in Ev<sub>o</sub> foreleg movements and vibrations were very subtle and often undetectable. A single Ev display occurred after a Ti series (Fig. 4). As the Tick-Rev Motifs were repeated, the male's forelegs gradually moved down during each Ev display (Fig. 4). In general, there were more Ti displays in early Tick-Rev Motifs than later motifs within a movement (Fig. 4). After several Tick-Rev Motifs, there was often a Thump Burst Bridge (TB) which demarcated the ending of a movement (see below; Fig. 6).

#### 3RD LEG MOTIFS (FIGS 5, 6)

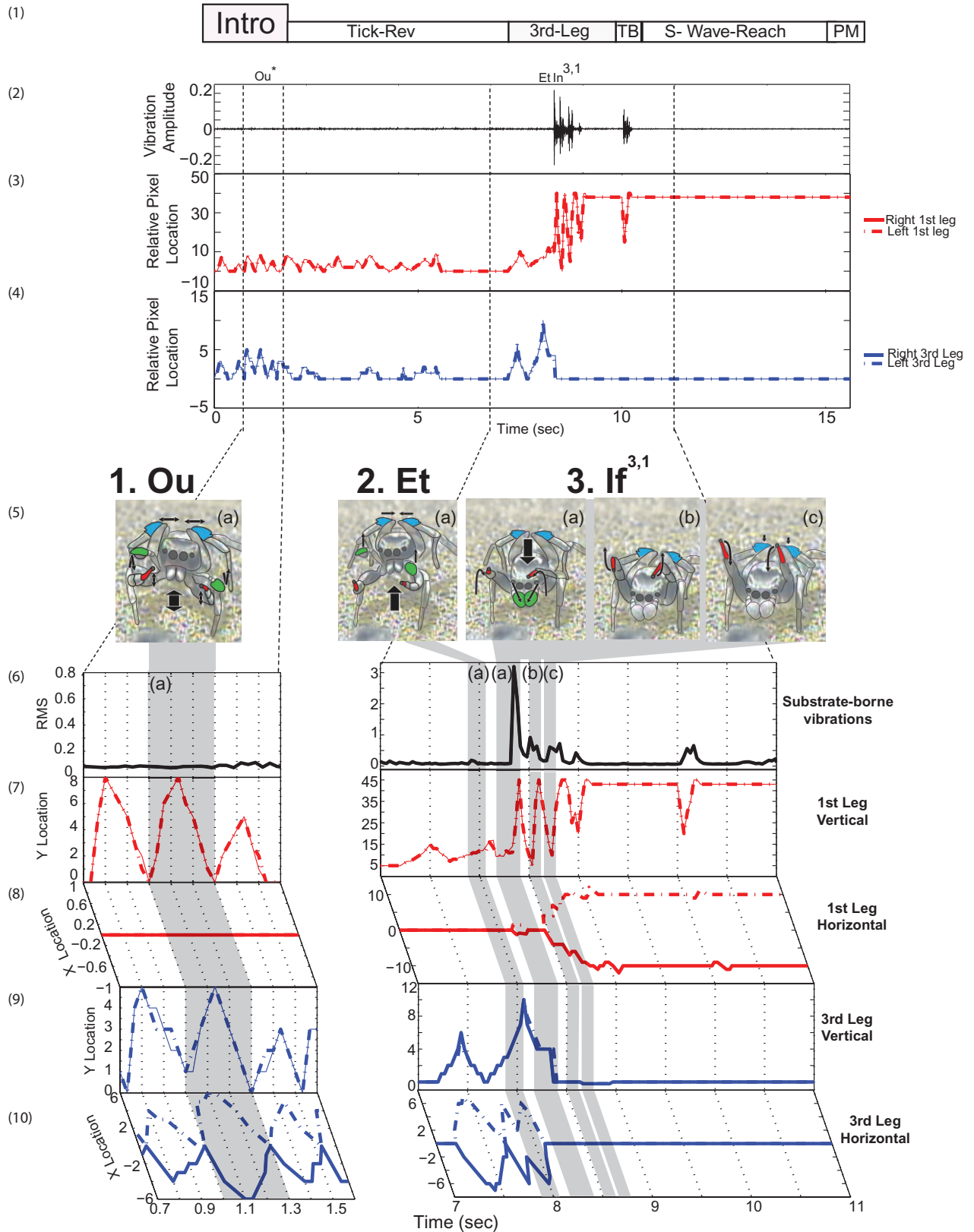
3rd Leg Motifs usually followed Tick-Rev Motifs. There were several variations of 3rd Leg Motifs. Some species used different 3rd Leg Motifs in different movements and in these cases, 3rd Leg Motifs in early movements were simpler (had less motifs) than in later movements. 3rd Leg Motifs were made up of 4 different signal types: 3rd leg switches (Rd<sub>sw</sub>), 3rd leg slides (Rd), Body pops (Bo<sub>po</sub>), and Body shakes (Bo<sub>sh</sub>) (Table 3). The order of the three 3rd Leg Motif variations were:

**3rd Leg Motif variation 1:** (Rd<sub>sw</sub> Rd\*)\*\*

**3rd Leg Motif variation 2:** ((Rd<sub>sw</sub> Rd\*)\* (Bo<sub>po</sub> Rd<sub>sw</sub> Rd\*)\*)\*

**3rd Leg Motif variation 3:** ((Rd<sub>sw</sub> Rd\*)\* (Bo<sub>sh</sub> Rd<sub>sw</sub> Rd\*)\*)\*

The first signal type was a 3rd leg switch (Rd<sub>sw</sub>). Rd<sub>sw</sub> always began a 3rd Leg Motif and consisted of motion and vibratory components. Rd<sub>sw</sub> occurred when a male in typical courtship posture, moved one of his 3rd legs up in a diagonal direction so that his 3rd leg was



**Figure 3.** Introductory Motif. Intro Motifs begin all displays and consist of three display elements (Ou, Et, If). 1st Row, overall timeline of display. Enlarged tab (in this case, Intro) represents the motif described in detail in the remaining panels (in this and subsequent figures). 2nd Row, oscillogram of entire Intro Motif. 3rd row, 1st leg position (red) during entire Intro Motif. Solid lines represent right 1st leg, dashed lines represent left 1st leg. 4th Row, 3rd leg position (blue) during the Intro Motif. Solid lines represent right 3rd leg, dashed lines represent left 3rd leg. 5th Row, drawings and video stills from courtship recordings. Each number represents a signal element (1–3) and each letter (a–c) represents a component of each signal element. Arrows show the direction of motion and thicknesses of arrows indicate the relative amplitude of motion. Grey bars indicate the times within the display that are represented by the drawings (5th row) and the corresponding details of substrate-borne vibrations (6th row), vertical (7th row) and horizontal (8th row) 1st leg movements, and horizontal (9th row) and vertical (10th row) 3rd leg movements. Display quantified from *Habronattus coecatus*.

**Table 1.** Introductory Motif

Species	Motif order
<i>Habronattus anepsius</i>	In <sup>3,1</sup>
<i>Habronattus borealis</i>	Simple Form: Ou Complex Form: Ou Et In <sup>3or4</sup>
<i>Habronattus brunneus</i>	Ou Et In <sup>4,1</sup>
<i>Habronattus coecatus</i>	Ou Et In <sup>4</sup>
<i>Habronattus cuspidatus</i>	Ou Et In <sup>3</sup>
<i>Habronattus festus</i>	Ou Et In <sup>3,1</sup>
<i>Habronattus klauserii</i>	Ou Et In <sup>4,1</sup>
<i>Habronattus mexicanus</i>	Ou Et <sub>o</sub> In <sup>2</sup>
<i>Habronattus pyrrithrix</i>	Ou Et In <sup>2</sup>
<i>Habronattus schlingerii</i>	Ou Et In <sup>3,1</sup>
<i>Habronattus virgulatus</i>	Et <sub>o</sub> In <sup>3</sup>

positioned higher than the tips of his forelegs (Fig. 5.1a). During these 3rd leg motions, males produced a relatively long broadband vibration (Fig. 5.1a; see also Supporting information, Table S3). Rd<sub>sw</sub> vibrations were similar to Rd vibrations in spectral content (see below) but were longer in duration (Fig. 5.1a; see also Supporting information, Table S4). 3rd Leg sweeps (Rd) followed Rd<sub>sw</sub> and consisted of horizontal movements of the raised 3rd leg (Fig. 5.2a) and coordinated broadband vibrations (Fig. 5.2a; see also Supporting information, Table S4). The raised 3rd leg alternated between successive Rd<sub>sw</sub> displays. Alternating presentation of 3rd legs was a property of all 3rd Leg Motifs. In the second and subsequent Rd<sub>sw</sub> displays, as the male's 3rd leg was raised (Fig. 5.1a), the previously raised leg was lowered, once again tightly near the body. The third type of display Bo<sub>po</sub> consisted of stereotyped motions and associated vibrations. Bo<sub>po</sub> began with the male crossing his raised 3rd leg with his lowered 3rd leg. The male then rapidly shifted his raised 3rd leg down (Fig. 5.3a), which caused his entire body to shake back and forth (Fig. 5.3b). During this rapid motion, he produced a loud 'pop' which may be have been caused by the release of 3rd leg tension, although this mechanism has not been determined (Fig. 5.3b). Pops were broad-

band and had the properties of percussive signals. Males alternated the legs that they used in successive displays (Fig. 5). Body shake (Bo<sub>sh</sub>), was the fourth type of signal. Bo<sub>sh</sub> occurred after Rd displays (Fig. 6.1a) and began when the raised 3rd leg was lowered down. During this movement, the male began to pivot his entire body back and forth repeatedly by approximately 30° (Fig. 6.2a). After his 3rd leg was lowered tightly against his body, the male continued to 'shake' his body by pivoting it back and forth. The shakes were produced along with a low intensity broadband vibration (Fig. 6; see also Supporting information, Table S4). After several 3rd Leg Motifs, there was often a Thump Burst Bridge (TB), which punctuated the ending of a movement (see below; Fig. 7).

