



# Post-Contest Stridulation Used Exclusively as a Victory Display in Mangrove Crabs

Paul Z. Chen, Luis R. Carrasco & Peter K. L. Ng

Department of Biological Sciences, National University of Singapore, Singapore

## Correspondence

Paul Z. Chen, National University of Singapore, 14 Science Drive, Singapore 117543, Singapore.  
E-mail: a0023944@nus.edu.sg

Received: October 18, 2013

Initial acceptance: December 15, 2013

Final acceptance: February 1, 2014  
(M. Manser)

doi: 10.1111/eth.12226

**Keywords:** Brachyura, fighting, signalling, *Perisesarma eumolpe*, Sesarmidae

## Abstract

Victory or triumph display is a post-contest signal, performed only by winners and not by losers. While much is unknown about its function, there is mounting evidence that victory displays are widespread among animals. However, evidence remains anecdotal in crabs. Sesarmid crabs belonging to the genera *Parasesarma* and *Perisesarma* are known to have characteristic stridulatory structures on their chelipeds. In *Perisesarma eumolpe*, a mangrove crab, stridulation has been anecdotally purported as a triumph display. We examined whether stridulation in *P. eumolpe* is a victory display and the factors affecting it by staging 17 contest trials among males and investigating the factors influencing stridulations and fight outcome in 55 fights. Using generalised linear mixed-effects models, we find that stridulations were generally performed by winners and after fights, especially when the fights were intense. In addition, stridulation was only observed in the context of a contest, never before or outside of it. Stridulation in *P. eumolpe* is likely a victory display, and, unlike other forms of victory display described for other species, it appears exclusively used for asserting victory.

## Introduction

Fights in animals are seldom fatal (Maynard Smith & Price 1973; Grafen 1987); nevertheless, they remain costly (e.g. Thorpe et al. 1995; Hack 1997; Riechert 1988). To reduce the cost of fighting, animals have commonly employed non-contact signalling (e.g. Logue et al. 2010). Signalling allows opponents to interact mutually without the need for physical contact, thereby reducing unnecessary escalation of the fight and the cost associated with it. This has led many studies to examine how signals, before and during fights, achieved cost reduction in animal contests (e.g. Andersson 1980; Waas 1991; Hasson 1997; Brown et al. 2006). However, signalling behaviours are not limited only to those moments. Post-contest displays are commonly reported, but, thus far, have remained relatively poorly studied and understood (Bower 2005; Matsumura & Hayden 2006). These displays may not aid in the reduction of cost in the current contest. However, the displays are likely to influence the cost of potential fights in the near future.

Victory display, performed by the winner and not the loser (Bower 2005), is an example of a post-contest signal. Although not well understood, victory display could reduce the risk of future conflict by discouraging the loser of a recent contest (browbeating rationale) and/or nearby onlookers (advertisement rationale) from initiating a new contest (Bower 2005). A recent study using game theory suggests that which role victory display would function as, to browbeat opponent or to advertise victory to neighbours, in a species, is dependent on the degree dominance advantage has on reproduction (Mesterton-Gibbons & Sherratt 2006). Thus, in species where dominance results in high reproductive benefit, victory display is predicted to browbeat the loser into a more permanent subordination (browbeating rationale; Mesterton-Gibbons & Sherratt 2006). On the contrary, in species with low reproductive benefit from dominance, victory display should discourage neighbouring onlookers from further aggression by announcing recent victory (advertisement rationale; Mesterton-Gibbons & Sherratt 2006). A recent study on little

blue penguins, *Eudyptula minor*, a species with low reproductive advantage from dominance, corroborated the advertisement rationale: victory display in little blue penguin increases the heart rate of nearby potential competitors but not that of mates (Mourtede et al. 2012). It remains to be seen whether victory display serves to browbeat loser of a recent fight, in a species where reproductive advantage of dominance is high.

