



Research

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Animal behaviour

Contests with deadly weapons: telson sparring in mantis shrimp (Stomatopoda)

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Mantis shrimp strike with extreme impact forces that are deadly to prey. They also strike conspecifics during territorial contests, yet theoretical and empirical findings in aggressive behaviour research suggest competitors should resolve conflicts using signals before escalating to dangerous combat. We tested how *Neogonodactylus bredini* uses two ritualized behaviours to resolve size-matched contests: meral spread visual displays and telson (tailplate) strikes. We predicted that (i) most contests would be resolved by meral spreads, (ii) meral spreads would reliably signal strike force and (iii) strike force would predict contest success. The results were unexpected for each prediction. Contests were not resolved by meral spreads, instead escalating to striking in 33 of 34 experiments. The size of meral spread components did not strongly correlate with strike force. Strike force did not predict contest success; instead, winners delivered more strikes. Size-matched *N. bredini* avoid deadly combat not by visual displays, but by ritualistically and repeatedly striking each other's telsons until the loser retreats. We term this behaviour 'telson sparring', analogous to sparring in other weapon systems. We present an alternative framework for mantis shrimp contests in which the fight itself is the signal, serving as a non-lethal indicator of aggressive persistence or endurance.

1. Introduction

Game theoretical models of aggressive behaviour (reviewed in [1–3]) and empirical tests in both vertebrates [4,5] and invertebrates [6,7] find that competitors use signals to resolve contests before escalating to dangerous combat. Some mantis shrimp species (Stomatopoda) use their raptorial appendages to crack and kill hard-shelled prey with strikes that deliver forces exceeding their body weight by a thousand times or more [8,9]. During territorial contests, both sexes also use their appendages to strike competitors [10]. These conspecific strikes may be as damaging as those delivered to prey; thus, mantis shrimp should resolve contests by signalling before escalating to combat.

Some mantis shrimp species use a visual display and the ritualized exchange of strikes during territorial conflicts (reviewed in [10]). During the 'meral spread' visual display, the raptorial appendages are spread laterally and ventrally such that several parts of the appendage are presented to the competitor and the individual displaying the meral spread is biomechanically unable to strike (figure 1) [10]. The meral spread is considered a signal of aggressive motivation [10–12] and possibly performance [1]. In addition, competitors exchange strikes using a ritualized 'telson coil' behaviour [10,13], in which the receiver of a strike coils its tailplate, or telson, in front of its body to receive the blow (figure 1). How these behaviours actually resolve conflicts has yet to be examined in this system. More broadly, studying processes of conflict resolution is essential for understanding the evolution of deadly weapons for both inflicting and circumventing injury.

Here we test how *Neogonodactylus bredini* competitors use meral spreads and telson strikes to resolve sex- and size-matched contests. We predicted that few contests would escalate to striking, and instead most contests would be resolved by meral spread displays. We also predicted that appendage morphological

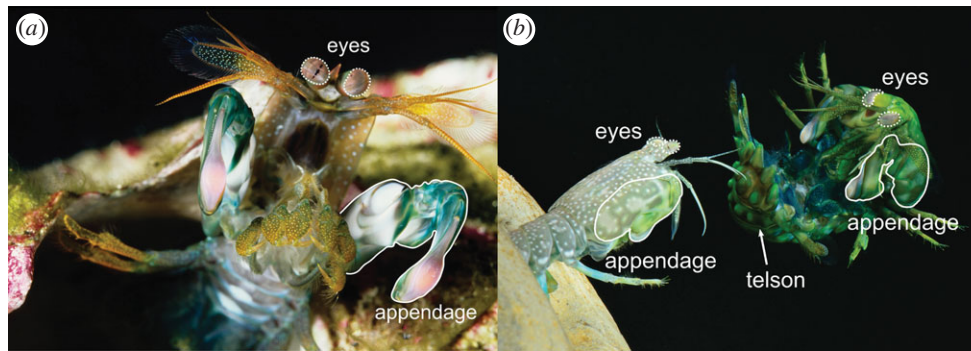


Figure 1. During aggressive contests, mantis shrimp often present meral spread displays (a). When receiving a strike during a ritualized fight (b), an individual coils its tailplate in front of its body in a ‘telson coil’ posture. Eyes (dotted lines), one raptorial appendage (solid lines) and telson (arrow) are labelled. (a) *Neogonodactylus wennerae* and (b) *Neogonodactylus oerstedii*. Images courtesy of Dr Roy Caldwell. (Online version in colour.)

components presented during meral spreads act as index signals [14] of strike performance (*sensu* [15]) via a strong correlation between the size of appendage components and maximum strike force (e.g. [16]). Finally, based on other studies of weapon performance in size-matched contests [16–18], we predicted that winners of contests would strike with greater maximum force than losers.