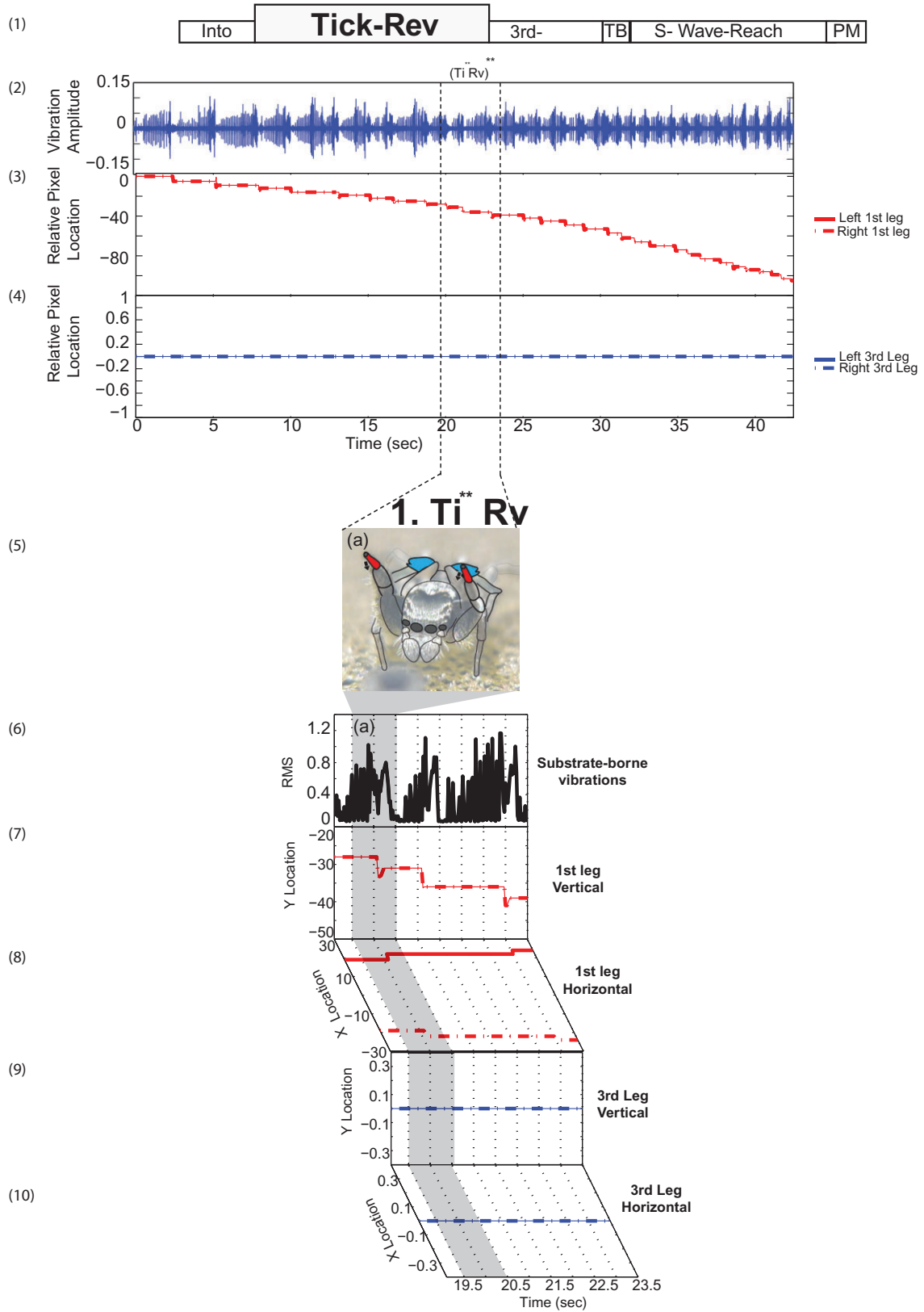
#### THUMP BURST BRIDGE (FIG. 7)

Thump Burst Bridges (TB) served as the bridge between most movements. TB displays occurred after Tick-Rev, 3rd Leg displays, and Reprise Bridges (see below). TB displays bridged these displays to new Tick-Rev Motifs. In our scoring of displays, TBs usually marked the end of a movement. TBs were made up of flicks (Fl), which were produced in rapid succession. In most species (9/11 species), the number of Fl displays was stereotyped, whereas, in other species, (3/11 species), the number of Fl displays varied within a small range (Table 4).

**TB Bridge:** Fl<sup>x</sup> where *x* is an integer in the range 2–5

Fl displays were associated with motions and substrate borne vibrations (Fig. 7). These displays typically began after an Rd display when one of the 3rd legs was raised and the other was held tight against the body (Fig. 7.1a). First, the male arched both his forelegs rapidly upwards so that his legs were almost completely vertical with the tips pointing upwards (Fig. 7.1a). This was followed by the male arching both his forelegs rapidly downwards until the foreleg tarsi and tips were pointing downwards (Fig. 7.1b). This pattern was repeated for every Fl display. In the final Fl display of the TB, the raised 3rd leg was





**Figure 4.** Tick-Rev Motif. Tick-Rev Motifs consist of two display elements (Ti, Ev). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.

**Table 2.** Tick-Rev Motif

Species	Motif order
<i>Habronattus anepsius</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus borealis</i>	Simple Form: none Complex Form: Ev**
<i>Habronattus brunneus</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus coecatus</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus cuspidatus</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus festus</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus klauserii</i>	(Ti** Ev <sub>lo</sub> )**
<i>Habronattus mexicanus</i>	(Ti** Ev <sub>hi</sub> )**
<i>Habronattus pyrrithrix</i>	(Ti** Ev <sub>hi</sub> )**
<i>Habronattus schlingerii</i>	(Ti** Ev <sub>hi</sub> )**
<i>Habronattus virgulatus</i>	(Ti** Ev <sub>hi</sub> )**

brought down so that it was close to the body, resetting the male to the typical courtship posture (Fig. 7.1c, d, e). Coordinated with each foreleg motion was a vibratory signal. Vibratory components of Fl displays were short, intense, broadband ‘thumps’ that occurred in two parts (Fig. 7; see also Supporting information, Table S5). Each part was associated with abdominal movements: one occurring on the downward deflection and the other on the upward deflection. Substrate borne vibrations preceded foreleg motions in all species.

FORELEG WAVE MOTIFS (FIGS 8, 9, 10, 11)

Foreleg Wave Motifs (S-Wave-Reach) were made up of two distinct parts and occurred in several variations. Foreleg Wave Motifs were made up of eight distinct signal elements: 3rd Leg Raises (Ra), Waving displays with low vibratory rumbles (Wa<sub>lo</sub>), Waving displays with high intensity vibratory buzzes (Wa<sub>hi</sub>), Waving displays with no vibrations (Wa<sub>0</sub>), Short Side Flicks (Sf<sub>lo</sub>), Large Side Flicks (Sf<sub>hi</sub>), Single Contact Lunges (Co<sub>si</sub>), and Multiple Contact Lunges (Co<sub>mu</sub>) (Table 5). The orders of the four Foreleg Wave Motif variations were:

**Foreleg Wave Motif variation 1:** Ra ((Wa<sub>lo</sub> Sf<sub>lo</sub> or hi)\*\* Wa<sub>lo</sub> Sf<sub>hi</sub> Co<sub>s</sub> (Wa<sub>lo</sub> Sf<sub>lo</sub> or hi)\*\*)\*

**Foreleg Wave Motif variation 2:** Ra((Wa<sub>lo</sub> Sf<sub>hi</sub>)\*\*Wa<sub>lo</sub> Sf<sub>hi</sub> Co<sub>si</sub> Co<sub>mu</sub>\*)\*

**Foreleg Wave Motif variation 3:** Ra(Wa<sub>hi</sub> Sf<sub>lo</sub>)\*\*((Wa<sub>hi</sub> Sf<sub>lo</sub>)\*\*(Wa<sub>hi</sub> Sf<sub>hi</sub> Co<sub>si</sub>)\*\*)\*\*

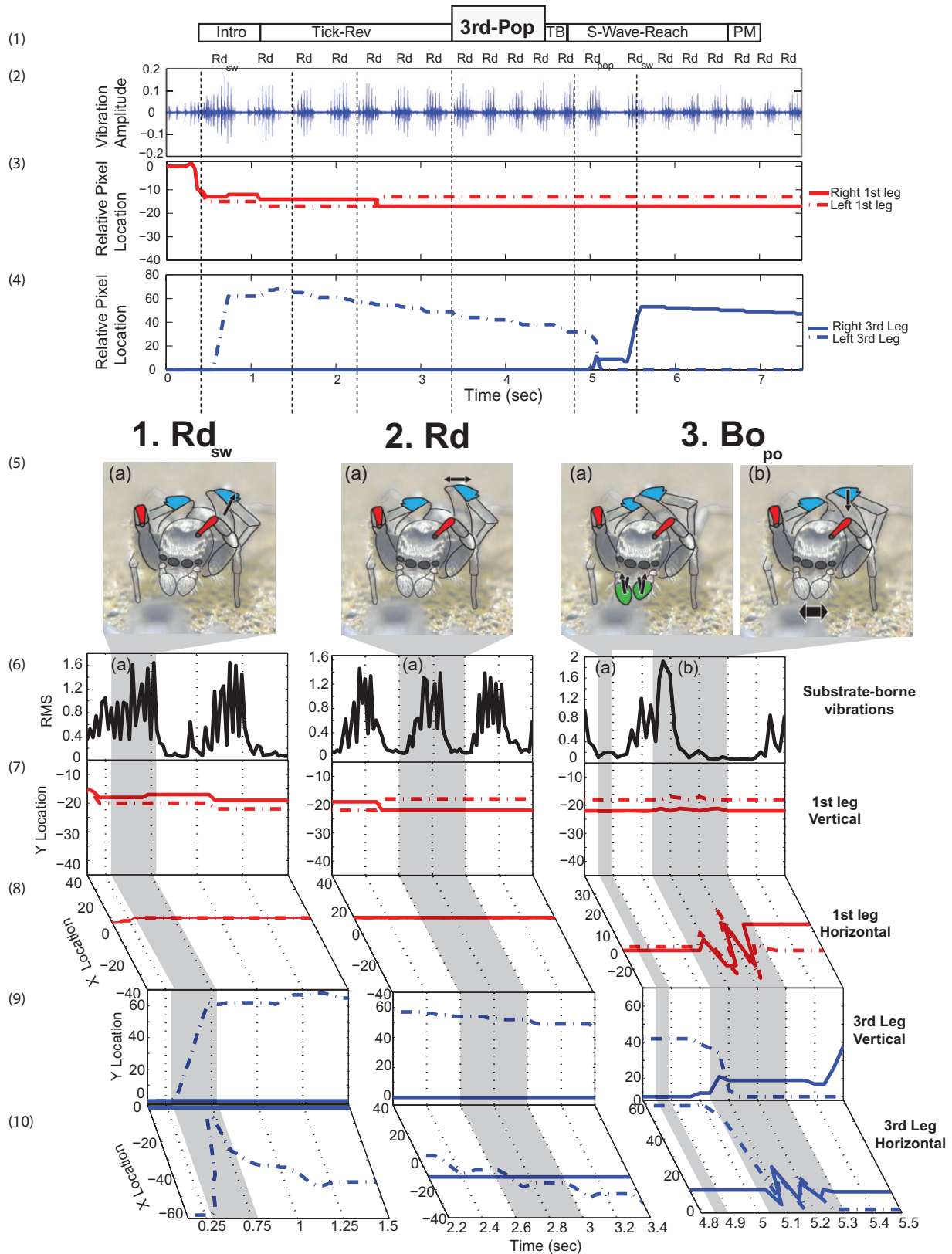
**Foreleg Wave Motif variation 4:** Ra((Wa<sub>lo</sub> Sf<sub>hi</sub>)\*\*(Wa<sub>0</sub> Sf<sub>hi</sub> Co<sub>si</sub>)\*\*)\*

