The sounds of fighting: contests between violet vinegar crabs, *Episesarma versicolor* (Tweedie, 1940) (Decapoda: Brachyura: Sesarmidae), are resolved through acoustic communication

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ABSTRACT

Sound plays an important role in animal communication. Sesarmid crabs (family Sesarmidae) are semi-terrestrial crabs found in tropical and temperate regions, and are known to communicate through acoustic signals. The violet vinegar crab *Episesarma versicolor* (Tweedie, 1940) is a tree-climber known to possess sound-producing structures. The significance of sounds produced by *E. versicolor* during intraspecific contests, however, remains unknown. We investigated the context in which sound production occurs by staging 27 trials using male crabs. Three main types of acoustic behaviours were documented: rapping, leg stamping, and vibration. With the exception of vibration, these behaviours were also observed in female crabs. The air or the wood substrate was utilised to transmit acoustic signals, with each sound having unique spectral and temporal features serving different purposes. Rapping and leg stamping may be an advertisement of the sender's resource-holding potential for territorial defence and asserting dominance during fights. Vibration is likely a victory display that discourages the contest loser as well as individuals in the vicinity from engaging the victor in another fight. *Episesarma versicolor* can therefore produce acoustic signals that may contain information about the sender, minimising costs associated with direct conflicts.

Key Words: behaviour, bioacoustics, resource-holding potential, signalling, sound production, tree-climbing crabs, victory display

INTRODUCTION

Communication plays a vital role in animal contests as a means of conveying information between individuals. Wilson (1975) presented a classical interpretation of communication: it takes place when an organism emits or displays a signal that is perceived by another, influencing behavioural patterns in a manner that benefits the sender, the perceiver, or both, in terms of reproductive success or survival. In particular, acoustic signalling can reduce the costs of engaging in or escalating fights by advertising one's fighting capability to an opponent, i.e., signalling one's resource-holding potential (RHP) (Parker, 1974). RHP is a measure of the probability of an animal to win in a fight, and is determined by factors such as body size, weaponry, strength, and energy reserves (Parker, 1974; Smith, 1982; Marden & Waage, 1990). RHP should also be considered in conjunction with the value of the resource, as well as the motivation level of each competitor.

Animals have evolved assessment strategies to avoid injury and the needless expansion of energy on prolonged fights. These assessment strategies fall under two categories: self-assessment and mutual assessment. In mutual assessment, both parties gather information about the other's RHP as the contest progresses, and compare it with their own RHP. Acoustic signalling can be an effective tool for advertising RHP during mutual assessment, as it is able to influence the behaviour of the receivers (Smith, 1982). The characteristics of the sounds produced can be correlated with the sender's fighting ability. This is best exemplified by the size-frequency relationship, where larger bodies are better able to generate and radiate low frequency sounds (Fitch & Hauser, 2003). Other acoustic features that reflect the user's RHP include signalling rate, duration, and sound amplitude (Clutton-Brock & Albon, 1979; Fischer *et al.*, 2004; Wyman *et al.*, 2008).

Crustaceans offer a unique perspective on contest signalling as they have developed a wide repertoire of acoustic signals to

convey information during agonistic interactions. More than 20 families and 50 genera have sound-producing mechanisms (Schmitz, 2002). Several genera of the family Sesarmidae, such as *Parasesarma* De Man, 1895, *Perisesarma* De Man, 1895, *Selatium* Serène & Soh, 1970 and *Sesarma* Say, 1817, have stridulatory structures on their chelipeds that they rub together to produce sound (Dumortier, 1963; Schmitz, 2002; Schubart *et al.*, 2009; Chen *et al.*, 2014). Brachyurans usually respond aggressively when approached by another crab by striking out with their chelae or ambulatory legs, and such agonistic behaviours are often accompanied by acoustic and seismic signals (Christy & Wada, 2015). Chen *et al.* (2014) found that *Perisesarma eumolpe* (De Man, 1895) uses stridulation exclusively as a post-contest victory display to dissuade the contest loser and any spectators in the vicinity from starting another contest. Another example is the mangrove tree-dwelling crab *Selatium brockii* (De Man, 1887), which is known to stridulate and strike wood during contests, possibly to communicate its strength and stamina to its opponent (Godsall & Smallegange, 2011).

An important consideration for acoustic communication by crustaceans is the transmission medium. In semi-terrestrial environments such as mangrove forests, hard substrates such as tree trunks and branches are readily available. When sound travels through air, spherical energy loss occurs as the finite energy spreads out, with much of this energy reaching areas where there are no receivers (Forrest, 1994; Greenfield, 2002). Making use of the wood allows the same energy to be linearly channelled to receivers, especially since the signal tends to be trapped within the substrate (Bennet-Clark, 1998; Greenfield, 2002). As compared to air, the substrate is a quieter environment where the prevailing background noise is restricted to very low frequencies (less than 200 Hz) (Popper *et al.*, 2001). The substrate is therefore a more effective communication channel compared to air, due to the lower noise levels and attenuation rates (Salmon, 1983; Bennet-Clark, 1998; Greenfield, 2002; Caldwell, 2014).

Many crustaceans have external (setae or sensory hairs), internal (statocysts), and joint (chordotonal organs) mechanoreceptors to receive acoustic signals (Bush & Laverack, 1982; Popper *et al.*, 2001). Another important sensory organ in semi-terrestrial brachyuran crabs is the Barth's myochordotonal organ, which is located in the merus of each ambulatory leg (Barth, 1934; Boon *et al.*, 2009). This organ primarily detects vibrations carried through the substrate, as seen in fiddler crabs. The organ is sensitive to airborne sounds in ghost crabs as well (Salmon *et al.*, 1977; Herberholz, 2007). The Barth's myochordotonal organ enhances the abilities of both fiddler and ghost crabs to detect sounds at frequencies above the noise band of 200 Hz in the substrate, but still below the higher frequencies that face greater attenuation rates (Salmon, 1983; Popper *et al.*, 2001).

The violet vinegar crab *Episesarma versicolor* (Tweedie, 1940) (family Sesarmidae) is likewise a semi-terrestrial brachyuran crab that possesses stridulatory structures. It is one of the five species of tree-climbing crabs found in the mangroves of Singapore, parts of Southeast Asia, and southern China (Serène & Soh, 1967; Tan & Ng, 1994; Ng, 1998). *Episesarma versicolor* commonly inhabits the main mangrove forests, where they reside within burrows in the mud or at the base of trees (Ng, 1998; Sivasothi, 2000). They are known to be facultative climbers, climbing up trees during high tides to avoid marine predators, and then remaining still to avoid detection from terrestrial predators (Sivasothi, 2000). Males of *E. versicolor* possess 40–50 tubercles on the dorsal margin of the dactylus and a longitudinal pectinated ridge with 65–80 fine tubercles on the dorsal margin of their chelae; females and juveniles do not have this ridge and have less prominent tubercles (Lee *et al.*, 2015). These tubercles represent stridulatory organs that can be used to generate sound, as seen in some other species of sound-producing crustaceans (Ng, 1998; Schmitz, 2002).