Despite the substantial consequences that victory display may have on the cost of future fight, it has received little attention. Accounts of plausible victory display have been recorded in a range of species (e.g. in birds [Waas 1990; Kraaijeveld & Mulder 2002], in amphibians [Wells 1978], in crickets and wetas [Hack 1997; Kelly 2006] and in crustaceans [Tweedie 1954]). However, many of these have remained as side notes and anecdotes. To date, only a few studies have specifically examined for the presence of victory display in animals (Grafe & Bitz 2004; Lippold et al. 2008; Bertram et al. 2010; Mourtede et al. 2012). Among these studies, all with the exception of Lippold et al.'s (2008) have positively identified post-contest signals to be victory displays. Instead of a victory display, Lippold et al.'s (2008) found that post-contest behaviours in black-capped chickadees, *Poecile atricapillus*, are performed by only losers and not by winners. Yet, not all post-contest displays, performed by the winners, are necessarily victory displays. Some are probably agonistic displays in anticipation of further aggression (Bower 2005). Thus, to gain a better understanding on the function of victory display and its importance in animal fights, verifying and examining the presence of victory display in animals are fundamental steps. Here, we aim to verify that the post-contest stridulation of a mangrove crab, *Perisesarma eumolpe*, is a victory display. To our knowledge, this is the first of such behaviour verified in brachyurans and possibly decapod crustaceans.

Stridulatory behaviour of *P. eumolpe* was first described anecdotally, by Tweedie (1954), and later in detail by Boon et al. (2009). Stridulation has often been associated as one of the many contest behaviours of *P. eumolpe*. When detailing the behaviour, Boon et al. (2009) noted that stridulation usually occurs after the occurrence of contact fight. However, it was not mentioned whether stridulations were performed by winners only or whether they signalled the conclusion of contests – conditions necessary to qualify as a victory display (Bower 2005). Nevertheless, when Tweedie (1954:123) first described the stridulatory behaviour in *P. eumolpe*, he annotated the behaviour as a 'gesture of defiance or triumph', purporting it is as a sort of victory display.

Identifying victory displays can prove challenging, because post-contest displays, performed by the winners, could probably be agonistic displays in anticipation of further aggression (Bower 2005). Hence, to verify whether the stridulatory behaviour of *P. eumolpe* is a victory display, we followed the proposed criteria set by Bower (2005). His criteria for a victory display are that (1) the display is restricted to winners, (2) it is performed in a post-contest context, and (3) it has unique features, differing – even subtly – from other agonistic behaviours (Bower 2005). Firstly, we investigate whether stridulatory behaviours are restricted only to winners. Secondly, we examine whether stridulations occur at the conclusion of contest. Lastly, we assess the factors that influence the probability of stridulation.

## Materials and Methods

### Collection of Specimens

Male crabs were hand collected from the Pasir Ris mangrove, north-east of Singapore (1°22'39" N, 103°57'09" E), during low-tide periods between June and September 2012. Only crabs that were in the intermoult stage without any loss of appendages were used. The crabs were housed individually in an open laboratory for a week, prior to the experimental trial. Acclimation was necessary to minimise the effect of prior fighting experience and habituate individuals to laboratory conditions. Each crab was housed individually in a perforated rectangular container (46 × 35 × 24 cm height), filled with black aquarium sand (diameter of 1–2 mm) to a depth of 3 cm, and a shelter (flower pot laid on the side, 5.5 cm diameter, 5 cm height) placed in the middle of one end of the container's length. Transparent acrylic lids were used to prevent crabs from escaping, but allowed natural light to enter. To keep the crabs moist, the substrates were wet with artificially constituted sea water (30–35‰) at the start of the acclimation period, thereafter every alternate day till the experimental trial. Similarly, a food pellet (JBL NovoCrabs) was fed to each crab on the second day of the acclimation period, thereafter every alternate day till the experimental trial. Uneaten feeds were removed before new ones were provided.