2. Material and methods

See the electronic supplementary material for additional details. We collected individuals from burrows in coral rubble. We measured body length, body mass and three morphological components visible during meral spreads that are biomechanically important for storing elastic energy and delivering strikes. Strike performance was defined as the maximum peak force from 10 strikes, following standard organismal performance methodology [16–18].

We paired 68 unique individuals in 34 sex- and body length-matched (mean difference $2.0\% \pm 1.2\%$; range <0.01 – 4.0%) contests over access to a body length-matched artificial burrow [19] following commonly used methods in contest behaviour research [7,11,12,18,20]. After giving the burrow resident 3–6 h to acclimate, we acclimated a second individual (the ‘intruder’) behind an opaque barrier for 10 min. We then lifted the barrier and recorded contest behaviours until one competitor was deemed the winner (see the electronic supplementary material videos). The winner was defined as the individual that resided in the burrow after the other made a clear, directed retreat toward the edge of the arena. Burrow residents have been found to win contests more often [11–13], yet we saw no resident advantage (perhaps due to brief residency time) and did not use residency as a factor in our analyses.

To test whether meral spreads occurred at the beginning of contests to avoid escalation to striking, we compared the number of contests that began with competitors displaying meral spreads to those that began with other behaviours, including striking, visually tracking competitors, and flicking antennae. We also asked whether meral spreads were used to resolve conflicts by comparing the number of contests resolved by meral spreads to the number that escalated to striking.

When contests escalated to striking, we tested how telson strikes were used in conflict resolution. We analysed the contest videos and counted the number of strikes received on a competitor’s telson compared with other parts of the body. We also tested whether winners and losers of contests differed in strike force, the number of strikes delivered during a contest, body length (within the size-matched range) and body mass.

We tested whether meral spreads displayed index signals of strike force by correlating maximum strike force with body

length, body mass and the size of three appendage morphological components (generalized linear model: gamma error distribution, log-link function; reduced using Akaike information criterion simplification [21]). We calculated partial correlation coefficients (partial r^2) between maximum strike force and the independent effect of each morphological component. A high amount of variation (low partial r^2) between a morphological component’s independent effect and maximum strike force suggests that the size of that component, independent of the size of other components or body size, does not reliably signal strike force [22]. Alternatively, a high partial r^2 suggests component size may reliably signal strike force [16].

3. Results

Meral spreads were not used to avoid escalation to strikes. Meral spreads were not more common than other behaviours at the beginning of contests (one-sided proportions test: $\chi_1^2 = 0.266$, $p = 0.246$), and 33 of 34 contests escalated to striking, even after competitors presented meral spreads (17/18 contests).

Meral spreads also did not display index signals of strike force: there was only a weak correlation between appendage morphological components and strike force. Saddle length, the component with the highest partial r^2 , accounted for only 5.9% of variation in strike force (electronic supplementary material, table S1 and figure S1). In comparison, other studies have described potential index signals with r^2 values greater than 0.40 [16,23].

Winners of contests did not have greater maximum strike force than losers; instead, winners struck a greater number of times during contests (table 1 and figure 2). Winners also had greater body mass than losers, although this variable was collinear ($r^2 = 0.31$) with body length.

When contests escalated to striking, almost every strike (214/227, 94.3%, one-sided proportions test: $\chi_1^2 = 176.2$, $p < 0.001$) was received on the competitor’s telson in a telson coil posture. In rare cases, as the loser was retreating the winner escalated past striking to stabbing. During stabbing, the raptorial appendage was used to puncture the competitor’s abdomen, resulting in significant injury.

4. Discussion

In contrast to our predictions, *N. bredini* competitors did not use meral spreads to resolve size-matched contests by presenting