As compared to other species of *Episesarma*, *E. versicolor* occurs in larger numbers in Singapore's mangrove forests (Sivasothi, 2000; Lee *et al.*, 2015). Yet, sound production in *E. versicolor* and its significance in intraspecific communication remains unknown. We address the role of sound production in *E. versicolor* in an effort to provide a stepping-stone to understanding sound production in tree-climbing crabs, and complement the current knowledge of acoustic communication in other species of mangrove crabs. Our study aims to address three main questions: 1) Do individuals of *E. versicolor* produce sounds during contests, and can this behaviour be observed in other contexts?, 2) What are the characteristics of the sound generated and does it vary with the size of the crab or its opponent?, and 3) How do acoustic signals help *E. versicolor* in resolving conflicts?

MATERIALS AND METHODS

Collection of specimens

The study site was located at Pasir Ris Park mangrove forest on the northeastern coast of Singapore (1°22′25″N, 103°57′17″E). A total of 36 adult crabs, comprising of 30 males and six females, were collected using small aquarium-fish nets from December 2016 to January 2017. Only adults with no missing appendages were collected. Their carapace widths ranged within 9.4–31.1 mm for males and 14.7–23.5 mm for females, whereas chela length ranged within 2.8–26.5 mm for males and 6.5–13.8 mm for females. They were housed in individual perforated plastic containers (14 × 10 × 9 cm) filled with some mud and mangrove leaves. The crabs were allowed to acclimatise to laboratory conditions for at least three days before initiating laboratory experiments in order to reduce the effects of any recent agonistic interactions.

Experimental setup and procedure

Contests were staged between male crabs of similar and/or different RHP in order to investigate whether the sounds generated by *E. versicolor* during antagonistic contests are affected by the RHP of the combatants. A study of the shore crab *Carcinus maenas* (Linnaeus, 1758) revealed that weapon size (measured by chela length) was found to be a better indicator of RHP than body size (carapace width) (Sneddon *et al.*, 1997). As *E. versicolor* possesses stridulatory structures on their chelae, chela length could be an important factor influencing the characteristics of the sound generated. The length of the major chela was thus used to categorise male crabs into three size classes: small (S; 2.8–5.0 mm), medium (M; 5.1–8.0 mm), and large (L; 8.1–26.5 mm). The size classes were determined by calculating the quantiles (i.e., tertiles) from measurements of major-chelae lengths of all males to obtain three groups containing 10 individuals each. We measured the lengths of the left and right chelae with a dial calliper (± 0.1 mm). All *E. versicolor* collected were observed to be homochelous, with an absolute difference of less than 0.5 mm between the left and right chelae. Both the chela length and carapace width ratio of each experimental pair was calculated by dividing the length of the major chela or carapace width of the larger crab by that of the smaller crab respectively.

Two male crabs were made to compete against each other in trials. Each trial might contain one or more contests (fights) between the crabs. A male was randomly selected as the focal crab in each of the experimental pairs. It was noted that the behaviours of the two crabs during a contest were not independent of each other. In order to obtain independent observations, only the sounds produced and behaviour of the focal crab were considered (rather than that of both crabs) in analyses of acoustic parameters such as sound amplitude and duration. Focal crabs (S, M, L) were

randomly paired with opponent crabs (S, M, L), such that there were nine treatment combinations, to obtain data on staged contests between all possible categories of crabs. Each of the nine treatment combinations was replicated three times, resulting in a total of 27 staged trials. All contests were conducted in a random order. Crabs were reused no more than twice, with the subsequent trial spaced at least two days apart to reduce any winner/loser effects from the previous contest (Hsu & Wolf, 2001). Each experimental pair always consisted of individuals that had not interacted before.

The arena consisted of a plastic tank (35 × 20 × 24 cm). All trials were staged during the evening and night, when *E. versicolor* is naturally active. Trials were recorded from above

Figure 1. The acoustic behaviours of *Episesarma versicolor*, in which they are rapping a chela (**A**), leg stamping (**B**), and vibrating an ambulatory leg (**C**).

the tank, using a HDC-SD80 camcorder (50 frames per second) (Panasonic, Osaka, Japan) and a DR-22WL handheld recorder (TASCAM, Montebello, CA, USA), with minimal lighting to provide adequate illumination for the recordings. A piece of mangrove wood was propped up against one side of the tank in the centre of the arena. The wood provided a tilted, natural platform for the crabs, as their distinctive tree-climbing habits suggest that their vertical positions on the tree could influence the outcome of the match (Godsall & Smallegange, 2011). The pair was placed on opposite sides of the arena, with two opaque dividers separating them from each other and the piece of wood. The crabs were allowed to settle for 15 min to recover from the stress of being handled before the dividers were simultaneously removed, signalling the start of the trial. The two crabs were then allocated 45 min to interact without the presence of humans.

Fights were split into two categories: minor fights and intense fights. A minor fight was defined as any physical interaction between the two crabs, beginning from the first moment of contact, however brief. A fight was considered to be intense if at any point during the contest, the chelae of either crab made contact with any part of the opponent's body, or if they locked their ambulatory legs together. Both types of fights were regarded to have ended when one crab retreated from the other and the crabs were at least 5 cm apart. The fight was considered to have continued if the crab re-engaged within 10 sec. The contest victor was defined as the crab that carried out the last aggressive action that caused the other crab to retreat.

Mixed-sex trials were also conducted, in which a female was paired against a randomly selected male, to examine whether *E. versicolor* produce sounds in other contexts. These trials were conducted in the same fashion as the staged contests, whereby the pair was placed in the plastic tank containing a piece of mangrove wood and allowed 45 min to interact.

Sound analysis

All sounds generated by the focal crab were extracted using the audio-editing software Audacity (Audacity Team, 2013), and the duration of these sounds were determined (± 0.001 sec). Sound analysis was then carried out with the programming language Python (Van Rossum, 1995). The fast Fourier transform (FFT) algorithm (Proakis & Manolakis, 1995) was used to compute the average power spectral density (PSD) of both the signals of interest and the background noise in the recorded data. The difference was then used to plot the signal-to-noise ratio (SNR), which shows at which frequencies the energy of the signal of interest is above that of the background noise. The spectral features (dominant frequency and frequency range) and temporal features (average duration of acoustic components in each sound type) of these signals were then examined. The frequency range was defined as the range within which the top 10 decibels (dB) of the SNR was found.
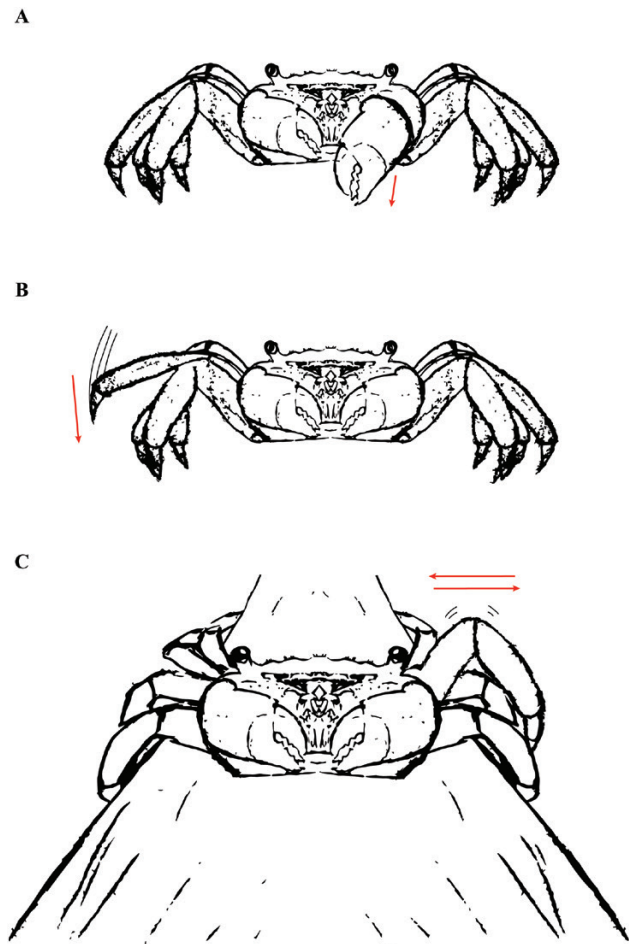
Table 1. Summary of temporal and spectral features of the sounds produced by *Episesarma versicolor*.