### Experimental Set-up

The experimental arena, in which all trials were conducted, had the identical layout of the housing container. To keep the arena moist, it was submerged in

artificially constituted sea water (30–35‰), only deep enough to keep the substrate moist without ponding. Two 15 W natural sunlight lamps (2% Ultraviolet B, Acardia) were used to light the arena. The arena was covered with a modified lid, where only 4 cm of the border of the arena was covered. This was to ensure that maximum light could enter the arena without allowing the crabs to escape. Lighting was a particular concern as studies have suggested that the coloured face band of crabs may be important in contest (Huang et al. 2008; Todd et al. 2011). All trials were recorded from above with a video camera (Sony HDR-SR8E) mounted on a tripod, without the presence of the experimenter. Trials were conducted from 09:00 to 17:00 h. Individuals were randomly paired and were used only once. After the experiment, males were returned to their original habitat.

### Experimental Trial

In each trial, paired males were introduced separately by means of two PVC pipes (6 cm diameter, 23 cm height) at two corners of the experimental arena, directly opposite the side of the shelter. They were allowed to acclimatise to the arena for 15 min. After which the pipes were removed simultaneously, and the crabs were allowed to interact for 45 min before the trial was terminated. Upon trial termination, the males' carapace width, right chela and left chela length ( $\pm 0.05$  mm) were measured with a dial calliper. The interactions between individuals were reviewed via video recording, and the winner and loser of each fight were determined. The contest

behaviours of each individual were scored based on a compiled ethogram (Table 1). In addition, the timing, duration, grappling duration and individual contest intensity of each fight in a trial were recorded. The nature of each fight, as to whether the fight was over the possession of the shelter or not, was also recorded. Lastly, the timing of stridulations, if they occurred, was noted. To remove inconsistency in judgment, measurement of crab body size and scoring of contest behaviours were all carried out by a single observer (P. Z. Chen, pers. obs.).

A fight was defined as any interaction between individuals where contact was made, even briefly. The start of the fight was defined as the moment where contact was made. The fight was determined to have ended, when the pair broke contact for more than 5 s and was more than 5 cm away from each other. Any physical interaction thereafter was considered to be a new fight. To determine the contest behavioural repertoire of *P. eumolpe*, 10 trials were chosen at random and scored for distinctive contest behavioural elements by a single observer (P. Z. Chen, pers. obs.). The scored behaviours were compiled into an ethogram (Table 1). A cumulative plot of new contest behavioural elements found in each successive trial scored suggested that the compiled ethogram was sufficiently comprehensive.

To quantify the contest intensity of a fight, each behaviour in the ethogram was assigned an intensity level. The contest intensity of a fight corresponds to the highest level of intensity reached. However, such mean of quantification may overlook important information that can differentiate fights with similar

**Table 1:** Agnostic ethogram and their respective intensity score

Behaviour	Description	Level of intensity
Stationary	Moment of inactivity towards opponent	0
Back away	Moving backwards for a short distance slowly	0
Disengage	Release of interlocking chelipeds with opponent	0
Retreat	Quick movement away from opponent	0
End	Opponents are at least 10 cm away from each other.	0
Stridulation	Stereotypic rubbing of stridulatory organ of one chela with that of another chela	0
Face opponent	Orientate body to face opponent	1
Leg touch	Slow approach from the side with 2nd ambulatory legs touching opponent	1
Side rubbing	Rubbing of cheliped against pterygostomial region	1
Advance	Move forward towards opponent	1
Claw extend	Extending chelipeds towards (with or without pushing) opponent	2
Jump	Quick lunge towards the opponent	2
Claw Swing	Chelae held pointing down and swing side to side	2
Claw tap	Striking opponent with the tip of cheliped	3
Grappling	Jostling while interlocking chelipeds with opponent	3
Jump strike	Quick lunge towards the opponent, while striking opponent with tip of cheliped(s)	3
Start of contest	Opponents within 5 cm of each other	
End of contest	Opponents are more than 5 cm away of each other and do not have physical contact for more than 5 s	

