Communicating male size by tremulatory vibration in a Columbian rainforest katydid, *Gnathoclita sodalis* (Orthoptera, Tettigoniidae)

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Summary

In the South American rainforest katydid *Gnathoclita sodalis* (Orthoptera, Tettigonidae), bouts of acoustic (airborne) and vibratory (substrate-borne) signals occur in the context of male agonistic interactions. We characterized the physical form for both sound and substrate signals and evaluated their role in male–male interactions. In a tournament design larger males retained sites against smaller opponents: the probability of winning was predicted by both male size and the incidence of tremulating vibrations. Substrate signaling by long-bodied rainforest katydids is a widespread and important modality of communication which embraces both female attraction and male rivalry.

Keywords: acoustic, communication, katydid, aggression, tremulation, vibration.

1. Introduction

Two mechanical modalities convey signals between katydids (Orthoptera, Tettigoniidae): airborne sound (Gerhardt & Huber, 2002) and plant-borne vibration (Virant-Doberlet & Cokl, 2004; Cocroft & Rodriguez, 2005). Most

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katydids live on plants rather than the ground, and can be expected to have evolved extensive use of plant-borne vibrations.

Katydid females respond to the physical structure of airborne sounds (calls/songs) made by males, choosing which song to approach (e.g., *Tettigonia* spp.; Schul, 1998). They also respond to plant-borne substrate signals generated by tremulation (to tremulate an insect oscillates its abdomen, usually without percussion, imparting vibrations to plant-perch substrates through its feet (Busnel et al., 1956; Morris, 1980)). In the katydid *Conocephalus nigropleurum* females choose to approach tremulatory vibrations with repetition rates indicating larger males (Deluca & Morris, 1998) (the effectiveness of tremulation in evoking katydid vibrotaxis was first demonstrated for *Ephippiger* sp. by Busnel et al., 1955, 1956).

Tremulation is reported in many animals (Virant-Doberlet & Cokl, 2004; Elias et al., 2008; Caldwell et al., 2010). It occurs in katydids, especially within the Conocephalinae and Pseudophyllinae (Morris, 1971, 1980; Belwood & Morris, 1987; Morris et al., 1994; Romer, 2010) in exchange between male and female and as a male calling signal, i.e., generated endogenously by a male in the absence of any conspecifics (Belwood & Morris, 1987). Despite its prevalence tremulation is poorly studied. There is no previous instance of experimentation among katydids into the role of tremulatory vibration in the context of male–male agonistic interaction (Simmons & Bailey, 1993 showed that the incidental vibrations accompanying stridulation in *Kawanaphila navtee* are effective in mediating male interactions).

Gnathoclita sodalis (Brunner v. Wattenwyl, 1895) is a rarely found false-leaf katydid (Pseudophyllinae) with vivid yellow and green markings (Figure 1), native to premontane rainforest in southern Colombia. Males produce an audible calling song at night (Montealegre & Morris, 1999). The species exhibits sexual dimorphism (Montealegre & Morris, 1999) and is now discovered to tremulate. We had access to a number of living specimens transported from South America. The males were observed to exchange both airborne sound and tremulatory vibratory signals. An experiment was designed to study the role of sound and vibration in relation to body size in this species.

Asymmetry in body size figures commonly in the resolution of animal fights (Arnott & Elwood, 2009). Among Orthoptera, in the Texas field cricket, *Gryllus integer*, heavier males are more likely to win aggressive contests when matched with lightweight males (Dixon & Cade, 1986). Males of the cricket *Gryllus pennsylvanicus* win fights in proportion to their larger

Figure 1. Male of *G. sodalis* (lower) gripped by the female's genitalia, mating at night in the field near Bitaco in Colombia. The insects are flightless, with reduced forewings that function only in male stridulation. Photo by Dita Klimas. This figure is published in colour in the online edition of this journal, which can be accessed via http://www.brill.nl/beh

heads, maxillae and mandibles (Judge & Bonanno, 2008). Among Wellington tree weta, head size predicts fight outcomes and retention of resources (Kelly, 2006). Time-domain components of airborne sound in the aggressive calls made during fighting between males of *Acheta domesticus*, correlate with body size and predict fight outcomes (Brown et al., 2006), but size is not always implicated: in fights between orthopterans, among *Cyphoderris mon-*

strosa males (insects related to crickets and katydids; Mason, 1996) winning was uncorrelated with body size and related instead to calling duty cycle.