Foreleg waves always began with a 3rd Leg Raise (Ra). 3rd Leg Raises began after an Rd display and consisted of the male’s 3rd leg that was close to the body being raised until it was on the same horizontal

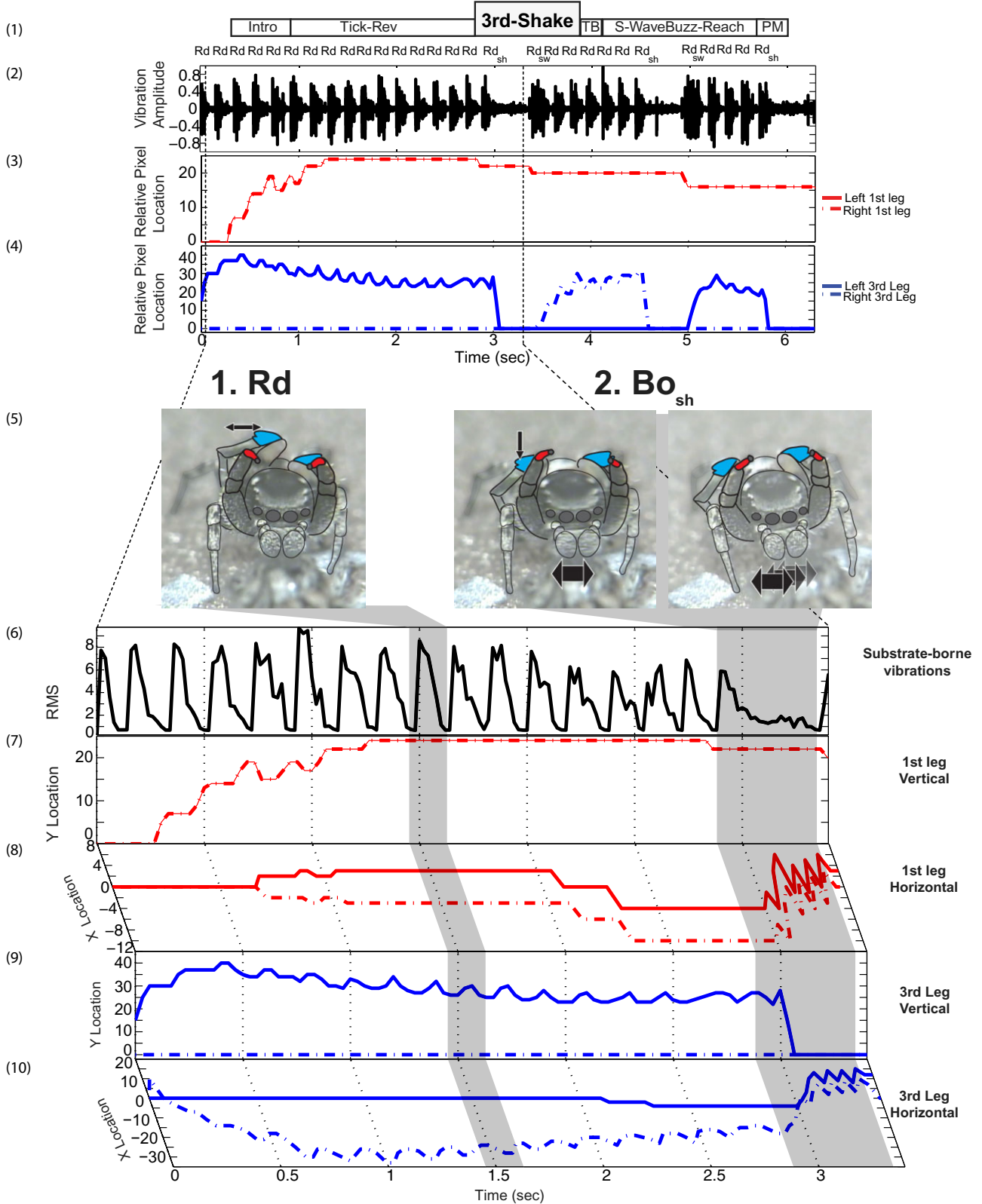
**Table 3.** 3rd Leg Motif

Species	Motif order
<i>Habronattus anepsius</i>	(Rd <sub>sw</sub> Rd*)*
<i>Habronattus borealis</i>	Simple Form: Rd* Complex Form: (Rd <sub>sw</sub> Rd*)* (Bo <sub>po</sub> Rd <sub>sw</sub> Rd*)*
<i>Habronattus brunneus</i>	Early movements: (Rd <sub>sw</sub> Rd* Rd <sub>sw</sub> )*
<i>Habronattus coecatus</i>	Late movements: (Rd <sub>sw</sub> Rd* Rd <sub>sw</sub> ) <sup>1</sup> (Rd* Bo <sub>sh</sub> Rd <sub>sw</sub> )*
<i>Habronattus cuspidatus</i>	Early movements: (Rd <sub>sw</sub> Rd*)* Late movements: Rd <sub>sw</sub> Rd* (Bo <sub>po</sub> Rd <sub>sw</sub> Rd*)*
<i>Habronattus festus</i>	Early movements: (Rd <sub>sw</sub> Rd*)* Late movements: (Rd <sub>sw</sub> Rd*)*Bo <sub>po</sub>
<i>Habronattus klauserii</i>	(Rd <sub>sw</sub> Rd*)*
<i>Habronattus mexicanus</i>	Early movements: (Rd <sub>sw</sub> Rd*)* Late movements: Rd <sub>sw</sub> Rd*(Bo <sub>sh</sub> Rd <sub>sw</sub> Rd*)*
<i>Habronattus pyrrithrix</i>	Early movements: (Rd <sub>sw</sub> Rd*)* Late movements: Rd <sub>sw</sub> Rd* (Bo <sub>po</sub> Rd <sub>sw</sub> Rd*)*
<i>Habronattus schlingerii</i>	Early movements: (Rd <sub>sw</sub> Rd*)* Late movements: Rd <sub>sw</sub> Rd* (Bo <sub>sh</sub> Rd <sub>sw</sub> Rd*)*
<i>Habronattus virgulatus</i>	Early movements: Rd <sub>sw</sub> Rd* (Bo <sub>po</sub> Rd <sub>sw</sub> Rd*)* Late movements: Rd <sub>sw</sub> Rd*(Bo <sub>po</sub> Rd*)*(Bo <sub>po</sub> Rd <sub>sw</sub> Rd <sup>4or5</sup> )**

plane as the raised leg. Both 3rd legs were positioned at their highest possible point with their patellas touching. Vibrations produced during this behaviour were virtually indistinguishable from vibrations produced during Rd<sub>sw</sub> displays and were variable (Fig. 8.1a). This posture was typical for all Foreleg Wave Motifs. After Ra displays, males produced a Waving display. Waving displays had three variations depending on the vibratory signals that co-occurred (or did not in one instance). The motion component of waving displays consisted of the male’s extended forelegs waved extremely fast, alternating the foreleg waved, typically in the range of 10–35 waves/s (Fig. 8.2a). Coupled with this motion was either (1) a low frequency, narrow band ‘hum’ (Wa<sub>lo</sub>; Fig. 8.2a; see also Supporting information, Table S6); (2) a higher frequency, broad band ‘buzz’ (Wa<sub>hi</sub>; Fig. 9.2a; see also Supporting information, Table S6), or (3) no vibrations (Wa<sub>0</sub>). In three species, *Habronattus festus*, *Habronattus klauserii*, and *H. schlingerii*, the



**Figure 5.** 3rd Leg Motif: 3rd – Pop variation. 3rd Leg Motifs consist of three of four possible display elements ( $Rd_{sw}$ ,  $Rd$ ,  $Bo_{po}$ ,  $Bo_{sh}$ ). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.



**Figure 6.** 3rd Leg Motif: 3rd – shake variation. 3rd Leg Motifs consist of three of four possible display elements (Rd<sub>sw</sub>, Rd, Bo<sub>po</sub>, Bo<sub>sh</sub>). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus brunneus*.