maximum fight intensity (see Bertram et al. 2010). Thus, we adapted Bertram et al.'s (2010) method to derive contest intensity. Firstly, individual, but not overall, contest intensity was considered. To quantify contest intensity of each individual, as in past practices, each contest behaviour was assigned an intensity level – one, two or three, one being the lowest and three being the highest. Intensity level was assigned based on the perceived energetics required (Table 1). All except for one (Grappling; see Table 1), behaviours were regarded as events, and each occurrence was considered distinctively unique. Grappling behaviour was more a behavioural state, and duration of occurrence was important. Thus, for grappling behaviour, the intensity level was the assigned value multiplied by the duration for which it occurred. The score of contest intensity was then the sum of intensities that occurred, based on the scored contest behaviour of each individual, divided by the total duration of the contest, to normalise between different fights.

### Analysis

All analyses were made using the statistical software R (R Core Team 2013) and the relevant R packages. Body and chelae dimensions, in crabs, are often good estimate of an individual resource holding potential (RHP) (Sneddon et al. 1997). However, the size variables (carapace width, right and left chela length) showed high multicollinearity, as estimated using the *car* package (Fox & Weisberg 2011). To avoid problems of multicollinearity, a new estimate for RHP, combination of the size variables, was constructed. This was carried out using principal component analysis, after obtaining a Kaiser–Meyer–Olkin measure of 0.723, using the *rela* package (Chajewski 2009), from the size measurements. Generalised linear mixed-effects models (GLMM) with binomial errors in the *lme4* package (Bates et al. 2012) were used to examine which variables influence whether individuals stridulate at the end of a contest or not. Generalised linear mixed-effects model were selected because the dependent variable was binary (stridulation; no = 0, yes = 1), and the data were not independent within trials, time and within individuals. The latter was dealt with using different random effects structures. The independent variables (fixed effects) of the initial model were duration of contest, RHP of the individual, outcome of fight (winner or loser), individual intensity and whether fight was over the limited resource (shelter) or not. The random effects of the model represented the nesting of the observations within individuals and within trials. The timing at

which each fight occurred was initially fitted as a random slope in the random effects part of the model, but was removed after comparing it with a simpler random intercept model using the Akaike's information criterion (AIC). Once the random structure was selected, we proceeded to obtain the final model by removing the main effects in a stepwise manner using likelihood ratio tests.

### Results

A total of 55 fights from 17 trials were recorded, of which 34 (61.8%) fights resulted in stridulations. The average duration of the fights was 51.2 s (SE,  $\pm$  6.86). Stridulation was never observed to occur before any antagonistic interaction. No individual stridulated more than once in one contest. Of the 37 stridulations observed, 31 (83.8%) occurred after the conclusion of the contest and were all performed by winners. Of the remaining observations, two losers stridulated during the contest. However, in those trials, the winner stridulated almost immediately after and resumed engaging the loser. In the other situation, where winners stridulated during the fight, losers were unable to distance themselves from the winner after stridulation, due to confinement at the corner of the arena. Fights were observed to resume after stridulation until the losers could distance themselves from the winners.

Five stridulations were observed to occur after agonistic interactions, but without physical contact (fighting). While these interactions were not fights, they are still agonistic in nature. These non-contact agonistic behaviours include dashing and jumping towards the opponent.

The statistical analysis was also consistent with the above observation (Table 2); winning a fight significantly increased the probability of stridulation (GLMM:  $\beta = 3.91$ , SE = 0.80,  $\chi^2 = 43.64$ ,  $p < 0.001$ ). In addition, individuals who fought more intensely were also more likely to stridulate (GLMM:  $\beta = 0.62$ , SE = 0.25,  $\chi^2 = 6.63$ ,  $p = 0.018$ ). The duration of fight, RHP of an individual and the context of the fight all do not predict the likelihood of whether an individual will stridulate.