Acoustic behaviour	Number of events	Temporal features			Spectral features (Hz)			Transmission medium
		Number of trains	Average duration of each train (sec)	Average number of elements per train	Frequency range	Dominant frequency	Modulation frequency	
Rapping	159	1.80 ± 0.33	0.994 ± 0.161	2.87 ± 0.32	20–5500	3050	-	Air and wood substrate
Leg stamping	17	2.33 ± 0.48	0.523 ± 0.195	1.47 ± 0.23	350–12000	10200	-	Air and wood substrate
Vibration	14	4.33 ± 0.32	1.264 ± 0.119	12.63 ± 0.93	20–1700	290	24	Air
					20–11000	220	29	Wood substrate
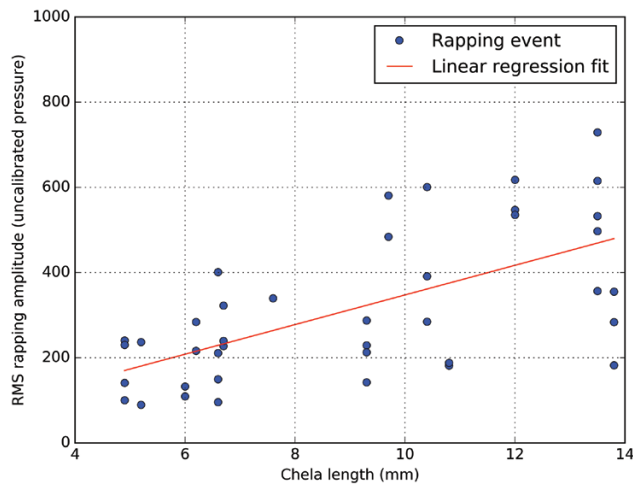
Figure 2. A linear regression of 40 randomly selected rapping events in *Episesarma versicolor* indicated that RMS rapping amplitude increased with chela length. This figure is available in colour at *Journal of Crustacean Biology* online.

An additional analysis was undertaken to determine the modulation frequency of the vibrational sounds, as their amplitudes were observed to follow a modulated pattern. The signal-processing algorithm employed to find the modulating waveform's frequency is known as DEMON (detection of envelope modulation on noise). An enhanced version of DEMON that accounts for impulsive noises in the environment was utilised to obtain a more robust estimate of the modulation frequency (Hari & Chitre, 2017).

Statistical analysis

We tested eleven hypotheses. All statistical computations were done with Python (Van Rossum, 1995), and a significance level of $\alpha = 0.05$ was adopted. To assess if sounds produced by *E. versicolor* varied with the size of their chela or carapace, simple linear regression was used to test for linear relationship of: 1) root mean square (RMS) rapping amplitude against chela length (using 40 randomly selected rapping events), 2) RMS leg stamping amplitude against carapace width, 3) vibration duration against chela length ratio, and 4) major chela length against carapace width. b_0 denotes the intercept and b_1 denotes the slope of the linear fit, while SE denotes the standard error. A Spearman's rank correlation test was also used to determine if there was a monotonic relationship between vibration duration and chela length ratio.

We also investigated whether the relative size of the crab's chela or carapace (in comparison to its opponent) has an effect on the duration and outcome of the fight. We used linear regression to test for a linear relationship between 5) contest duration and chela length ratio, and binary logistic regression to test 6) contest outcome (defined as whether the larger crab won or lost) against chela length ratio, and 7) contest outcome against carapace width ratio. Subsequent to the linear regression, a nonlinear (exponential) model was fitted to the dataset of contest duration *versus* chela length ratio using a model in which fight duration would not take on negative values, in order to determine whether this would provide a better fit. This model was of the form $y = ab^{(x-1)}$, where y refers to the contest duration, x is the chela length ratio ($x \geq 1$), and a and b are the model parameters to be fitted. In order to gain a better understanding of when vibration occurs and which contestant is likely to vibrate, a one-tailed paired t-test was carried out on 8) the number of vibrations produced by contest winners *versus* contest losers. McNemar tests were also conducted on 9) the proportion of contest winners *versus* contest losers that vibrated, and

10) the proportion of intense fights that were followed by vibration *versus* minor fights that were followed by vibration. Lastly, rapping events were studied to determine if the number of raps generated differed between the winner and loser of the contest. Hence, a one-tailed paired t-test was carried out on 11) the number of raps made by contest winners *versus* contest losers, for raps that occurred within one minute before or after a fight.

RESULTS

Analysis of sound characteristics

Three main types of acoustic behaviours (sounds) were documented during this study: rapping, leg stamping, and vibration (Fig. 1). All these sounds were made against the substrate. Although mating was not observed during the mixed-sex trials, it was noted that females generated sounds via rapping and leg stamping. These sounds were generated in the same manner as that of males, and contained spectral and temporal features similar to the respective acoustic signals mentioned above. Vibration was the only acoustic behaviour that was exclusively recorded during the staged contests with males, whereas rapping and leg stamping were observed in both contests and mixed-sex trials.

All sound recordings were generally made up of pulses (an individual sound unit), pulse trains (a series of discrete pulses), impulses (an almost instantaneous pulse), and impulse trains (a series of discrete impulses). A pulse or impulse was considered to be part of the same train if they were spaced less than 0.5 sec apart. If the interval between successive trains was more than 5 sec, it was considered to be a new acoustic event. Each type of signal has unique spectral and temporal features that allow a particular sound to be easily distinguished from another (Table 1).