**Table 4.** Thump Burst Bridge

Species	Bridge
<i>Habronattus anepsius</i>	Fl <sup>2or3</sup>
<i>Habronattus borealis</i>	Simple Form: none Complex Form: Fl <sup>2</sup>
<i>Habronattus brunneus</i>	Fl <sup>3or4</sup>
<i>Habronattus coecatus</i>	Fl <sup>3</sup>
<i>Habronattus cuspidatus</i>	Fl <sup>3</sup>
<i>Habronattus festus</i>	Fl <sup>3</sup>
<i>Habronattus klauserii</i>	Fl <sup>4</sup>
<i>Habronattus mexicanus</i>	Fl <sup>3</sup>
<i>Habronattus pyrithrix</i>	Fl <sup>2</sup>
<i>Habronattus schlingerii</i>	Fl <sup>3</sup>
<i>Habronattus virgulatus</i>	Fl <sup>4</sup>

frequency of  $Wa_h$  changed in the display ( $Wa_{hi1}$  and  $Wa_{hi2}$ ). In the early portion of Foreleg Wave Motifs,  $Wa$  displays were followed by Short Side Flicks ( $Sf_{lo}$ ).  $Sf_{lo}$  were displays where the male's forelegs were moved horizontally away from his body (Fig. 8.3a) and then rapidly returned (Fig. 8.3b). In some species, the patellas of the 3rd legs were brought towards the body as the forelegs were moved away from the body (Fig. 9.3a). As the male's legs were returned to their initial position, males produced a high intensity, broadband 'thump' using their abdomen (Fig. 8.3a, b). As this early stage progressed, the separation between adjacent Sf pairs became increasingly longer as the tempo of the display slowed down (Figs 8, 9).

At later stages of  $Wa$  displays (Figs 10, 11), they were sometimes followed by Large Side Flicks ( $Sf_{hi}$ ).  $Sf_{hi}$  were displays where the male's forelegs were moved horizontally away from his body until the femur of his forelegs were almost parallel to the floor (Fig. 10.1a).  $Sf_{hi}$  motion components were produced concurrently with high intensity, broadband 'thumps' similar to  $Sf_{lo}$  displays, although they tended to be shorter in duration (Figs 10.1b, 11.2b; see also Supporting information, Table S6).  $Sf_{hi}$  were often followed by Contact (Co) displays. Co displays came in two varieties: Single Contact Lunges ( $Co_{si}$ ) and Multiple Contact Lunges ( $Co_{mu}$ ).  $Co_{si}$  displays consisted of one or two extremely rapid foreleg flicks, where the male arched one of his forelegs downwards towards the female, making contact with the female's legs, palps, or face. Concurrently with this flick, males produced a narrow band 'rev' (Figs 10.2a, 11.3a; see also Supporting information, Table S6). In one species (*H. schlingerii*),  $Co_s$  motions occurred at the beginning of  $Wa_{hi}$  vibrations and were virtually indistinguishable from  $Wa_{hi}$  vibrations. In some species, this rapid  $Co_{si}$  display was followed by a  $Co_{mu}$  display.  $Co_{mu}$  displays were much slower than  $Co_{si}$  displays and

occurred when the same foreleg that was used in  $Co_{si}$  display was waved in front of the female's face, often touching the ground directly in front of her. Concurrently with this  $Co_{mu}$  motion component, males produced a series of narrow band 'revs' (Fig. 10.3) that were lower in frequency than  $Co_{si}$  displays (see Supporting information, Table S6).

#### REPRISE BRIDGE

Reprise Bridges (RB) only occurred after Foreleg Wave Motifs and served to bridge these displays to Tick-Rev Motifs. In our scoring of displays, RBs served to end later display movements. RBs appeared to use a hodgepodge of elements from previous motifs with the addition of a Back Reset (Ba) display (Table 6). The typical order of a RB was:

**Reprise Bridge:**  $Ba^n$  ( $Rd_{sw}$  or  $Rd$  or  $Bo_{sh}$  or  $po$  or  $Ti^*$  Ev)  $Fl^x$  where  $x$  is an integer number

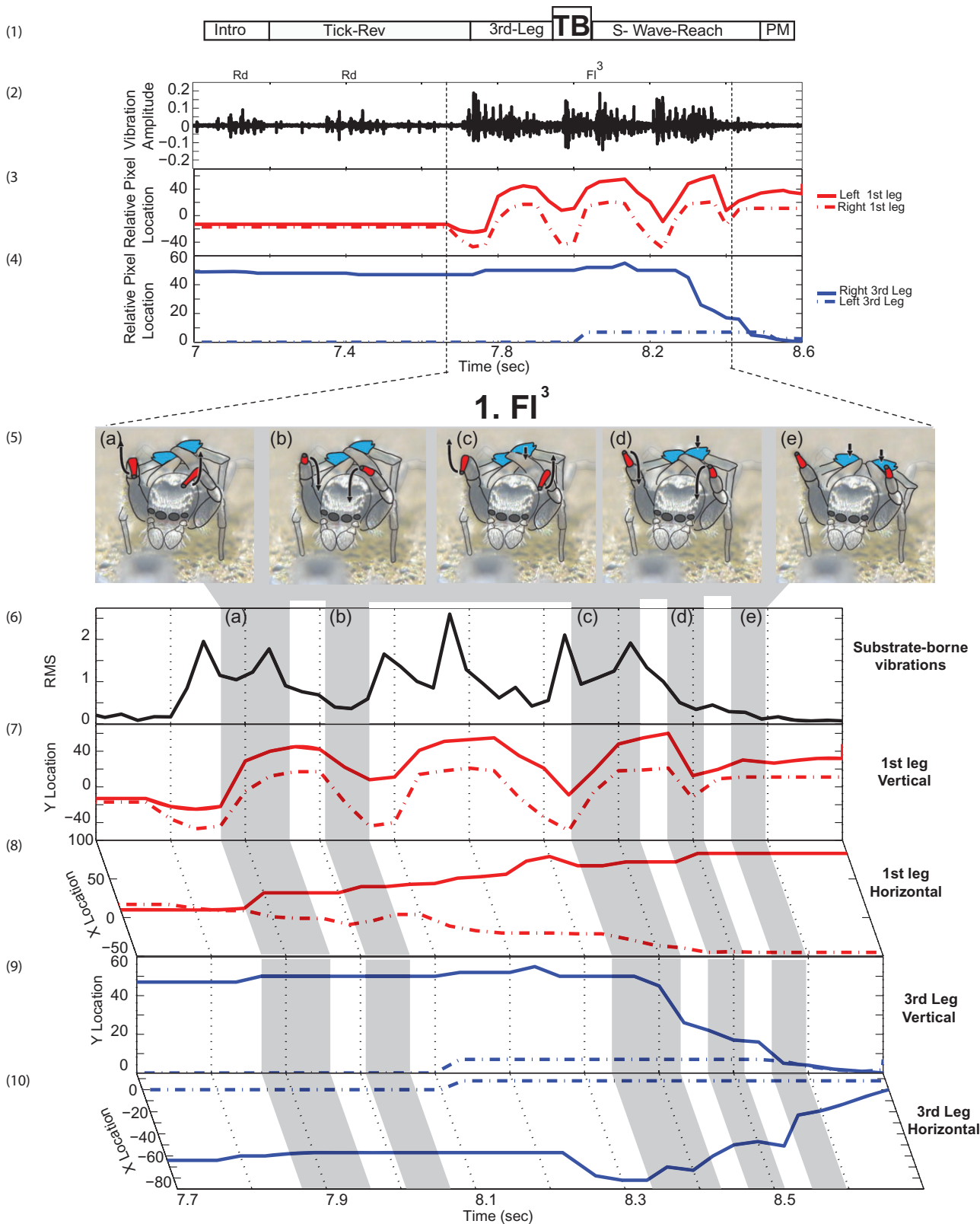
Reprise Bridges appeared to facilitate the switch from Foreleg Wave postures to 'typical' postures. From the Foreleg Wave posture (forelegs horizontally oriented just above the female), males produced a Back Reset (Ba) display. In Ba displays, the male's forelegs were raised upwards until his forelegs were once again positioned in an almost vertical position. During each backwards movement, a coordinated broad-band 'rev' was produced. After the forelegs were positioned, males produced a display that was previously produced in other motifs [either a 3rd leg switch ( $Rd_{sw}$ ), a Body Shake ( $Bo_{sh}$ ), a Body Pop ( $Bo_{po}$ ), or a Tick-Rev ( $Ti^*Ev$ )]. At the end of these displays, males produced a Thump Burst Bridge (TB), except in *H. borealis*. For some species, we did not record any RB displays. It was unclear whether these species did not produce this display or whether this was result of the absence of multiple Foreleg Wave Motifs.

#### PRE-MOUNT MOTIF (FIG. 12)

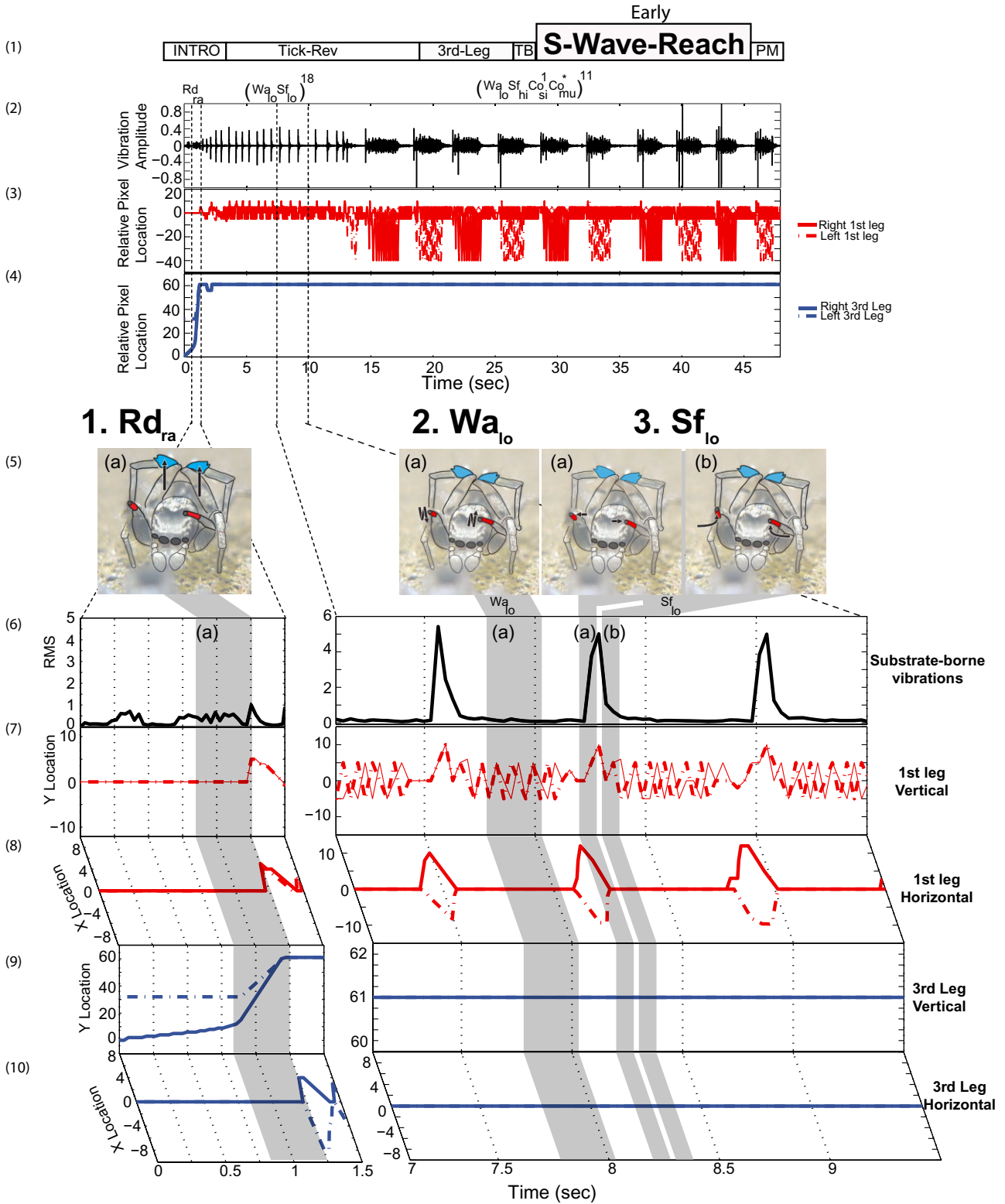
Pre-Mount Motifs were the finale of a display composition and occurred just before an attempted copulation (Table 7). Because we did not use live females, courtship recordings were terminated as soon as males attempted to copulate with females. In preliminary observations with live females, all *H. coecatus* group males produced a different set of vibrations during copulation (copulatory courtship). Pre-Mount Motifs included a single display element Pr with the general pattern:

**Pre-Mount Motif:**  $Pr^*$

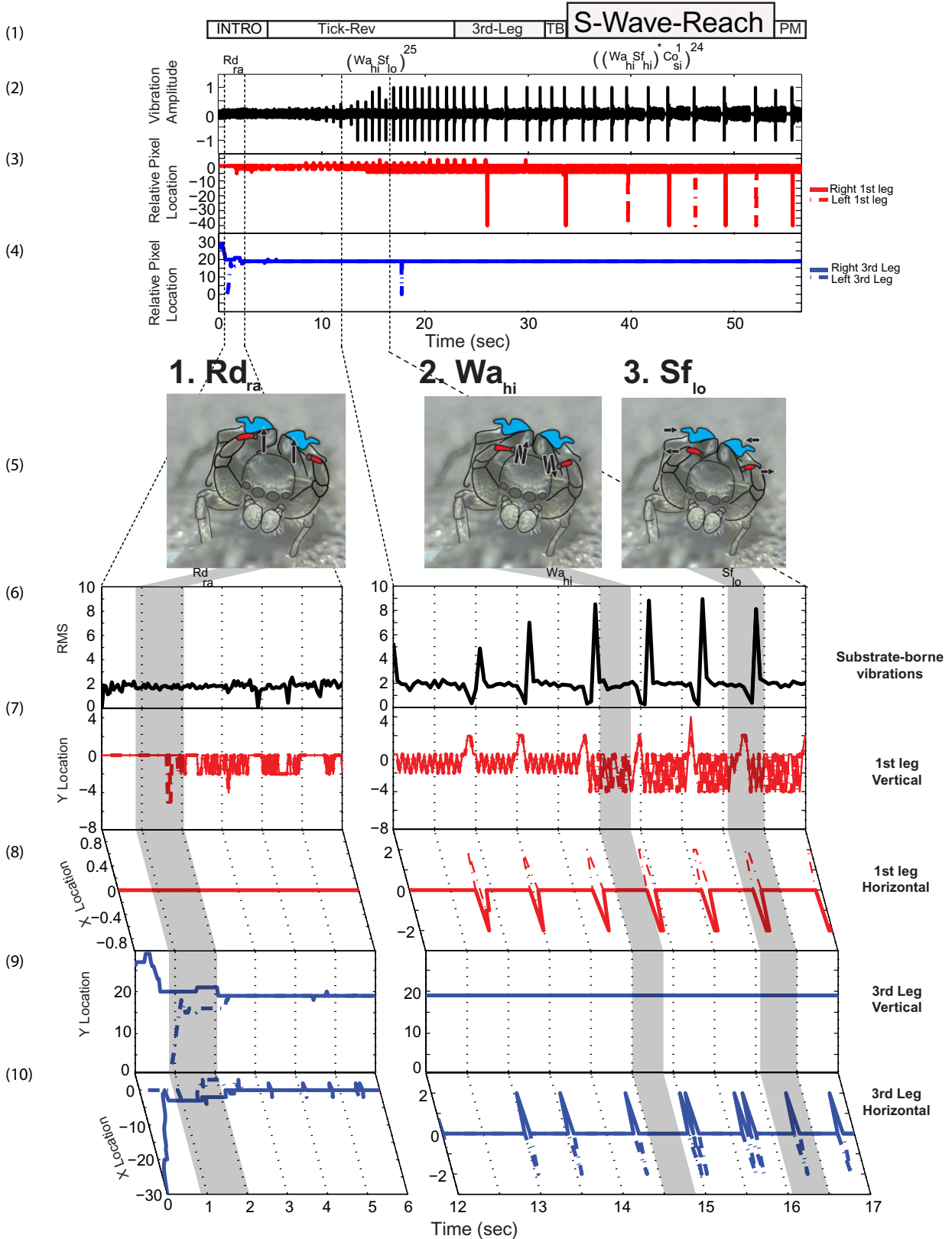
Pr displays followed Foreleg Wave Motifs and consisted of both motion and vibratory components. During Pr displays, a male arched his forelegs toward



**Figure 7.** Thump-Burst (TB) Bridge. TB displays bridge Tick-Rev Motifs with other Tick-Rev Motifs or 3rd Leg Motifs with Tick-Rev Motifs and consists of one repeated display element (F1). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.

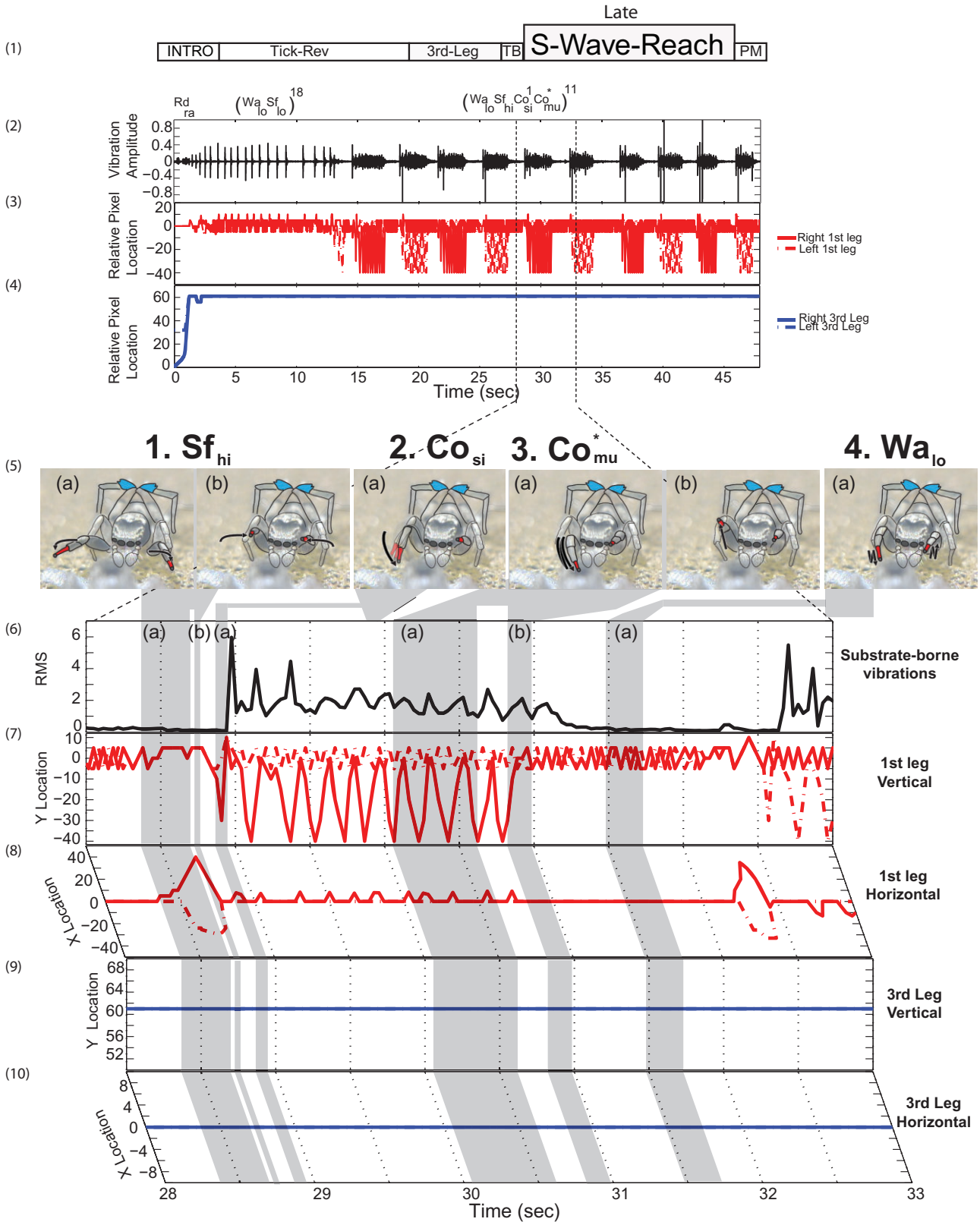


**Figure 8.** Early portion of Foreleg Wave Motif:  $Wa_{lo}$  variation. Early Foreleg Wave motifs consist of three of six possible display elements ( $Ra$ ,  $Sf_{lo}$ ,  $Sf_{hi}$ ,  $Wa_{lo}$ ,  $Wa_{hi}$ ,  $Wa_0$ ). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.