### Discussion

#### Victory Display in *P. eumolpe*

Our analyses suggest that stridulation in *P. eumolpe* is a victory display. Firstly, it fulfils all three criteria of a victory display (Bower 2005). Stridulations were, gen-

**Table 2:** Generalised linear mixed-effects model investigating the effects of contest outcome and fight intensity on the probability of stridulation

	Effect size ( $\beta$ )	SE	p (Wald statistic)
Full model			
RHP of individual	0.035	0.180	0.843
Total contest duration (s)	0.002	0.004	0.578
Outcome of fight (winner or loser)	3.955	0.811	<0.001
Fight intensity	0.622	0.264	0.018
Whether fight is over shelter or not	0.426	0.629	0.498
	Effect size ( $\beta$ )	$\chi^2$ (df)	p value
Final model			
Outcome of fight (winner or loser)	3.910	43.641 (1)	<0.001
Fight intensity	0.618	6.630 (1)	0.010

erally, (1) restricted to winners, (2) performed after contests and (3) distinctive from other agonistic behaviours. In fact, stridulations were not only distinctive; they were never seen used in any agonistic context other than to exert victory. This exclusive use of behaviour type for victory display has yet to be reported. Typically, victory displays in many species consist of agonistic behaviour types already in use throughout the contest (Bower 2005). For instance, songs and stridulations were showed to be victory displays in birds (e.g. Waas 1990; Grafe & Bitz 2004), and wetas and crickets (e.g. Kelly 2006; Bertram et al. 2010), respectively. However, songs and stridulations are well-known common agonistic behaviours used throughout fights in birds, and crickets and wetas, respectively. As a result, this report may be the first record where a behaviour type is exclusively used for victory display. Secondly, while contest duration was not found to predict the likelihood of winners stridulating (Mesterton-Gibbons & Sherratt 2012), winners were found more likely to stridulate after intense agonistic interactions. This is consistent with Mesterton-Gibbons and Sherratt (2012) suggestion that victory displays should only occur when the cost of fighting is sufficiently high. Intensity of fight, such as contest duration, is a mean of measuring of the cost of fighting, could be used as surrogates for each other and provided that the intensity per unit time was approximately constant. As a result, as the intensity of fight (cost of fight) increases, the probability of winners stridulating also increases. Our results indicate, however, that in the case of *P. eumolpe*, contest intensity, and not contest duration, may be more reflective of the cost of fighting in this case. Further research with

other species could be directed to ascertain the role of intensity and duration on the probability of winners signalling. Consequently, these results collectively suggest that stridulation in *P. eumolpe* is likely to be a victory display.

While stridulations, in *P. eumolpe*, are generally consistent with the predictions of a victory display, there were some exceptions. For example, losers were found stridulating during the contest in two independent trials. Those stridulations were likely claims of victory, albeit mistaken ones. Winners were observed to stridulate immediately after – seemingly challenging the losers' stridulation. In addition, winners resumed further agonistic interactions immediately after. The losers, in these fights, could have mistakenly perceived that the fights have concluded and that they were the winners. These mistakes could have led losers and winners to stridulate during the fight, rather than after.

In two trials, winners were found to stridulate during the contest instead of after. However, these stridulations are probably post-contest victory display too. In these instances, after the winner had stridulated, the losers, due to the spatial constraint of the experimental arena, were unable to put adequate distance between themselves and the winners. As a consequence, the fights resumed – always initiated by the winners. Hence, it is probable that winners continued exhibiting aggression towards losers despite them having already yielded; thus, appearing like these stridulations were performed during a fight rather than after.

Lastly, some stridulations were seen elicited after agonistic interactions without physical contact. These are also likely victory display. While agonistic behaviours without physical contact do occur in nature, establishing a good criterion to include them in our analysis was difficult. Therefore, for a more accurate analysis, we limited our definition of fights to agonistic interactions with physical contact. As such, stridulations arising from non-physical agonistic interactions were likely performed in the same context as those elicited after physical ones. Thus, these stridulations are not inconsistent with the definition of victory display.