Rapping involves striking the dactylus and pollex of the chela against the substrate. Individuals of *E. versicolor* were observed to either alternate chelae or use a single chela throughout the entire rapping event. The amplitude of the rapping signal increased linearly with the major chela length of the crab generating the signal (linear regression: $P = 1.40 \times 10^{-5}$, $N = 40$, $R^2 = 0.395$, $b_0 = -0.43$, $SE(b_0) = 66.88$, $b_1 = 34.79$, $SE(b_1) = 6.98$) (Fig. 2). Rapping events can occur as a crab approaches another crab, regardless of whether there is a contest, but not during the physical fight itself. Contest winners rapped a greater number of times as compared to the corresponding contest losers (paired t-test: $P = 0.00480$, $N = 43$ rapping events). Each rapping event is made up of pulse trains that consist of pulses (synonymous with rap trains and rap elements in this case) (Fig. 3A, B). The frequency of a rapping signal ranged from 20–5500 Hz, with the dominant frequency at 3050 Hz (Fig. 3C).

Leg stamping, where a crab raises an ambulatory leg above its body and swiftly brings the dactylus down to strike the substrate, was the second acoustic behaviour observed. The second or third ambulatory leg may be utilised in this motion. The amplitudes of the acoustic signals generated by leg stamping increased linearly with the carapace widths of the crabs generating them (linear regression: $P = 1.07 \times 10^{-4}$, $N = 17$, $R^2 = 0.644$, $b_0 = -7828.04$, $SE(b_0) = 2357.07$, $b_1 = 774.26$, $SE(b_1) = 148.77$) (Fig. 4). Leg stamping may occur in the moments leading up to a fight as a crab approaches its opponent, as well as during the physical engagement. One leg stamping event consists of impulse trains that are made up of impulses (Fig. 5A, B). Leg stamping also has a wider frequency range (350–12000 Hz) and a higher dominant frequency (10200 Hz) as compared to rapping (Fig. 5C).

The third acoustic behaviour observed was vibration, where the crab raises an ambulatory leg slightly in the air and vibrates it rapidly before placing it back onto the wood. The rapid vibrations in the air produced a very low frequency sound ranging from 20–1700 Hz, with the highest SNR at a dominant frequency of
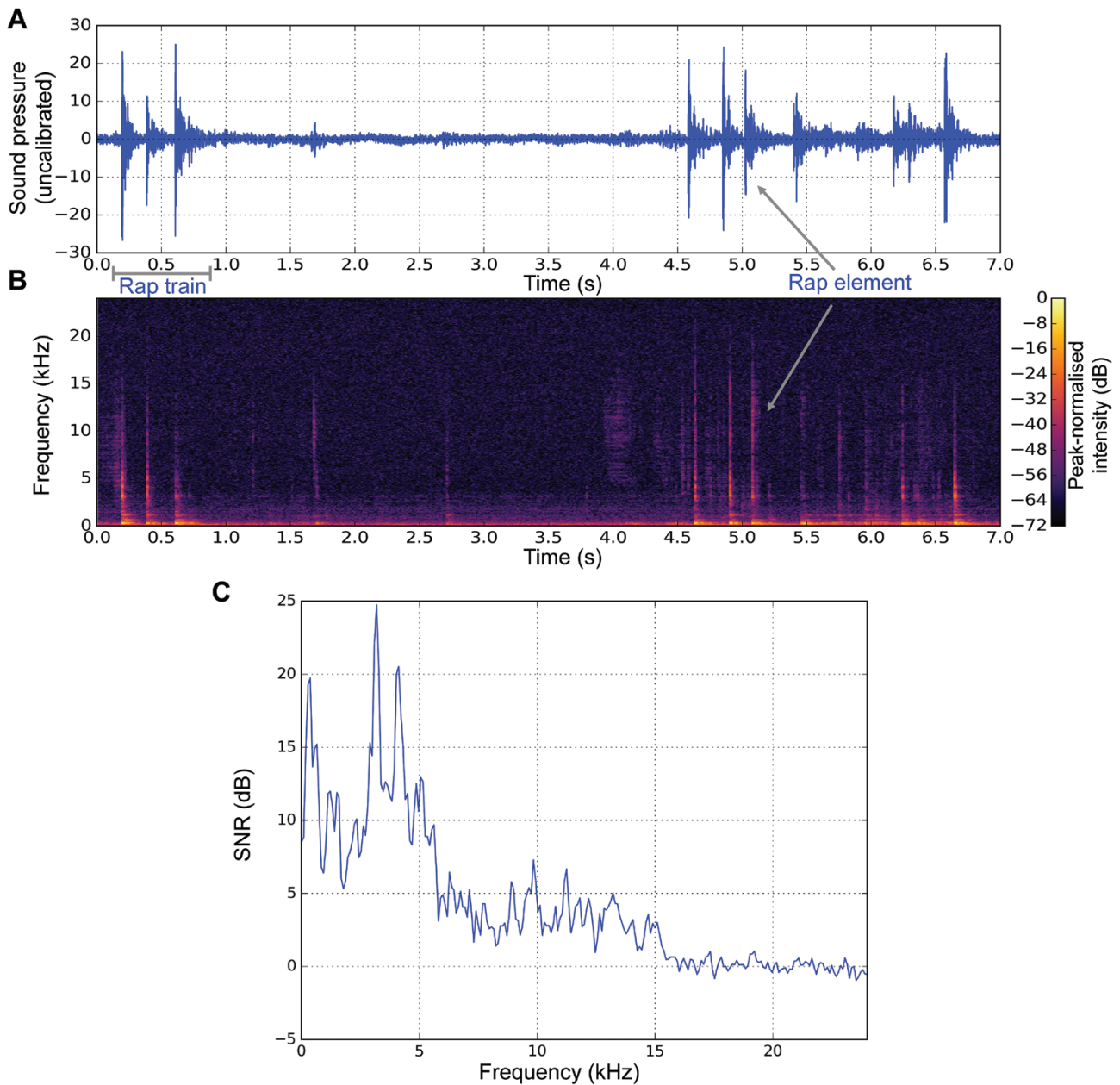
Figure 3. A timeseries (**A**) and spectrogram (**B**) of a rapping event in *Episesarma versicolor* that had three rap trains with three, four, and three rap elements respectively. The SNR was highest at a frequency of 3050 Hz (**C**). This figure is available in colour at *Journal of Crustacean Biology* online.

290 Hz (Fig. 6D). Alternatively, the vibrating leg may come into contact with the wood, generating a more audible sound over a broader frequency range of 20–11000 Hz, with a lower dominant frequency at 220 Hz (Fig. 7D). This process (known as one pulse train) was repeated an average of 4.33 ± 0.32 (1 SE) times, with the crab sometimes alternating between vibrating its second or third leg. In each pulse train, there was an average of 12.63 ± 0.93 (1 SE) pulses made within 1.264 ± 0.119 sec (1 SE) (Figs. 6A–C, 7A–C). Unlike rapping or leg stamping, the amplitude of the signal was observed to vary with time at a modulating frequency of 24 Hz when in the air (Fig. 6E) and 23 Hz when against the substrate (Fig. 7E). We were unable to detect any significant linear correlation or rank correlation between vibration duration and chela length ratio of the pair (linear regression: $P = 0.136$, $N = 14$, $R^2 = 0.175$, $b_0 = 8.02$, $SE(b_0) = 4.94$, $b_1 = 6.58$, $SE(b_1) = 4.12$; Spearman's rank correlation: $P = 0.140$, $N = 14$, $R^2 = 0.17$). Nevertheless, vibration only occurred after an intense fight

and was exhibited only by the contest winner in all of our experiments. The number of vibrations employed by the winning crabs was more than the corresponding losing crabs (paired t-test: $P = 0.0323$, $N = 27$), and the proportion of winning crabs that vibrated was more than the proportion of losing crabs that vibrated (McNemar's test: $P = < 0.0001$, $N = 27$). Moreover, the proportion of intense fights that were followed by vibration was more than the proportion of non-intense fights that were followed by vibration (McNemar's test: $P < 0.0001$, $N = 27$).