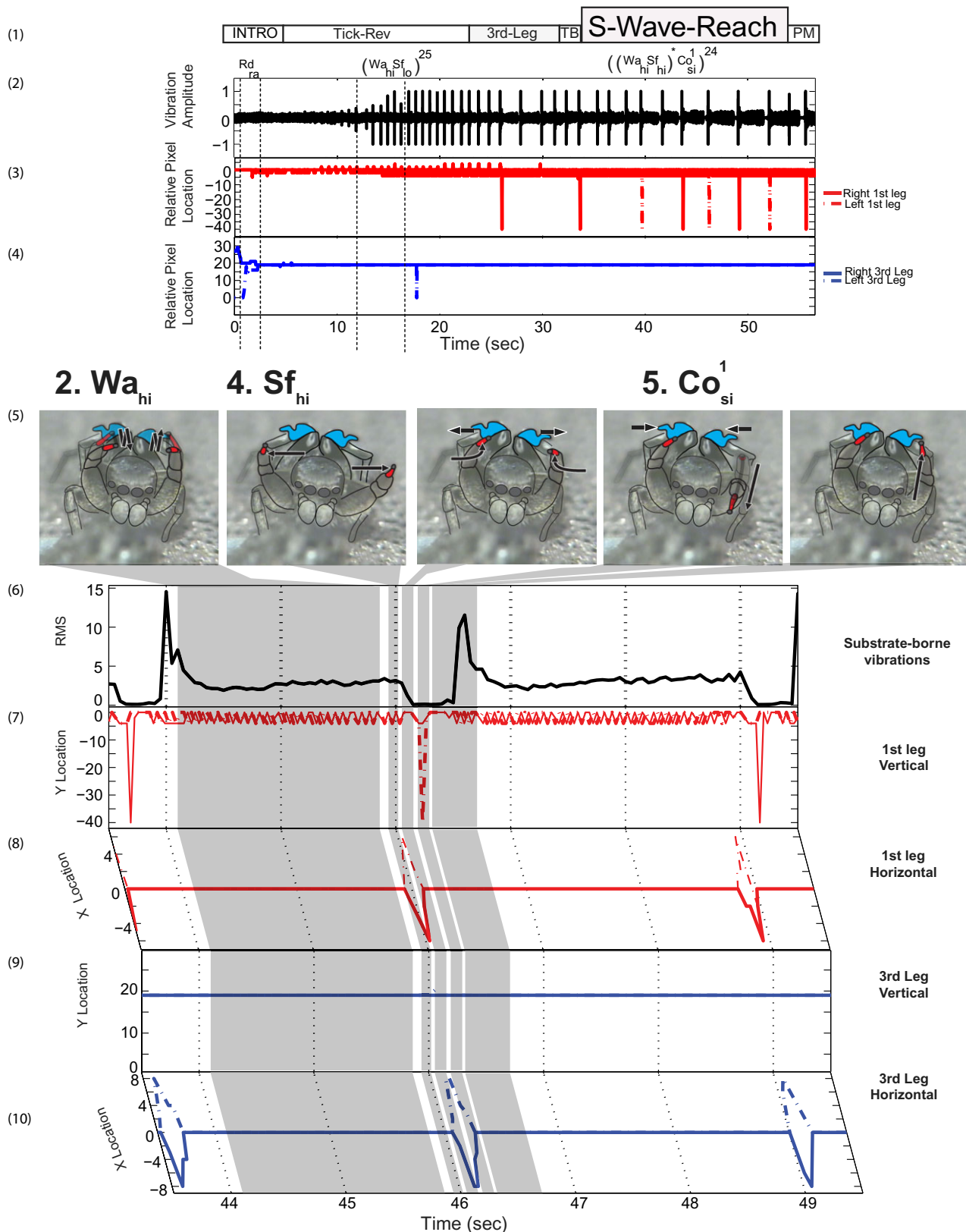


**Figure 9.** Early portion of Foreleg Wave Motif:  $Wa_{hi}$  variation. Early Foreleg Wave motifs consist of three of six possible display elements ( $Ra$ ,  $Sf_{lo}$ ,  $Sf_{hi}$ ,  $Wa_{lo}$ ,  $Wa_{hi}$ ,  $Wa_0$ ). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus schlingerii*.





**Figure 10.** Late portion of Foreleg Wave Motif:  $Co_{si} - Co_{mu}$  variation. Late Foreleg Wave motifs consist of three to four of nine possible display elements ( $Sf_{lo1}$ ,  $Sf_{lo2}$ ,  $Sf_{hi}$ ,  $Wa_{lo}$ ,  $Wa_{hi1}$ ,  $Wa_{hi2}$ ,  $Wa_o$ ,  $Co_{si}$ ,  $Co_{mu}$ ). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.



**Figure 11.** Late portion of Foreleg Wave Motif:  $Co_{si}$  alone variation. Late Foreleg Wave Motifs consist of three to four of nine possible display elements ( $Sf_{lo1}$ ,  $Sf_{lo2}$ ,  $Sf_{hi}$ ,  $Wa_{lo}$ ,  $Wa_{hi1}$ ,  $Wa_{hi2}$ ,  $Wa_0$ ,  $Co_{si}$ ,  $Co_{mu}$ ). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus schlingerii*.

**Table 5.** Foreleg Wave Motif

Species	Motif order
<i>Habronattus anepsius</i>	Ra (Wa <sub>1</sub> Sf <sub>1</sub> )*((Wa <sub>1</sub> Sf <sub>h</sub> Wa <sub>1</sub> Sf <sub>h</sub> Co <sub>s</sub> Co <sub>m</sub> <sup>1</sup> (Wa <sub>1</sub> Sf <sub>h</sub> )*)
<i>Habronattus borealis</i>	Simple Form: none *Complex Form: (Wa <sub>0</sub> Sf <sub>h</sub> ** Co <sub>s</sub> Co <sub>m</sub> *)*
<i>Habronattus brunneus</i>	Ra (Wa <sub>1</sub> Sf <sub>1</sub> ) <sup>1</sup> (Wa <sub>1</sub> Sf <sub>h</sub> Co <sub>m</sub> ) <sup>1</sup> (Wa <sub>1</sub> Sf <sub>1</sub> ) <sup>1</sup>
<i>Habronattus coecatus</i>	Ra (Wa <sub>0</sub> Sf <sub>h</sub> )**(Wa <sub>0</sub> Sf <sub>h</sub> Co <sub>s</sub> Co <sub>m</sub> *)**
<i>Habronattus cuspidatus</i>	Ra(Wa <sub>h</sub> Sf <sub>1</sub> )** ((Sf <sub>h</sub> Wa <sub>1</sub> )* (Sf <sub>h</sub> Co <sub>s</sub> <sup>2</sup> Wa <sub>1</sub> )**)*
<i>Habronattus festus</i>	Ra (Wa <sub>h1</sub> Sf <sub>1</sub> )***(Wa <sub>h2</sub> Sf <sub>1</sub> )* (Wa <sub>h2</sub> Sf <sub>h</sub> Co <sub>s</sub> )**
<i>Habronattus klauserii</i>	†(Wa <sub>h</sub> Sf <sub>11</sub> )***(Wa <sub>h</sub> Sf <sub>12</sub> )* (Wa <sub>h</sub> Sf <sub>12</sub> Co <sub>s</sub> <sup>2</sup> )***
<i>Habronattus mexicanus</i>	Ra ((Wa <sub>h</sub> Sf <sub>h</sub> )** (Wa <sub>h</sub> Sf <sub>h</sub> Co <sub>s</sub> Co <sub>m</sub> *Wa <sub>1</sub> )*)*
<i>Habronattus pyrrithrix</i>	Ra (Wa <sub>1</sub> Sf <sub>h</sub> )* (Wa <sub>1</sub> Sf <sub>h</sub> Co <sub>s</sub> Co <sub>m</sub> *)*
<i>Habronattus schlingerii</i>	Ra ((Wa <sub>h</sub> Sf <sub>1</sub> )** ((Wa <sub>1</sub> Sf <sub>h</sub> )** (Wa <sub>1</sub> Sf <sub>h</sub> Co <sub>s</sub> )**)***
<i>Habronattus virgulatus</i>	Ra (Wa <sub>0</sub> Sf <sub>h</sub> )**(Wa <sub>0</sub> Sf <sub>h</sub> Wa <sub>0</sub> Co <sub>s</sub> )**

\*Co<sub>m</sub> for *H. borealis* has no vibratory component. †*H. klauserii* has no Ra display; instead 3rd legs get raised gradually during the Wa<sub>h</sub> display. First of Co<sub>s</sub> pair contains percussive component and tends to be lower in peak frequency.

**Table 6.** Reprise Bridge

Species	Bridge order
<i>Habronattus anepsius</i>	Ba <sup>1or2</sup> Bo <sub>sh</sub> Rd* Fl <sup>2</sup>
<i>Habronattus borealis</i>	Simple Form: none Complex Form: Ba Bo <sub>po</sub> Rv*
<i>Habronattus brunneus</i>	Ba Rd <sub>sw</sub> Fl <sup>3</sup>
* <i>Habronattus coecatus</i>	n/a
<i>Habronattus cuspidatus</i>	Ba <sup>2</sup> Ev <sub>Wah</sub> * Rd* Fl <sup>3or4</sup>
<i>Habronattus festus</i>	Ba <sup>2</sup> Ev* Fl <sup>3</sup>
<i>Habronattus klauserii</i>	BaFl <sup>2or3</sup>
<i>Habronattus mexicanus</i>	Ba Ti* Ev Fl <sup>2or3</sup>
<i>Habronattus pyrrithrix</i>	Ba Ti* Ev Fl <sup>2</sup> Ba Ti* Ev Rd* Bo <sub>po</sub>
<i>Habronattus schlingerii</i>	Ba Ev Rd Fl <sup>2or3</sup>
<i>Habronattus virgulatus</i>	Ba <sup>4</sup> Fl <sup>5</sup>

\*Ev<sub>Wah</sub> = Ev followed by vibratory component *alone* of Wa<sub>h</sub>.