We describe the physical form of the substrate-borne vibratory signal exchanged between males. Using staged male–male encounters in a tournament model, we test the hypothesis that sound, vibration and size are involved in determining the probability of agonistic outcomes. To our knowledge, no previous study has demonstrated a role for tremulatory vibratory signals in agonistic interactions between male katydids. We also improve the sample size for measures of physical parameters of the acoustic signal of this species.

2. Materials and methods

The following terms are used to describe sound signal parameters: Chirp (call) period (Figure 2A), time measured from the start of a chirp to the

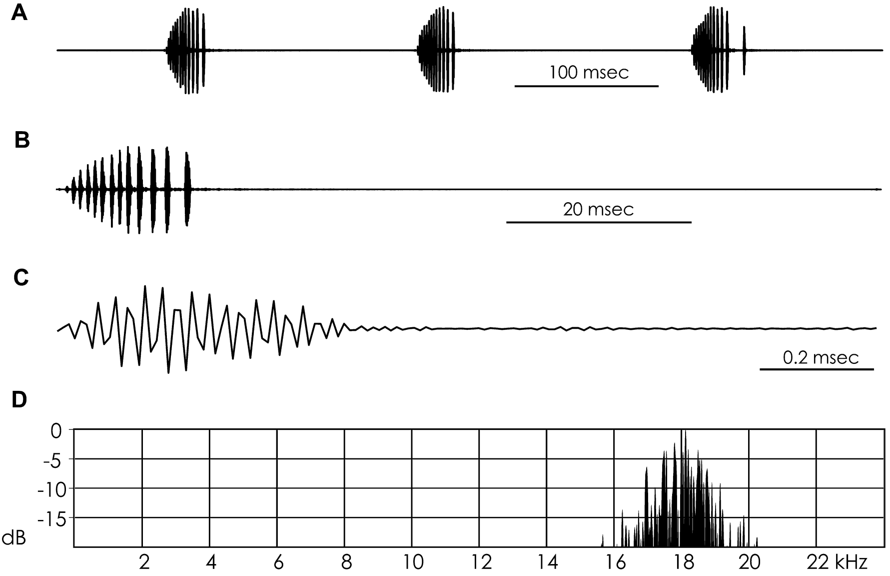

Figure 2. Song of *G. sodalis*. (A) Three successive chirps (zips). (B) Single chirp at higher time resolution comprised of a train or series of sinusoidal pulses. (C) Single pulse at high resolution; the insect's pulse is actually quite sinusoidal; its jagged appearance here is an effect of nearing the limits of an adequate sampling rate: in digitizing a sound, at least 2 points must be calculated per the shortest wavelength of interest (Nyquist theorem, see Materials and Methods). (D) Power spectrum of a single chirp: the width of the frequency band (20 dB down) is 15.6–20.3 kHz. Peak centres at 18 kHz.

start of the next chirp; pulse period (Figure 2B), time measured from the beginning of a pulse to the beginning of the next pulse; power spectrum (Figure 2D), a fast Fourier transform (FFT) calculated on a single chirp; chirp (call) duty cycle, expressed as a per cent, as used here this is the total sound output 'uptime' within a series of 10 chirps, divided by the overall duration; pulse duty cycle, expressed as a percent, this is the summed 'uptime' of the constituent pulses within a single chirp, divided by the duration of that chirp. Kilosample/s is preferred to kHz in the context of digitizing sound waves: it refers to the rate at which the digitizer writes values. 'Nyquist' (see legend to Figure 2) refers to the theorem that assures sampling without aliasing: sample rates must exceed twice the highest sound frequency of interest.