Analysis of contests

A total of 165 contests (34 intense fights and 131 minor fights) were recorded in the 27 trials conducted. The mean contest duration of intense fights was 29.12 ± 3.26 sec (1 SE), while minor fights lasted approximately 4.08 ± 0.60 sec (1 SE). Fights usually
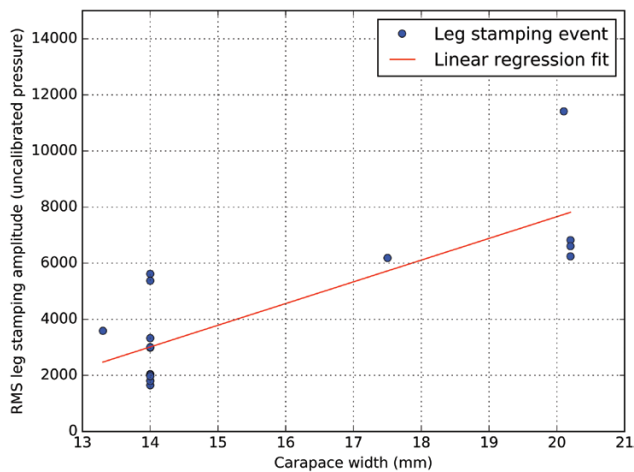
Figure 4. A linear regression of all 17 leg stamping events in *Episesarma versicolor* showed that RMS leg stamping amplitude increased with carapace width. This figure is available in colour at *Journal of Crustacean Biology* online.

involved one crab slowly approaching the other. The aggressor would rap or stamp as it made its approach, while the other crab would respond by either rapping or backing away. When the crabs were sufficiently close to each other, one crab might extend a leg out in the direction of the other, sometimes even successfully trapping the other under its leg. The crabs were also capable of leaping small distances, either to pounce toward or to escape from another crab. In intense fights, the crabs would either lock their legs together and jab at each other with their chelae, or latch onto each other and tumble around the arena in a ball.

The duration of both intense and minor fights was found to decrease linearly as the chelae length ratio of the contesting pairs increased, i.e., became more asymmetrical (linear regression: $P = 0.0264$, $\mathcal{N} = 165$, $R^2 = 0.0298$, $b_0 = 17.26$, $SE(b_0) = 3.87$, $b_1 = -5.34$, $SE(b_1) = 2.42$) (Fig. 8). The dependence between duration and chela length ratio was also well-explained using a nonlinear regression model, in which fight duration would not take on negative values and decreased nonlinearly with an increase in chelae length ratio (nonlinear regression: $P = 0.0358$, $\mathcal{N} = 165$, $R^2 = 0.0267$). The length of the major chela is linearly correlated with carapace width (linear regression: $P < 0.0001$, $\mathcal{N} = 36$, $R^2 = 0.900$, $b_0 = -7.96$, $SE(b_0) = 0.98$, $b_1 = 1.01$, $SE(b_1) = 0.06$) (Fig. 9), understandably because both these parameters would increase simultaneously as a function of the size of the crab. Although crabs with larger chelae won significantly more fights as chela length ratio increased (binary logistic regression: $P = 0.0147$, $\mathcal{N} = 165$, $b_0 = -3.94$, $SE(b_0) = 2.49$, $b_1 = 5.07$, $SE(b_1) = 2.08$), there is insufficient evidence to conclude that crabs with larger carapace widths won more fights as carapace width ratio increased based on the analyses (binary logistic regression: $P = 0.0530$, $\mathcal{N} = 165$, $b_0 = -4.01$, $SE(b_0) = 3.31$, $b_1 = 5.61$, $SE(b_1) = 2.90$).

DISCUSSION

We found that *E. versicolor* did not use the tubercles on their chelae for sound production. It was also observed that when the ratio of the chela length increased, contest duration decreased as fights became more one-sided. This trend was well captured by a linear model, as well as by the nonlinear fit. The latter ensures that the model-predicted values of contest duration do not go below zero when chela length ratio was large, which is more in line with reality. Moreover, the contest outcome favoured crabs with larger chelae as chela length ratio increased. A larger chela size would confer a fighting advantage to the crab, as the chela is involved

in most agonistic behaviours, and can be used as both a weapon and for visual displays (Sneddon *et al.*, 1997; Yoshino *et al.*, 2011). Unlike chela size, however, a larger carapace did not seem to give the crabs a fighting edge. This suggests that RHP might be better reflected by the size of the chelae of *E. versicolor* rather than its body size. Additional studies may be required to further evaluate this disparity.

Rapping

Rapping was the most common behaviour displayed by *E. versicolor* ($\mathcal{N} = 159$), as compared to leg stamps ($\mathcal{N} = 17$) and vibrational events ($\mathcal{N} = 14$). Rapping is most likely used for territorial defence. This acoustic behaviour was only observed when a crab approached another crab, regardless of whether a fight would ensue. A similar acoustic behaviour can be seen in the ghost crab *Ocypode jousseaumei* (Nobili, 1905), in which the number of rap elements and length of rap train increases as an intruder crab approaches a resident crab, irrespective of the species or gender of the advancing crab (Clayton, 2005). As rapping amplitude was also found to increase with chela length, and RHP is determined by factors such as weaponry (e.g., chelae), rapping could be an advertisement of RHP. By sending acoustic signals that reflect its RHP, the sender will be able to communicate its capability to intruders, which may deter them from entering the sender's territory (Pryke, 2013).

Rapping is often a repeated signal in which a series of raps (a rap train) may be repeated several times. The magnitude of the repeated signal also contains information about the sender. Although repetition is an energetically costly action, repeated signals allow the sender to showcase its stamina and ensure that the signal is accurately conveyed, as receivers may be erroneous during signal assessment (Enquist & Leimar, 1983; Payne & Pagel, 1997; Briffa & Elwood, 2000). Repetition may allow a crab to demonstrate its RHP in the form of stamina, even though the maximum amplitude may be limited by its chela size. Crabs that are able to produce and maintain acoustic signals with high amplitudes and repetition rates are more likely to emerge as contest victors as compared to crabs that lack the capabilities to do so (Briffa *et al.*, 1998, 2003). This is consistent with our findings, as contest victors produced a greater number of raps and/or amplitudes than contest losers. The repetitive raps executed by *E. versicolor* are thus likely to enhance its advertisement of RHP by adding information about its stamina, and improve the reception of this information to avoid a costlier conflict.