While stridulation induced by non-physical interaction is a rarity in this experiment, this phenomenon is more commonly observed in the wild. The limited area of the experimental arena probably compelled individuals into physical interactions. However, in their natural habitat, individuals could avoid physical agonistic interactions by moving away from their aggressor. Thus, non-physical agonistic interactions and stridulations elicited from them are more common.

### Victory Display in Other Decapods

Besides *P. eumolpe*, victory displays are suspected in a number of species of astacidean crayfish (Mesterton-Gibbons & Sherratt 2006). Astacideans are known to direct urine towards opponents during agonistic interactions (e.g. Zulantz Schnider et al. 1999; Breithaupt & Atema 2000; Breithaupt & Eger 2002; Bergman et al. 2005; Moore & Bergman 2005; Katoh et al. 2008). As dominant individuals tend to release more urine (e.g. Breithaupt & Atema 2000; Breithaupt & Eger 2002; Bergman et al. 2005; Moore & Bergman 2005; Katoh et al. 2008), urination was thought to be a potential candidate for victory display (Mesterton-Gibbons & Sherratt 2006). However, urination in astacideans is unlikely to be a victory display. Firstly, the release of urine in most, if not all, species was reported to occur before and more actively during agonistic interactions (e.g. Breithaupt & Atema 2000; Breithaupt & Eger 2002; Bergman et al. 2005; Katoh et al. 2008). It does not appear that the urination is a post-contest behaviour in these animals. Secondly, urination is not exclusive to the winners; losers were also found releasing urine, but with less frequency (Breithaupt & Atema 2000; Breithaupt & Eger 2002; Bergman et al. 2005; Katoh et al. 2008). Hence, it is unlikely that urination in astacideans is a form of victory display. This suggests that *P. eumolpe*, and possibly its congeners, could be the only decapod that are known to exhibit victory display.

### Function of Victory Display

The function of victory displays remains poorly understood, even though victory displays are becoming evidently more widespread and common among gregarious animals. Two major hypotheses have since been brought forth (Bower 2005; Mesterton-Gibbons & Sherratt 2006). The first is the advertisement hypothesis, where victory display acts to announce recent win of the victor to bystanders, in the bid to reduce the probability of a new contest. The second is the browbeating hypothesis, where victory display served to decrease the probability of the loser from re-initiating another fight with the winner in the near future. A recent study has showed that victors alter the performance of victory displays, depending on the type and presence of bystanders (Fitzsimmons & Bertram 2013). This suggests that victory display, besides browbeating the loser, may also function similarly to an audience effect. Future studies should not neglect the effect of audience when examining the brow-

beating function of victory displays. Despite the difference, both hypotheses have assumed the reduction of cost in potential fight in the near future. According to game theory, whether the display was intended primarily to bystanders or loser depends largely on the reproductive advantage of winning (Mesterton-Gibbons & Sherratt 2006). When the reproductive advantage of winning is low, as in monogamous birds (e.g. Mourtede et al. 2012), victory displays serve more to inform bystanders of the victors. On the other hand, when the advantage is high, as in species practicing defence polygyny (e.g. Kelly 2006), victory displays function more to intimidate opponents.

Little is known as to whether males of *P. eumolpe* compete for females (female defence polygyny) or for resources, such as shelter, used by females (resource defence polygyny). Nevertheless, individual males were usually found with a number of females in their natural habitat (P. Z. Chen, pers. obs.). Although males do not necessary fight over the shelter provided in our analyses, winners plausibly have a greater reproductive advantage than losers. Males could be defending an area, rather than the specific shelter provided. Thus, it is likely that victory display in *P. eumolpe* functions more to browbeat the loser than to announce their victory to nearby conspecifics. Yet, there is a possibility that victory display in *P. eumolpe* serves to advertise recent victory to nearby conspecifics. Stridulatory signals of *P. eumolpe* are barely audible, and recording them has proved challenging. Recording of substrate-borne signals have borne out to be more promising. If stridulatory signals, in *P. eumolpe*, are indeed substrate-borne, signals could potentially reach a number of neighbours. Further research is being conducted in this direction to elucidate this question.