2.1. Collection and rearing

Specimens of *Gnathoclita sodalis* were obtained by Fernando Montealegre in 2002 from mountain rainforest localities in the western cordillera of southwestern Colombia near Bitaco. A male and two females (adults) were transported alive to Canada to the University of Toronto, Mississauga. Here the females laid eggs from which offspring were raised in an environmental chamber (22°C, 85% RH, photoperiod 12:12 h). They were housed initially in two large wood and screen cages (60 × 40 × 30 cm). They were fed fresh carrot and apple, pollen and a baked preparation of rolled oats, fish-food flakes, millet seed and pollen. Adults were separated by sex about 2 weeks before the start of the study into two groups, each in a communal cage. Later, mature males were housed individually in Plexiglas cages.

2.2. Trough arena

An early supposition that *G. sodalis* might live within tree cavities in the wild (F. Montalegre-Z., pers. commun.), led us to construct a trough-like wooden arena (Figure 3). A 71-cm-long hardwood dowel, diameter 2.3 cm, was mounted vertically, singly-screwed from below into a flat wooden, 40 × 35 cm, pressed-board base of thickness 1.3 cm. The sliding wooden trough was fashioned from a block of white pine (8 × 8 × 52 cm), cut-out to a depth and width of 4 cm, to create a 'cavity' bounded by walls 2 cm thick; the trough could be secured at a desired height on the dowel by a hand-screw. In order to understand how the resonant frequency of the apparatus might be affecting our records of the insect's vibrations we obtained recordings of

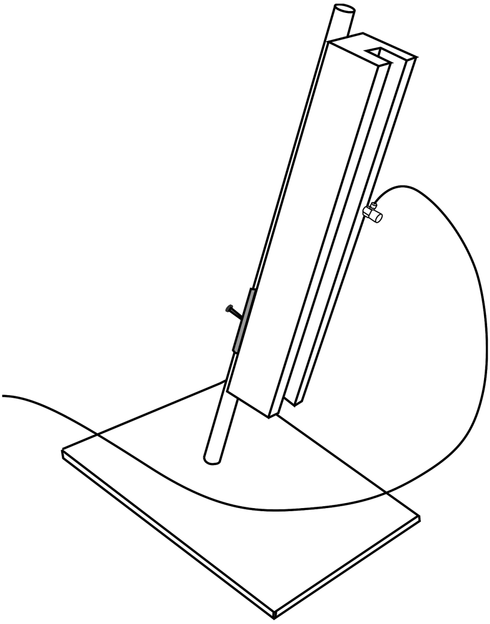

Figure 3. Wooden arena with attached accelerometer used to stage male interaction experiments.

the arena when lightly pulled and released; a similar test was made for a herbaceous potted plant, *Dieffenbachia* spp., approx. 60 cm high, to examine the form of signal vibrations in a herbaceous substrate.

2.3. Recordings

Recordings of stridulations were obtained with a TASCAM Digital Audio Tape Recorder (DA-P1) and Sennheiser microphone (ME66); the singers were individually caged in Aluminum-screen cages and microphones presented to their dorsal aspect at a 5-cm distance. Recordings were at a sampling rate of 48 kHz in an environmental chamber at temperatures of 18 to 24°C. A sample of 10 successive calls was obtained from each of seven males.

Recordings of vibratory signals were made in a sound-attenuating room under red light at temperatures of 25 to 30°C. Two males were released at the base of the arena and observed for 10 min. An accelerometer (Bruel & Kjær 4352) was attached to the trough of the wooden arena (Figure 3), with its sensitive axis normal to the long axis of the trough. The distance of the animal from the accelerometer at the moment of tremulation was noted. The accelerometer was connected to a sound level meter (Bruel & Kjær 2204) and its output digitized with a PC board (Tucker Davis Systems) at 40 kilosamples/s.