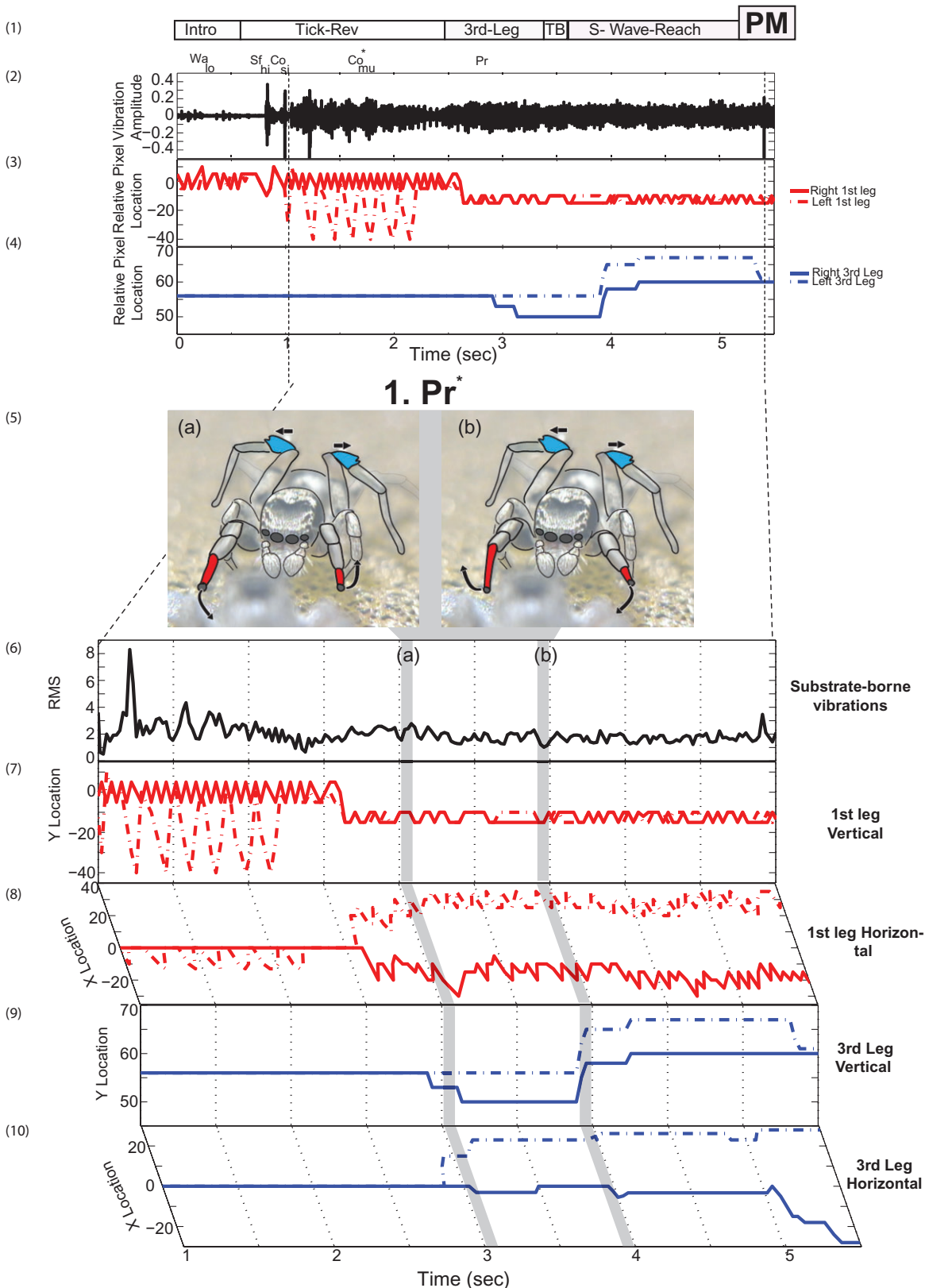
**Table 7.** Pre-Mount Motif

Species	Bridge
<i>Habronattus anepsius</i>	Pr*
<i>Habronattus borealis</i>	Simple Form: Pr* Complex Form: Pr*
<i>Habronattus brunneus</i>	Pr*
<i>Habronattus coecatus</i>	Pr*
<i>Habronattus cuspidatus</i>	Pr*
<i>Habronattus festus</i>	Pr*
<i>Habronattus klauserii</i>	Pr*
<i>Habronattus mexicanus</i>	Pr*
<i>Habronattus pyrrithrix</i>	Pr*
<i>Habronattus schlingerii</i>	Pr*
<i>Habronattus virgulatus</i>	Pr*

the female, twisting his foreleg tips towards and then away from the female. The forelegs alternated so that one foreleg was twisting towards the female, whereas the other was twisting away (Fig. 12). During these movements, males also moved their 3rd legs horizontally away from their body. Vibratory components were produced continuously in a Pre-Mount Motif, and consisted of high frequency 'buzzing' (see Supporting information, Table S8). In our scoring of components, a Pre-Mount Motif was the concluding movement (Fig. 12).

#### DISPLAY OF *H. BOREALIS*

Ten of the species observed shared the same progression of movements (some species did not include RBs; see above), although details such as the numbers of repetitions of elements and motifs, the exact paths of motions, the fine structure of vibratory signals, and the elements used in each motif differed (Table 8; see also Supporting information, Tables S2–S8). Three additional species for which we have partial data, likewise show the same overall sequence of visual elements (Table S1). *H. borealis*, however, stood out for several reasons. First, *H. borealis*, unlike other members of the species group, is drab and lacks the extensive ornamentation on the first and third legs that characterizes the group (Fig. 13). Because the complex ornaments of the group were lacking, and *H. borealis* falls phylogenetically within the larger clade with modified first and third legs (Maddison & Hedin, 2003), *H. borealis* displays are likely an example of evolutionary loss of display complexity. Second, unlike other *H. coecatus* group members where motifs are generally stereotyped, for *H. borealis*, it is variable. Maddison & Stratton (1988a) described briefly a complex display in specimens from Ontario; Richman & Cutler (1998) described a simple display in specimens from Kansas. In order to under-



**Figure 12.** Pre-Mount (Pr) Motif. Pr Motifs consist of one display element (Pr). For an explanation of figure organization, see Fig. 3. Display quantified from *Habronattus coecatus*.

**Table 8.** Element summary

Motif	Elements
Tick-Rev Motif	<b>Ti (10/11 species):</b> <i>anepsius</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Ev (11/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i>
3rd Leg Motif	<b>Rd<sub>sw</sub> (11/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Rd (11/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Bo<sub>po</sub> (4/11 species):</b> <i>borealis</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>virgulatus</i> <b>Bo<sub>sh</sub> (5/11 species):</b> <i>anepsius</i> , <i>brunneus</i> , <i>festus</i> , <i>mexicanus</i> , <i>schlingerii</i>
TB Bridge	<b>F1 (11/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i>
Foreleg Wave Motif	<b>Ra (9/11 species):</b> <i>anepsius</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Wa<sub>0</sub> (8/11 species):</b> <i>anepsius</i> , <i>brunneus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> <b>Wa<sub>hi</sub> (5/11 species):</b> <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>schlingerii</i> , <b>Wa<sub>0</sub> (2/11 species):</b> <i>coecatus</i> , <i>virgulatus</i> <b>Sf<sub>0</sub> (6/11 species):</b> <i>anepsius</i> , <i>brunneus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>schlingerii</i> <b>Sf<sub>hi</sub> (11/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Co<sub>si</sub> (10/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>coecatus</i> , <i>cuspidatus</i> , <i>festus</i> , <i>klauserii</i> , <i>mexicanus</i> , <i>pyrrithrix</i> , <i>schlingerii</i> , <i>virgulatus</i> <b>Co<sub>mu</sub> (6/11 species):</b> <i>anepsius</i> , <i>borealis</i> , <i>brunneus</i> , <i>coecatus</i> , <i>mexicanus</i> , <i>pyrrithrix</i>

stand this variation, we extensively recorded displays from individuals in one population in Ontario ( $N = 46$ ) and on a subset of these individuals ( $N = 25$ ) we recorded two courtship displays from the same individual separated by 2 weeks. No morphological differences are evident between Ontario and Kansas populations. Errors in the recording procedure prevented us from quantifying courtship length in 3 recordings, although data on display behaviour was noted.

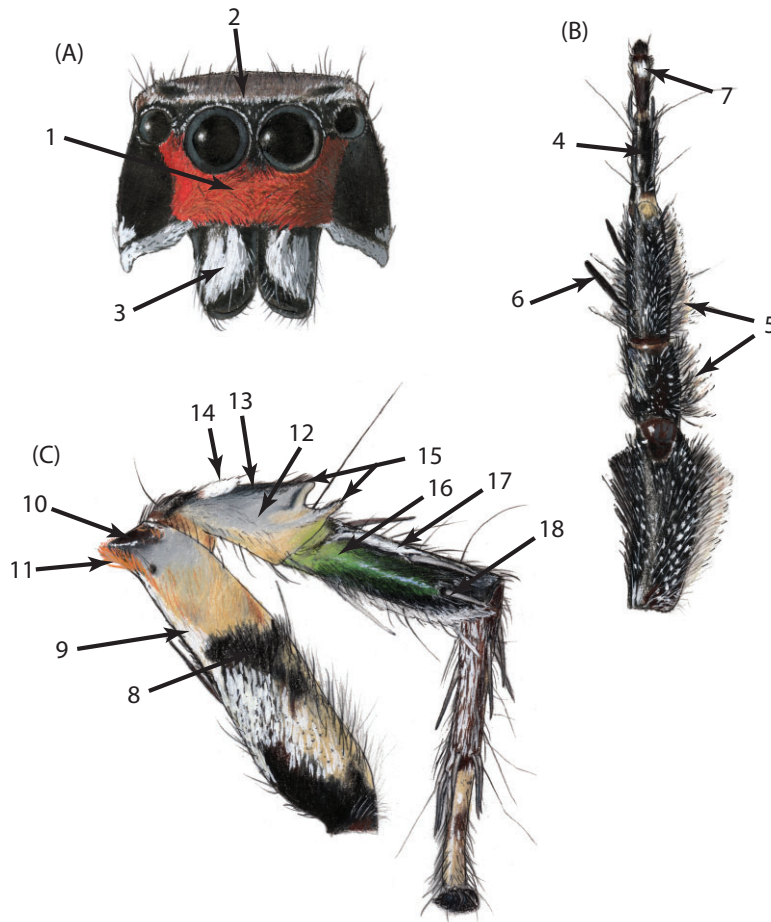
*Habronattus borealis* displays fell into two categories: (1) simple display compositions which were short ( $34.6 \pm 22.2$  s, range 14–80,  $N = 30$ ) and consisted of very few signal elements ( $3.07 \pm 0.27$  display elements; range 3–4,  $N = 30$ ) and (2) complex display compositions which were longer ( $296.8 \pm 311$  s, range 90–370 s,  $N = 13$ ) and consisted of more signal elements ( $5.4 \pm 0.8$  display elements; range 5–7 elements,  $N = 16$ ). Of the 46 individuals observed, most used simple display compositions in their first courtship recordings (30/46). For the majority of simple display compositions (77%; 23/30), males performed Ou displays (Introductory Motif) and then proceeded directly to Pr displays (Pre-Mount Motif). In the remaining seven displays, males included a second motif that consisted of a single courtship display