Leg stamping

Leg stamping is possibly used to assert dominance during fights. As in the case of rapping, it is only displayed as one crab approaches another ($\mathcal{N} = 17$). Individuals of *E. versicolor* were also seen stamping an ambulatory leg while physically engaged in the fight, even while they were grappling or striking at their opponents with their chelae (which would make it difficult for either crab to rap). Mowles *et al.* (2010) demonstrated that the locomotor capabilities of the hermit crab *Pagurus bernhardus* (Linnaeus, 1758) are correlated with contest victory for shell ownership, and thus serves as a good predictor of RHP. Information about RHP could similarly be communicated through the leg stamping performance in *E. versicolor*, e.g., by the number of stamps, the height to which the leg is raised, and the amplitude of the resulting sound.

Vibration

Vibration was only observed after an intense fight and was exhibited by the winners of the contests ($\mathcal{N} = 14$). Vibration could therefore be a form of victory display. Bower (2005) defines a victory display to be a post-contest behaviour that is exhibited
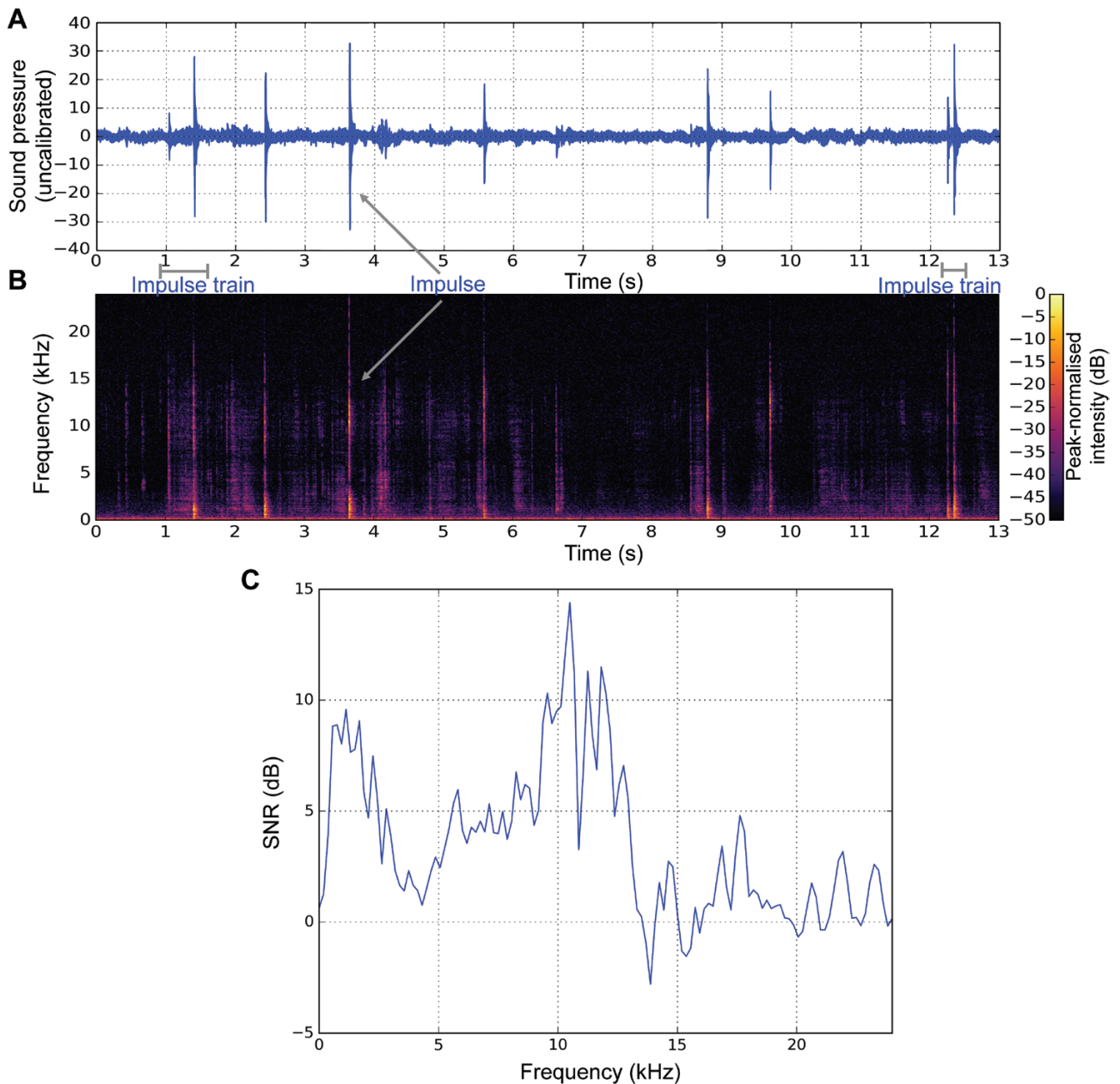
Figure 5. A leg stamping event in *Episesarma versicolor* containing two impulse trains separated by five impulses, as shown in the timeseries (**A**) and spectrogram (**B**). The SNR was highest at a frequency of 10200 Hz (**C**). This figure is available in colour at *Journal of Crustacean Biology* online.

by the contest winner, but not by the loser. Two functions have been proposed for victory displays: to communicate the victory to surrounding individuals that may not have been paying attention to the contest or are unable to ascertain the victor (i.e., advertisement), and to discourage the loser from re-engaging in a fight in the future (i.e., browbeating) (Mesterton-Gibbons & Sherratt, 2006). As vibration was the only acoustic display observed in males and not females (i.e., four males, though this could be due to the limited number of females observed), victory displays by *E. versicolor* may also be advertising the victor's prowess to female individuals in the vicinity to obtain a reproductive advantage (Fitzsimmons & Bertram, 2013).

A game-theoretical model by Mesterton-Gibbons & Sherratt (2012) considering the browbeating rationale predicted that winners did not signal in contests of shorter durations (that were relatively one-sided), but signalled in longer, more evenly matched

contests. This is consistent with the results in this study, where vibration was only displayed after intense fights, which were generally of longer duration than minor fights. This may be because there is a greater need for the winner to re-assert their dominance after a fight if both contestants are comparable in fighting ability (Mesterton-Gibbons & Sherratt, 2012). While the linear regression revealed that vibration duration does not vary linearly with chela length ratio, this could be due to the small sample size of vibrational events observed.