2.4. Sound and vibration analysis

For the seven males, the signal from the taped recordings was digitized into a computer at 48 kilosamples/s via a Sound Blaster PC card. High-pass filtering with a Krohn Hite (model 3352) at 5 kHz removed low-frequency noise arising from the cooling compressors of the holding chamber. We obtained 10 successive calls from each male, from regions of each recording where they engaged in steady acoustic calling. These files were then opened in Cool Edit (ver. 2000) and transformed using its Noise Reduction function, to eliminate additional low-frequency background noise (the Cool Edit noise-reduction function was tested to determine the absence of distortion on known signals). Measures of time parameters of the 10 successive chirps (single pulse trains) of each male were accomplished with DADiSP™ (DSP Development, ver. 2002): fast Fourier transforms were obtained in DADiSP for each chirp, each calculated on 1024 values, Welch-smoothed, with successive overlapping of 64 values through the time-course of each chirp/pulse-train sample.

Tremulations are body movements, that is, not themselves ‘vibrations’, but body oscillations that transmit the vibration signal via the legs into the substratum. In this insect one bout of tremulation produced a series of vibration events (e.g., Figure 4A shows a bout of three such events, each event a wave train arising from the body oscillations). Measures of the vibrations were analyzed as (i) bout duration, time from the onset of the event series to its termination (Figure 4A, B) and (ii) power density spectrum, FFT calculated on the bout, revealing the dominant frequency of the tremulation signal (Hz) within this particular substratum (arena) (e.g., Figure 4C). Bout durations of tremulation recordings were measured using DADiSP: we had learned, through observation of the insects during the making of the recordings, to distinguish the characteristic waveforms of tremulation from those arising from walking or jumping.

Coefficient of variation (CV) was calculated for all acoustic and tremulation data. A regression analysis was conducted to test for a relationship between body size and tremulation bout durations.

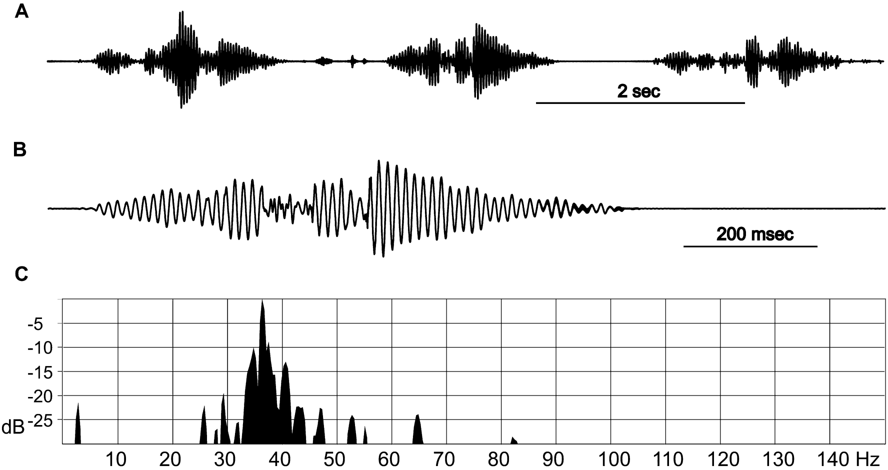

Figure 4. Tremulation signals of *G. sodalis*. (A) Three successive tremulatory vibrations from a single bout. (B) The middle wavetrain of the trace in A given at higher time resolution. (C) Spectrum of the wavetrains in B. These spectral frequencies reflect the interaction of the insect tremulations with the vibrational characteristics of the arena.

2.5. *Male–male interactions*

Male size as midline pronotum length was measured using a dissection microscope with a calibrated reticle. Male weights were also measured just prior to the staging of male interactions, but judged too variable for analysis.

Arena trials of all possible pairings (15) among the seven adult males were staged in a random sequence on a single day. Time intervals between trials were measured in minutes. To begin each trial the two males were released onto opposite sides of the trough arena. Simultaneously they were allowed to walk free from their containers, one lower down, the other higher up, out of each other's sight. High versus low individual allocation of the position of release was also randomly selected for each trial. An observation interval began when the males first encountered each other; it ended when one male clearly withdrew (walked) from the arena or after the lapse of 10 min. Interactions were video-taped with a Sony Camcorder and the retreating and remaining male noted (on one occasion a female was videotaped interacting with two males).