### Conclusions

Winners were found to fight more intensely and stridulate at the end of contests. In addition, stridulation was never observed before a contest or outside the context of a fight. Thus, we reckon that stridulation is used exclusively as a victory display in this species. The function of victory display in *P. eumolpe* is not known, and further studies are needed. We believe that these crabs could be good models to study the evolution and adaptation of victory display.

### Literature Cited

Andersson, M. 1980: Why are there so many threat displays? *J. Theor. Biol.* **86**, 773–781.

- Bates, D., Maechler, M. & Bolker, B. 2012: lme4: Linear mixed-effects models using Eigen and Eigenfaces. R package version 0.999999-0.
- Bergman, D. A., Martin, L. A. & Moore, P. A. 2005: Control of information flow through the influence of mechanical and chemical signals during agonistic encounters by the crayfish, *Orconectes rusticus*. *Anim. Behav.* **70**, 485–496.
- Bertram, S. M., Rook, V. L. M. & Fitzsimmons, L. P. 2010: Strutting their stuff: victory displays in the spring cricket, *Gryllus veletis*. *Behaviour* **147**, 1249–1266.
- Boon, P. Y., Yeo, D. C. J. & Todd, P. A. 2009: Sound production and reception in mangrove crabs *Perisesarma* spp. (Brachyura: Sesarmidae). *Aquat. Biol.* **5**, 107–116.
- Bower, J. L. 2005: The occurrence and function of victory displays within communication networks. In: *Animal Communication Networks*, 1st edn (McGregor, P., ed.). Cambridge Univ. Press, Cambridge, UK, pp. 115–126.
- Breithaupt, T. & Atema, J. 2000: The timing of chemical signaling with urine in dominance fights of male lobsters (*Homarus americanus*). *Behav. Ecol. Sociobiol.* **49**, 67–78.
- Breithaupt, T. & Eger, P. 2002: Urine makes the difference: chemical communication in fighting crayfish made visible. *J. Exp. Biol.* **205**, 1221–1231.
- Brown, W. D., Smith, A. T., Moskalik, B. & Gabriel, J. 2006: Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. *Anim. Behav.* **72**, 225–233.
- Chajewski, M. 2009: rela: Scale item analysis. R package version 4.1.
- Fitzsimmons, L. P. & Bertram, S. M. 2013: Playing to an audience: the social environment influences aggression and victory displays. *Biol. Lett.* **9**, 20130449.
- Fox, J. & Weisberg, S. 2011: *An {R} Companion to Applied Regression*, 2nd edn. Sage, Thousand Oaks, CA.
- Grafe, T. U. & Bitz, J. H. 2004: An acoustic postconflict display in the duetting tropical boubou (*Laniarius aethiopicus*): a signal of victory? *BMC Ecol.* **4**, 1–6.
- Grafen, A. 1987: The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.* **3**, 462–467.
- Hack, M. A. 1997: The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behav. Ecol.* **8**, 28–36.
- Hasson, O. 1997: Towards a general theory of biological signaling. *J. Theor. Biol.* **185**, 139–156.
- Huang, H., Todd, P. A. & Yeo, D. C. J. 2008: Inter- and intra-specific variation in the facial colours of *Perisesarma eumolpe* and *Perisesarma indiarum* (Crustacea: Brachyura: Sesarmidae). *Hydrobiologia* **598**, 361–371.
- Katoh, E., Johnson, M. & Breithaupt, T. 2008: Fighting behaviour and the role of urinary signals in dominance assessment of Norway lobsters, *Nephrops norvegicus*. *Behaviour* **145**, 1447–1464.