Vibration (both substrate-borne and air-borne) had the lowest dominant frequencies among all the sounds recorded. As compared to higher frequencies, lower frequencies have low attenuation rates in the air and substrate, and are thus able to propagate further in both mediums (Wiley & Richards, 1978; Popper *et al.*, 2001). This also facilitates acoustic advertisement of the victory to any surrounding eavesdroppers, who receive
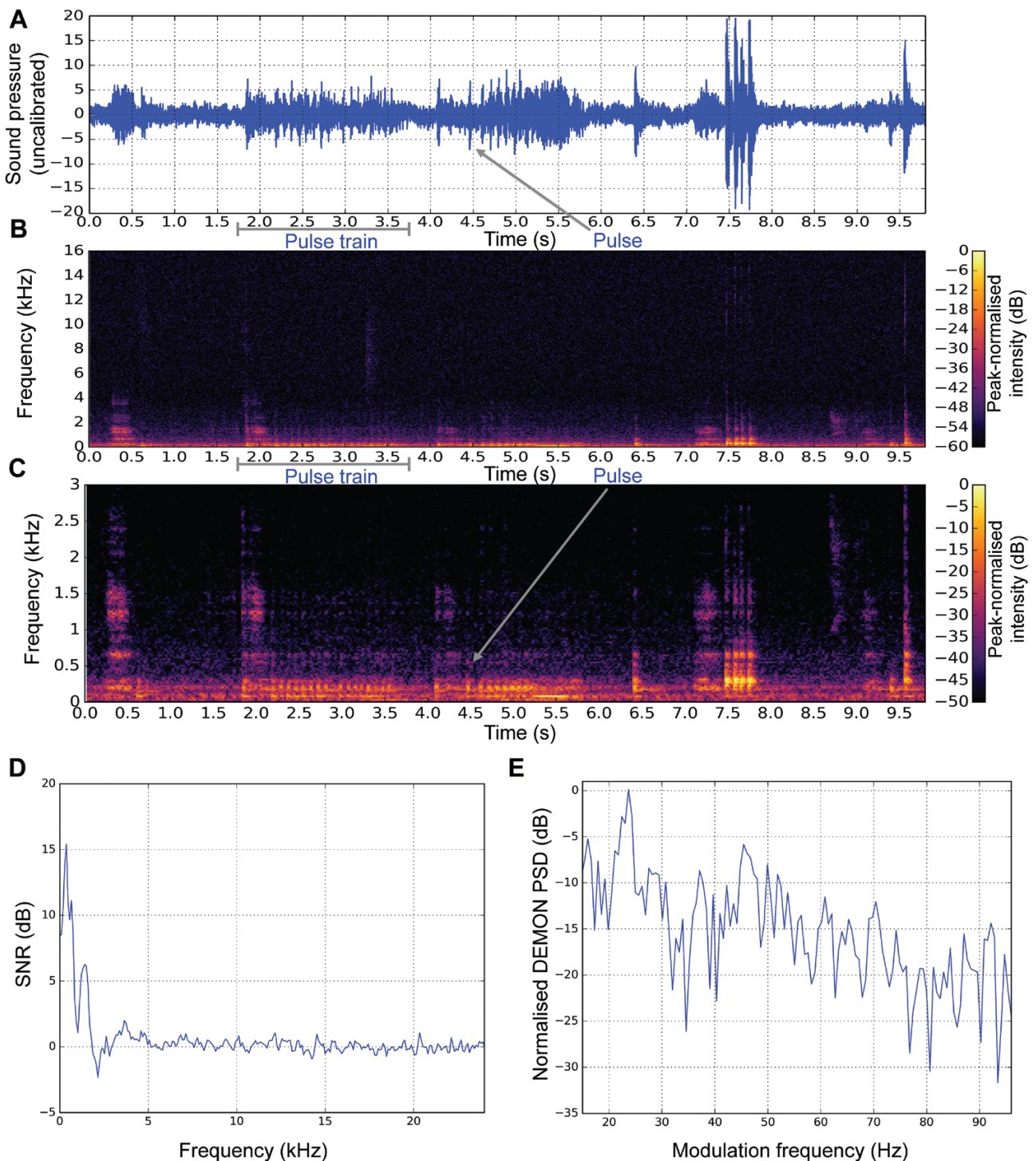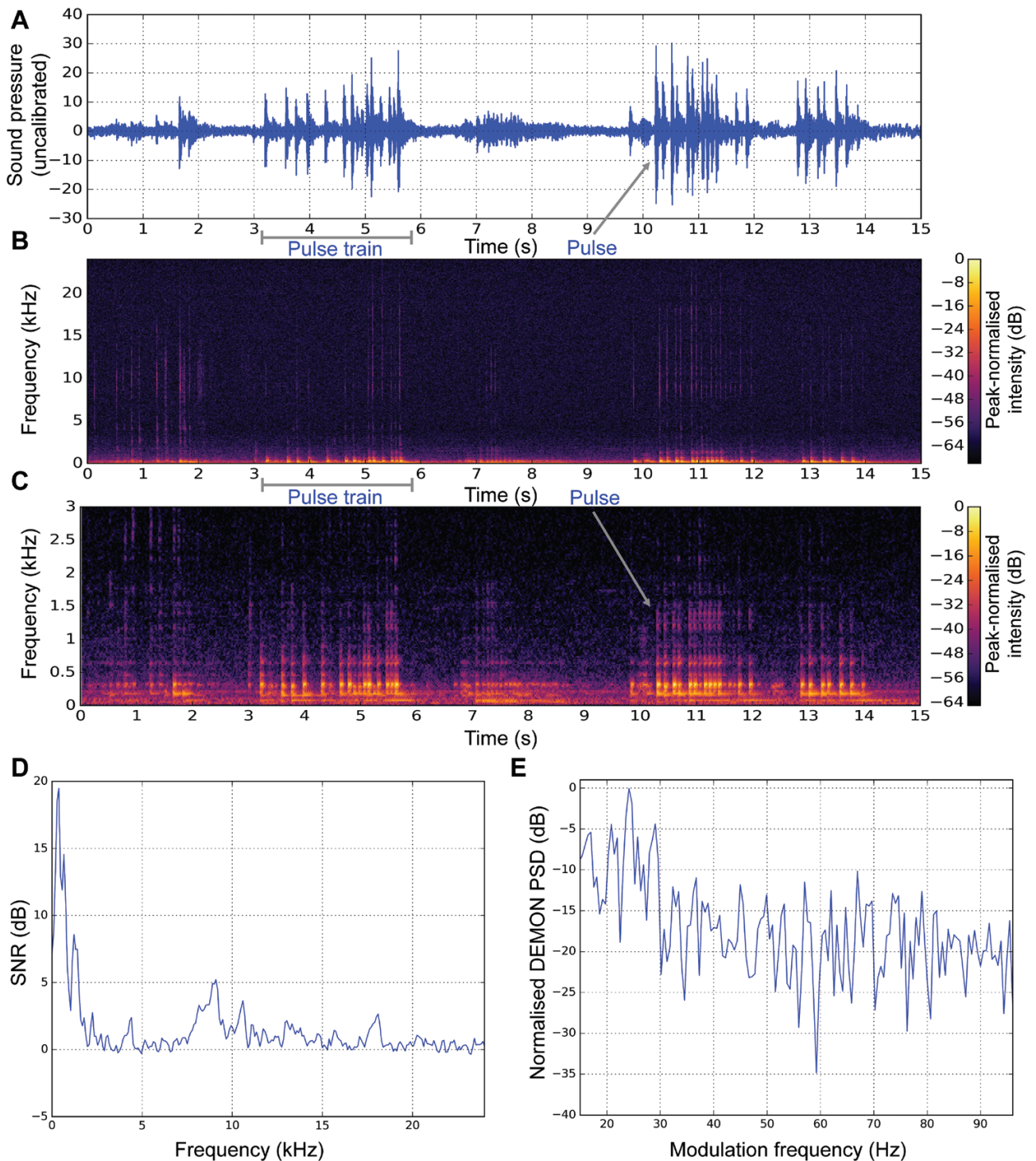
Figure 6. A vibro-acoustic signal in *Episesarma versicolor* transmitted through the air. The timeseries (**A**) shows several pulse trains. The individual pulses can be seen when the spectrogram (**B**) was zoomed-in (**C**). The SNR presented a dominant frequency at 290 Hz (**D**), while the first significant peak of the DEMON spectrum located away from the 0 Hz frequency indicated that the signal was modulating at a frequency of 24 Hz (**E**). This figure is available in colour at *Journal of Crustacean Biology* online.

information without the need for a direct confrontation, thus benefitting the contest winner and eavesdroppers (Dabelsteen, 2005). Additionally, vibration was the longest acoustic behaviour observed in *E. versicolor* (with the highest number of trains, elements per train, and longest train duration). This could be a representation of stamina, where victors showcase that they still have

excess energy that could be utilised against potential opponents (Fitzsimmons & Bertram, 2013).