We quantified the number of acoustic and vibratory signals both during the interaction and after the withdrawal. As all of the males were fought against one another in a tournament design, we used a modified Bradley–Terry model (Firth, 2005; e.g., Stuart-Fox et al., 2006; Kasumovic et al.,

2009) that would allow us to specifically partition the relative effects of size, the number of tremulations and the number of stridulations, while taking into consideration any experience effects. We standardized each of these values to a mean of zero and standard deviation of one, before using them in our model to allow direct comparison of the relative magnitude of each of the traits towards contest outcomes.

Assuming that winning has a positive effect and losing has a negative effect on future contests (e.g., Hsu & Wolf, 1999), we quantified experience by allotting a value of 1 each time an individual won a contest and a value of -1 each time an individual lost. We coded only the most recent experience in the analysis for two reasons. First, numerous studies demonstrate that the most recent contest experience has the greatest effect on contest outcomes (Hsu & Wolf, 1999; Stuart-Fox et al., 2006; Kasumovic et al., 2009). Second, our sample size was small and our goal was to examine the effects of intrinsic traits of fighting quality while taking into consideration any experience, rather than examining the effect of experience itself. We, thus, feel justified in only coding the immediately previous experience.

3. Results

3.1. Male acoustic signal analysis

A previous study, describes the physical parameters of the calling song (Montealegre & Morris, 1999) based on only two individuals. We now improve upon this analysis using our recordings of an additional seven males. We report song parameters as averages ($N = 9$). Song parameter measures were normally distributed with $p > 0.05$.

The call is a regular series of very short (about 50 ms) chirps interrupted irregularly at intervals of several seconds. More than a dozen short sinusoidal pulses make up each chirp, and there is a single-peak carrier at 15–16 kHz.

Each chirp is approximately 27 ms in duration. The number of pulses per chirp remained stable for all 10 calls sampled within the sequence of each male in the sample. The carrier frequency, as determined from a power spectrum of a single call, averaged 18.8 kHz. In all cases there was just one spectral peak with no harmonic peaks apparent. Frequencies measured for each male at -20 dB high and low relative to the carrier peak, gave a mean peak width of 6.7 kHz. The CV was low for both mean peak frequency and mean peak frequency range, at 0.5 and 4.3%, respectively. Mean chirp period was 208 ms and the mean pulse period was 2.4 ms.

3.2. *Male tremulatory/vibratory signal analysis*

In response to the close presence of either sex, males show bouts of tremulation. Females were not observed to tremulate. In slowed video of tremulations it was apparent that the males oscillate their abdomen relative to the thorax in a rapid succession of alternating dips and rises in the sagittal plane. The abdomen's vertical oscillatory amplitude increases distad during the display: the abdomen extremity oscillates up and down through several millimeters. An uninterrupted series of such movements constitutes a tremulation bout. Downtimes between bouts (bout intervals) were quite variable. It was determined from the accelerometer records and video recordings, that there were approximately 27–36 abdominal oscillations per bout of tremulation.

There was substantial variation in bout durations within individuals: CV ranged from 0 to 25%. The CV overall for bout durations was 51%. Body size was not predicted by tremulation-bout durations ($p = 0.25$). The largest male repeatedly gave his bouts as three in succession, these of highly uniform duration (247 ms); this male's bouts were unusual in the uniformity of their durations and also in their shortness in comparison with the durations of the other males. Average bout duration was 1672 ms (247–2773 ms). The mean principal frequency of the insects' vibrations was 36 Hz.

The arena is a vertically mounted cantilever. In tests to determine its natural frequency, we set it into vibration by a side pull and sudden release; the plant, made to vibrate similarly, showed a principal frequency of 15 Hz, while the arena oscillated at 6 Hz.

Slowed video recordings indicated abdomen movements in every frame and a changed direction of abdominal movement in almost every frame. This observation, given the frame speed of 30/s, is consistent with the accelerometer-measured vibration peak at 36 Hz, i.e., the phase of subsequent frames slowly lost ground to the pictures of the insect's 36-Hz wave.

3.3. *Male–male staged encounters*

Dominance was attributed to males that occupied the site of tremulation exchange after the withdrawal of their opponent. Following exchanges of

Table 1. The standardized coefficients from the Bradley–Terry model with experience coded by only previous experience.