- Kelly, C. D. 2006: Fighting for harems: assessment strategies during male-male contests in the sexually dimorphic Wellington tree weta. *Anim. Behav.* **72**, 727–736.
- Kraaijeveld, K. & Mulder, R. 2002: The function of triumph ceremonies in the black swan. *Behaviour* **139**, 45–54.
- Lippold, S., Fitzsimmons, L. P., Foote, J. R., Ratcliffe, L. M. & Mennill, D. J. 2008: Post-contest behaviour in black capped chickadees (*Poecile atricapillus*): loser displays, not victory displays, following asymmetrical countersigning exchanges. *Acta Ethologica* **11**, 67–72.
- Logue, D. M., Abiola, I. O., Rains, D., Bailey, N. W., Zuk, M. & Cade, W. H. 2010: Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song. *Proc. R. Soc. B* **277**, 2571–2575.
- Matsumura, S. & Hayden, T. J. 2006: When should signals of submission be given? – A game theory model. *J. Theor. Biol.* **240**, 425–433.
- Maynard Smith, J. & Price, G. R. 1973: The logic of animal conflict. *Nature* **246**, 15–18.
- Mesterton-Gibbons, M. & Sherratt, T. 2006: Victory displays: a game-theoretic analysis. *Behav. Ecol.* **17**, 597–605.
- Mesterton-Gibbons, M. & Sherratt, T. 2012: Signalling victory to ensure dominance: a continuous model. *Ann. Internat. Soc. Dynam. Games* **12**, 25–38.
- Moore, P. A. & Bergman, D. A. 2005: The smell of success and failure: the role of intrinsic and extrinsic chemical signals on the social behavior of crayfish. *Integr. Comp. Biol.* **45**, 650–657.
- Mourtede, S. C., Duganzich, D. M., Molles, L. E., Helps, S., Helps, F. & Waas, J. R. 2012: Triumph displays inform eavesdropping little blue penguins of new dominance asymmetries. *Anim. Behav.* **83**, 605–611.
- R Core Team 2013: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>.
- Riechert, S. E. 1988: The energetic cost of fighting. *Integr. Comp. Biol.* **28**, 877–884.
- Sneddon, L. U., Huntingford, F. A. & Taylor, A. C. 1997: Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav. Ecol. Sociobiol.* **41**, 237–242.
- Thorpe, K. E., Taylor, A. C. & Huntingford, F. A. 1995: How costly is fighting? Physiological effects of sustained exercise and fighting in swimming crabs, *Necora puber* (L.) (Brachyura, Portunidae). *Anim. Behav.* **50**, 1657–1666.
- Todd, P. A., Wang, W. Y., Huang, H., Belle, C. C., Lim, M. L. & Yeo, D. C. J. 2011: The function of colourful facial bands in mangrove crab (*Perisesarma*) communication. *J. Exp. Mar. Biol. Ecol.* **407**, 26–33.
- Tweedie, M. W. F. 1954: Notes on grapsoid crabs from the Raffles Museum, nos. 3, 4 and 5. *Bull. Raffles Mus.* **25**, 118–128.

- Waas, J. R. 1990: An analysis of communication during the aggressive interactions of little blue penguins (*Eudyptula minor*). In: Penguin Biology, (Davis, L. S. & Darby, J. T., eds). San Diego, CA, Academic Press, pp. 345—376.
- Waas, J. R. 1991: The risks and benefits of signalling aggressive motivation: a study of cave-dwelling little blue penguins. *Behav. Ecol. Sociobiol.* **29**, 139—146.
- Wells, K. D. 1978: Territoriality in the green frog (*Rana clamitans*): vocalizations and agnostic behaviour. *Anim. Behav.* **26**, 1051—1063.
- Zulandt Schnider, R. A., Schneider, R. W. S. & Moore, P. A. 1999: Recognition of dominance status by chemoreception in the red swamp crayfish, *Procambarus clarkii*. *J. Chem. Ecol.* **25**, 781—794.