element (3/30 included Sf<sub>0</sub>; 2/30 included Rd; 1/30 included Wa<sub>0</sub> wave). Only 29% of individuals used complex compositions in their first display. Of the 16 individuals that produced complex display compositions, 51% used Ou, Ev, Rd, and Pr display elements; 39% used Ou, Ev, Rd, Sf, Co<sub>m</sub>, and Pr displays; and 3% used all possible *H. borealis* display elements (Ou, Ev, Rd, Wa<sub>0</sub>, Sf, Co<sub>m</sub>, Pr).

To determine whether males maintain the same courtship elements in Ontario populations, we recorded the same individuals after a 2-week period ( $N = 24$ ). Of the males who had a complex courtship during the first trial, five remained complex and only one transitioned to a simple display composition. Of the males who had simple courtship during the first trial, 11 remained simple and seven transitioned to a complex display composition. Statistical analysis using McNemar's test for frequency of changes indicates no differences between switching and nonswitching rates ( $P = 0.221$ ), suggesting that males switch randomly between courtship types.

#### MORPHOLOGICAL ORNAMENTATION (FIG. 13)

We did not attempt to characterize fully the complexity of morphological structures involved with



**Figure 13.** *Habronattus coecatus* ornament diversity. Numbers represent distinct ornaments that are restricted to males and on body parts that are moved and visible to females during courtship. (A) *H. coecatus* face (B) *H. coecatus* 1st pair of legs. (C) *H. coecatus* 3rd pair of legs. The vast majority of *H. coecatus* group members are elaborately ornamented. Drawings by Wayne P. Maddison.

courtship, although a brief description of those found in *H. coecatus* (Fig. 13) shows how multifarious male ornamentation is in this species group. If we define an ornament as a morphological structure or colour pattern that is restricted to males and on body parts that are moved or visible to the female during courtship, then a male *H. coecatus* has 18 ornaments: (1) clypeus covered with bright red setae; (2) lateral stripes on carapace above the eyes; (3) chelicerae with a large distinct white spot (Fig. 13A); first leg (4) black beneath, with (5) lateral fringe of long setae, many with expanded white tips; (6) first tibia with spatulate macrosetae; (7) first tarsus with white spot below (Fig. 13B); (8) third femur with black bar centrally, (9) pale area distally, (10) prolonged into corner distally, and (11) with patch of orange setae distally; third patella (12) pale grey, with (13) black dorsal ridge, (14) white patch dorsobasally, and (15) two spurs dis-

tally; third tibia (16) green, with (17) ridge of white setae and (18) white macrosetae (Fig. 13C). Although the developmental biology of spiders is not well understood, it is likely that many independent genes are involved in these traits. Except in *H. borealis*, this type of ornamental complexity (ornamented face, fringed first leg, modified third leg) is generally consistent across the species group, with the species differing in colours and detailed shapes of the particular ornaments.

## DISCUSSION

In the present study, we show that *H. coecatus* group sexual displays are some of the most elaborate in the animal kingdom. Their displays combine intricate ornamentation with multicomponent substrate-borne vibrations and coordinated dances. Even in the most austere terms, one can say that their multimodal

displays are complex because some species have up to 18 ornaments (body segments with distinct coloured, patterned or formed structures; Fig. 13), a plethora of motions of various appendages (Figs 3, 4, 5, 6, 7, 8, 9, 10, 11, 12), and up to 20 distinct vibratory signals (Table 8). Displays in the *H. coecatus* group, however, cannot be described in simple terms because the entire display changes through time as males add new signal types and new signal combinations. In addition, the overall structure and tempo of the displays changes through time in an organized progression of element combinations (motifs), within which individual males may vary the duration and number of element repetitions. This temporal structuring of displays is more analogous to a musical composition than to language syntax; hence, our choice of nomenclature for display descriptions. Complex displays are a characteristic of the genus *Habronattus* (Griswold, 1987; Cutler, 1988; Maddison & Stratton, 1988b; Maddison & McMahon, 2000; Masta, 2000; Elias *et al.*, 2003, 2005, 2006c, d) and members of the *H. coecatus* group are the *maestros* of the genus. Understanding the patterns that led to evolution of such highly complex displays is a challenge.

In the *H. coecatus* group, one of the most unexpected observations is that the complex ornamentation of the group finds an equal counterpart in vibratory and motion displays. This appears to be at odds with prevailing ideas on multiple signal evolution (Moller & Pomiankowski, 1993; Pomiankowski & Iwasa, 1993, 1998; Iwasa & Pomiankowski, 1994; Johnstone, 1996). Theoretical work on signal evolution has suggested that, if signals are costly, multiple signals are unlikely to evolve and that females should prefer single indicators of quality (Moller & Pomiankowski, 1993; Pomiankowski & Iwasa, 1993, 1998; Iwasa & Pomiankowski, 1994; Johnstone, 1996). Simple signals are predicted to be more reliable indicators of mate quality and more likely targets of female choice (Schluter & Price, 1993; Iwasa & Pomiankowski, 1994), although this is not always the case in non-equilibrium conditions (van Doorn & Weissing, 2004). Furthermore, theoretical work on processing mechanisms in animals has suggested that information in signals only increases up to a point after which the value of any new information precipitously drops off (Ay, Flack & Krakauer, 2007). Under these conditions, an upper limit on the complexity of sexual displays is predicted (Krakauer & Nowak, 1999; Ay *et al.*, 2007).

Another unexpected observation is that there is molecular evidence for genetic introgression throughout *Habronattus*. Phylogenetic data points specifically to the *H. coecatus* group, including species examined in the preset study, as being involved in hybridization with other species groups (Maddison & Hedin, 2003).

Maddison & Hedin (2003) suggested that this puzzle (i.e. distant hybridization concentrated in a group with complex courtship) might be explained by a process of antagonistic coevolution driving the evolution of novel exploitative male traits (and subsequent female resistance; Holland & Rice, 1998). Complexity of *H. coecatus* group displays may be indicative of an active arms race, with females susceptible to intense novel signals, and therefore also to displays of other distantly related species. In one *Habronattus* species group (the *Habronattus pugillis* group), it has been suggested that sexual selection is driving diversification (Maddison & McMahon, 2000; Masta, 2000; Masta & Maddison, 2002; Hebets & Maddison, 2005). Interestingly, however, females of one population prefer males from foreign populations (Hebets & Maddison, 2005) whose displays have additional vibratory elements (Elias *et al.*, 2006a). Such xenophilia may have, during times of population contact, promoted hybridization. In a study on the *amicus*-species group, multiple lines of evidence demonstrated genetic introgression between two of the species: *Habronattus amicus* and *Habronattus ustulatus* (Hedin & Lowder, 2009). It was suggested that introgression occurred in only one direction, with *H. amicus* females mating with *H. ustulatus* males (Hedin & Lowder, 2009). *Habronattus ustulatus* male courtship includes elements lacking in *H. amicus* (D. O. Elias, unpubl. observ.). In both the *pugillis* and *amicus* groups, novel elements in male displays may, by exploiting naive female susceptibilities, promote hybridization in a particular direction. Alternatively, this pattern of hybridization may be promoted by a direct female preference for complex and/or novel display elements. In this scenario, females prefer males with more complex signalling repertoires, potentially as a signal of overall rigour (Byers, Hebets & Podos, 2010). New signalling elements gained through introgression could then be incorporated into the existing signalling repertoire over evolutionary time. Preferences for repertoire size have been studied extensively in bird song and are considered to be a major factor driving signal evolution (Searcy, 1992; Catchpole & Slater, 1995). The likelihood of making mating mistakes as a result of preferences for new display traits may also lead to the rapid de-evolution of complex displays, as is seen in *H. borealis* and in other species groups (D. O. Elias and W. P. Maddison, unpubl. observ.). Although we cannot currently test these two hypotheses, future work will explore these scenarios across the genus.

Although jumping spiders have long been held as one of the quintessential examples of visual displays in arthropods (Forster, 1982b; Jackson & Pollard, 1997; Land & Nilsson, 2002), we are now beginning to understand what we have overlooked in the past.

Courtship in many jumping spider groups is more complex than once assumed and includes colours and vibrations imperceptible to human observers without the aid of specialized technologies (Uhl & Elias, 2011). For systems such as the *H. coecatus* group, it will be important to not only understand how females utilize information in signals, but also why the group has evolved such multifaceted displays. Understanding the function and evolution of signals for a variety of species that differ in the complexity of their communication displays could be a window into general principals driving species evolution, as well as how nervous systems and decision-making processes are organized.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Table S1.** Additional *coecatus* group observations.
- Table S2.** Signal Properties for Intro Motif.
- Table S3.** Signal Properties for Tick-Rev Motifs.
- Table S4.** Signal Properties for 3rd Leg Motifs.
- Table S5.** Signal Properties for Thump Burst Bridge (TB).
- Table S6.** Signal Properties for Foreleg Wave Motifs (S-Wave-Reach).
- Table S7.** Signal Properties for Reprise Bridge (RB).
- Table S8.** Signal Properties for Pre-Mount Motif.
- Doc. S1.** Collection locales for all *Habronattus coecatus* group species.

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