	B	χ^2	p
Size	-1.48 ± 0.84	4.75	0.029
Tremulations	-1.63 ± 1.19	3.90	0.048
Experience	0.66 ± 0.99	1.02	0.31
Stridulations	-0.27 ± 0.76	0.65	0.42

acoustic and vibratory displays, one of the males would leave. The departing or subordinate male was noted. The smaller male in each staged encounter was typically the first to depart. In 11 of the 13 resolved encounters, it was the larger male that maintained his position and continued to tremulate and/or sing from his perch. Our Bradley–Terry model significantly explained the variation in male outcomes ($\chi^2 = 11.32$, df $= 4$, $p = 0.02$). Both size and the number of tremulations predicted contest outcomes (Table 1). Neither prior experience nor the number of stridulations had any effect on contest outcomes.

4. Discussion

Little is known about the living conditions of *G. sodalis*. It is nocturnally active on understory vegetation in rainforest. One pair was observed at night mating on a waist-height plant (Figure 1). The sexes are dimorphic with an unusual head enlargement in males, suggestive of adaptations for fighting (Montealegre & Morris, 1999, see their Figure 14), yet our observed interactions were marked by an absence of escalation to overt aggression, perhaps because any gain associated with excluding a rival is too modest. In the lab, males in proximity to conspecifics of either sex, repeated both the airborne and substrate-borne signals. It remains to be seen if females would exhibit any response to the tremulation signals. Perhaps these insects aggregate in refugia (F. Montalegre-Z., pers. commun.) and these same signals might serve to promote and maintain aggregation. Smaller males withdraw from larger on the basis of the vibrations, but not the airborne sound (the main result of our tournament); yet males frequently called acoustically during the interactions: perhaps these airborne signals are directed toward the females who may normally be within earshot. On one occasion when two males were caged and interacted with a female, the male's incidence of calling in the immediate vicinity of the female dramatically increased over that typical of male interactions.

4.1. Male–male interactions

Typically prior contest experience affects future contest outcomes; prior winners are more likely to win, while prior losers are more likely to lose (Hsu et al., 2006; Rutte et al., 2006). Given that experience effects are widespread throughout the animal kingdom and present in numerous Orthoptera (Hsu et al., 2006), it is surprising that we did not find any significant effects of experience on contest outcomes in our study. Especially so since the arena interactions were staged over a very short interval of time. Since physiological changes are thought to be responsible for experience effects (Hsu et al., 2006), the same hormonal changes should be occurring in *G. sodalis* as in other Orthoptera, suggesting that experience should be a relevant contributor to contest outcomes. The most likely explanation is that size and tremulations are so important in determining contest outcomes in *G. sodalis* that they significantly outweigh any experience effects that may exist. That a system where phenotypic and behavioural traits outweigh experience may exist is interesting and warrants further investigation with a larger sample size.

Our tournament analysis shows tremulation and size both predict interaction outcomes but airborne sound does not. This contrasts with other orthopterans such as field crickets, where calling song is implicated in conveying information about size. For example, experiments showed a positive relationship between male size and syllable duration in the field cricket, *Gryllus bimaculatus* (Simmons & Zuk, 1992). In *Acheta domesticus* greater size is indicated by a greater number of pulses per chirp (Gray, 1997) and the males make use of this information in fighting (Kiflawi & Gray, 2000). The aggressive song of *A. domesticus* was analyzed, showing that body size significantly related to pulse interval: larger males had shorter pulse intervals, producing more pulses within chirps and body size correlated positively with the number of pulses per chirp (Brown et al., 2006). It is possible that for insects living on and in the ground tremulation is less available as a basis of encoding body size.