These vibro-acoustic sounds were also observed to be amplitude modulated, which may be a means of encoding information in the signal. In electronic communication, notably in amplitude modulation (AM) radio transmission, information is embedded

Figure 7. A vibro-acoustic signal in *Episesarma versicolor* where vibrations were made against a wood substrate. The signal consisted of a few pulse trains containing several pulses each, as seen in the timeseries (**A**), spectrogram (**B**), and zoomed-in spectrogram (**C**). The SNR (**D**) indicated that the signal had a lower dominant frequency of 220 Hz when compared to vibrations in air, but the DEMON spectrum (**E**) showed that it had a similar modulation frequency of 23 Hz. This figure is available in colour at *Journal of Crustacean Biology* online.

in the signal (carrier wave) by modulating its amplitude (Frenzel, 2010). Amplitude modulation may be a reason why vibration is used as a victory display instead of rapping or leg stamping; vibration could be a specialised sound for this purpose as it carries additional information (of the sender being the victor) through amplitude modulation. The frequency at which AM signals are being modulated (i.e., modulation frequency) may even reflect

the sender's identity (Beeman, 1998). One example is when adult king penguins produce amplitude-modulated calls in search of their young, the chick is able to identify its parent's call at great distance, even amidst the calls of other adults (Aubin & Jouventin, 1998; Langemann & Klump, 2005). As an AM signal travels through a medium, it faces degradation in addition to frequency-dependent attenuation. This might be why the lower frequency

band (up to 1700 Hz) is amplitude modulated for the vibrational sounds produced in air. This could ensure that the sound travels a longer distance to its target, and thus receivers would be better able to discriminate these sounds in the densely vegetated mangrove forests.

Acoustic communication in the natural habitat of *Episesarma versicolor*

The natural habitat of *E. versicolor* in mangrove forests is a markedly different environment from that of a laboratory setting, particularly when examining acoustic communication. It was observed, for example, that individuals are naturally spaced apart in the mangrove. This spatial distribution has implications for how and when acoustic communication between conspecifics takes place. During the staged trials, males were made to fight in a small, confined space under experimental conditions. In the natural environment, in contrast, most acoustic communication is limited to

periods when the crabs are forced together by environmental factors like the rising tide. During the day high tide, crabs are forced out of their burrows and up onto trees (Sivasothi, 2000), where they immediately begin spacing themselves if there are multiple individuals on each tree. If the tide rises rapidly (e.g., during the bimonthly spring tides), however, they are forced to climb trees simultaneously, placing them in close proximity to one another. Perhaps this critical window may be when contests and agonistic acoustic signals are most commonly observed in the natural environment.
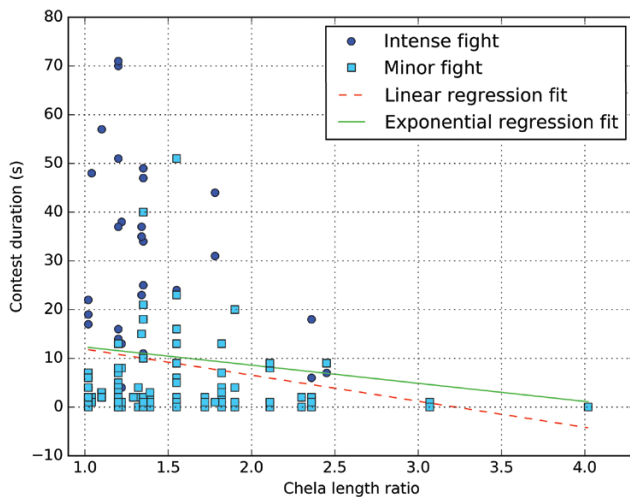
The rapping and leg stamping behaviours of *E. versicolor* require a hard substrate for the sound to be generated and transmitted effectively. Because the lifestyle of *E. versicolor* revolves around mangrove trees (for feeding, tide avoidance, and burrows at the tree base), a hard substrate is easily accessible. As compared to air, this would provide the crabs with a more effective channel for communication due to the lower noise levels and attenuation rates (Salmon, 1983; Bennet-Clark, 1998; Greenfield, 2002; Caldwell, 2014). Even if the signal is transmitted through air, such as in the case of air-borne vibrations generated by *E. versicolor*, the crabs' elevated positions on the tree can contribute to improved signal quality. Softer surfaces like the mangrove mud would cause air-borne signals to attenuate more than harder, less porous surfaces like wood, thus reducing sound amplitude (Forrest, 1994). If the crabs are approximately a meter above the mud, the soft ground's attenuation effect on the signal will decrease (Forrest, 1994). Acoustic communication in *E. versicolor* is therefore most effective above ground level when the crabs are perched on trees, especially if the wood substrate is utilised to transmit these signals.

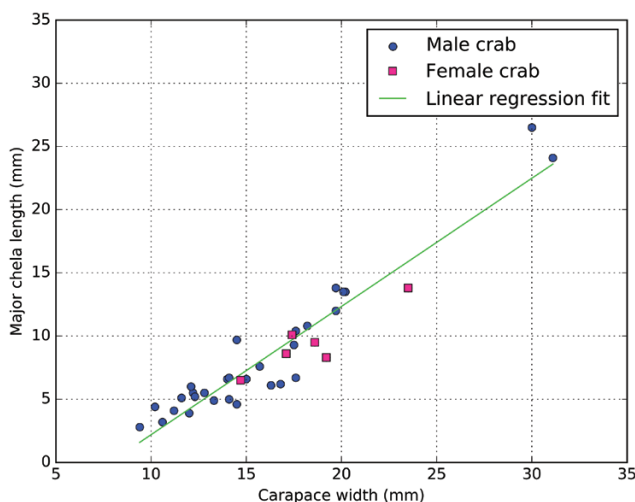**Figure 8.** Both the linear best-fit line and the nonlinear (exponential) fit showed a decrease in contest duration for all fights in *Episesarma versicolor* as chela length ratio of the two crabs increased. This figure is available in colour at *Journal of Crustacean Biology* online.

Figure 9. A linear regression analysis on 30 males and six females of *Episesarma versicolor* demonstrated that the length of the major chela increased linearly with carapace width. This figure is available in colour at *Journal of Crustacean Biology* online.

ACKNOWLEDGEMENTS

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