4.2. Selection for tremulation vs. sound

Katydids are vulnerable to bat predation (Belwood & Morris, 1987; ter Hofstede & Fullard, 2008; Romer et al., 2010; ter Hofstede et al., 2010). Substrate signaling represents a less public broadcasting of signal (Romer et al., 2010) that can reduce the cost of predator eavesdropping. There are several katydid species in which calling tremulations, interspersed between bouts of calling songs (airborne), are presumably aimed at attracting distant females: *Copiphora rhinoceros* (Morris, 1980), *Myopophyllum speciosum* and *Choeroparnops gigliotosi* (Morris et al., 1994). In *Docidocercus gigliotosi* (Romer et al., 2010) airborne vs. substrate attracting of potential mates varies with the lunar cycle and males spend more time substrate signalling under full-moon conditions: the airborne calls are interspersed among bouts of tremulation. The range of such vibrations will be determined in part by the plant substrate.

Tremulation has been supposed to evolve in a female-attracting context driven by selection from eavesdropping predators such as bats (Belwood & Morris, 1987). Such selection is unlikely to have produced the tremulating behaviour of *G. sodalis*. This is because the role of these vibrations is exclusively short-range, conveying information related to a contest between paired conspecifics, not designed to attract from a distance. There is likely no selection on *G. sodalis* tremulation for enhanced range or reduced range: just for stimulus intensity to convey dominance.

4.3. Frequencies of tremulatory vibrations probably do not matter

The vibratory frequency spectrum is strongly dependent upon the orientation of the signaller, his distance from the receiver and the physical composition of the substrate (Markl, 1983; De Luca & Morris, 1998). Plants act as filters (Virant-Doberlet & Cokl, 2004) and frequencies of bending waves proceed at different speeds within them (Michelsen, 1982). Our use of this particular wooden arena, or any other arbitrarily chosen artificial substrate, as a place upon which to stage the male interactions, is probably not affecting the observed behaviour. *G. sodalis* likely evolved contending with diverse substrates that confound the use of carrier frequency to encode information such as body size.

The principal vibration frequency in *G. sodalis* was measured at an average of 36 Hz; this changed to 20 Hz when tremulations were measured on a *Dieffenbachia* plant. This illustrates the strong effect of substrate on vibrational spectra and again the unlikely usefulness of such a parameter for encoding information such as size. Plants act like a filter, altering what is transmitted. The bout duration of an animal and other amplitude modulations would be more resistant to change.

The species *D. gigliotosi* is known to associate with one particular plant species, a terrestrial bromeliad (Romer et al., 2010). This insect might be able to 'count upon' a more consistent signalling substrate and so might evolve to utilize adaptive carrier frequencies. However this is unlikely to be the common case or the case with *G. sodalis*.

The problems presented by spectral frequency and its being affected by plant substrate, lend importance to our direct measures of tremulation using the video recorder. That is, it is important to follow exactly what the insect does with its body axis in the frames and as in this case, to determine that it oscillates body parts at 36 times a second, rather than to concern oneself with obtaining and measuring the filtered frequencies generated within the arena (plant tissue).

4.4. Cigar-shape an adaptation to tremulate?

Belwood (1990) observed a morphological trend among many species of Pseudophyllinae, conspicuous at night perched within neotropical rainforest understory. Many of these 'forest' katydids have elongate cylindrical bodies. This body form may be an adaptation to enhance tremulatory signalling, which is also a common behviour in many of these species (Belwood & Morris, 1987). The abdomen of insects is cantilevered rearward from their thorax. The force moments developed with the abdomen's oscillation during tremulation increase distad. Other things being equal, a longer katydid will make stronger tremulations. From *Copiphora rhinoceros* (Morris, 1980) through *Myopophyllum speciosum* and *Choeroparnops gigliotosi* (Morris et al., 1994) abdominal displacement during tremulation oscillations increments rearward: the tip of the abdomen shows the greatest displacement.

4.5. Final comment

Tremulation is common in Tettigoniidae, both temperate and tropical (unpub. obs., G.K. Morris). For a family of insects marked by lives spent moving about on plant surfaces, it seems likely that the vibrational modality has special importance. Researchers have been slow to grasp the widespread use by animals of the vibrational modality (Hill, 2008, 2009). Thus, our brief observation here of *G. sodalis*, with its indication of tremulation in male rivalry, appears unusual among tettigoniid species. This is likely an illusion: a lack of instances where tremulation mediates contests between male katydids is probably just the result of a lack of looking.

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