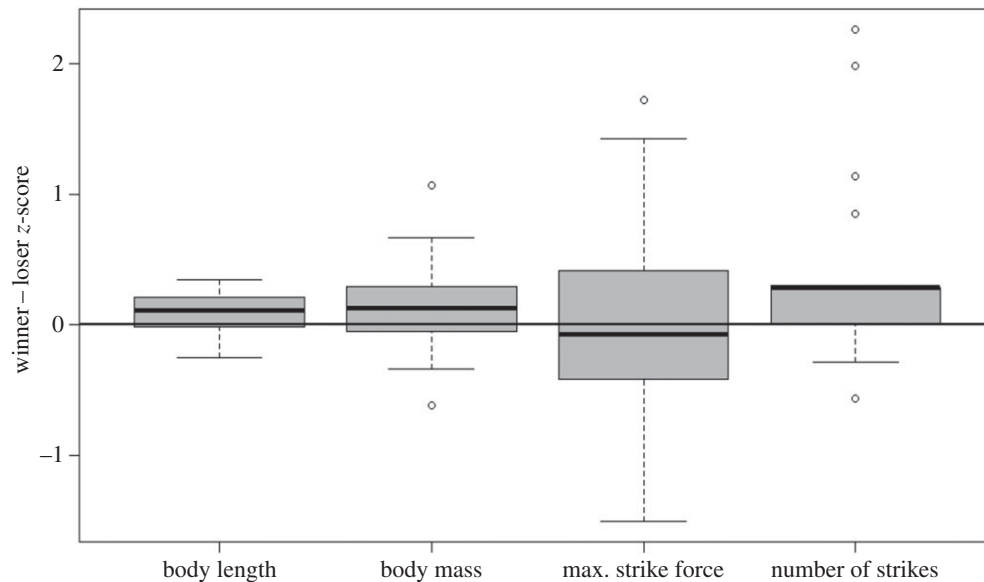


Figure 2. Winners of contests do not have greater strike force than losers; instead, winners strike a greater number of times during contests. Each variable was z-score transformed. The *y*-axis shows the winner minus loser z-score. Dark solid lines represent median z-score, box ends represent 25% and 75% quartiles, whiskers represent the most extreme values within $1.5\times$ the interquartile range and open circles represent values greater than 3 s.d. from the mean.

Table 1. Winners (*W*) of contests do not have greater strike force than losers (*L*); instead, winners strike a greater number of times during contests. The mean difference between winner and loser values is indicated for each variable followed by the statistical tests of these differences. Emboldened values represent significant differences ($p < 0.05$). Body length was correlated with body mass (see Results). See the electronic supplementary material for explanation of statistical analyses.

variable	<i>W</i> – <i>L</i> mean \pm s.e.	<i>p</i> -value	statistical analysis	Hedge's <i>g</i>	95% CI of Hedge's <i>g</i>
body length	0.31 \pm 0.16 mm	0.058	two-sided <i>t</i> -test	0.330	–0.023, 0.713
body mass	0.08 \pm 0.03 g	0.020	two-sided <i>t</i> -test	0.409	0.057, 0.735
maximum strike force	–2.48 \pm 9.31 N	0.604	one-sided <i>t</i> -test	–0.045	–0.392, 0.288
number of strikes	0.97 \pm 0.35 strikes	0.005	two-sided Wilcoxon	0.469	0.201, 0.659

index signals of strike force. Instead, most contests escalated to the ritualized exchange of strikes, and almost all strikes were received on the telson. These results evoke parallels to sparring in mammals [4,24], in which weapons are used in a ritualized manner and damage is unlikely. Thus, we introduce the term 'telson sparring' to describe the function of ritualized strikes in mantis shrimp contests. While the signalling function of sparring is often difficult to quantify, our finding that winners deliver more strikes than losers suggests that telson sparring may communicate aggressive persistence or physiological endurance. Alternatively, or additionally, sparring may signal performance other than peak strike force [25].

The close match between body and contested burrow size in the field [19] makes size-matched contests likely; however, future work should investigate the progression of behaviours in non-size-matched contests. One study found variation in the number of strikes and meral spreads given to larger or smaller competitors, but did not measure the progression of these behaviours throughout a contest [11], which is essential information for theoretical models of escalation [26].

Telson sparring illuminates how animals with lethal weapons potentially lower their risk of fatality by using ritualized fighting to signal persistence, endurance or performance [3]. Indeed, the telson's mechanical behaviour suggests that impact dynamics may inform competitor assessment. The telson dissipates a high percentage of impact energy and the amount of energy returned to the striker correlates with the

size of the receiving animal [27]. As body size can be difficult to visually assess in burrows, telson sparring may communicate a competitor's size. Telson sparring thus reveals multiple potential signalling functions for high-force strikes in mantis shrimp. These findings encourage new perspectives on other well-studied weapon systems, in which peak force has been the key measured variable, yet which may be using sparring strategies to reduce the risk of damage during contests.

Ethics. This work complied with animal welfare guidelines at both STRI in Panama and at Duke University, USA. Detailed animal welfare information is available in the electronic supplementary material.

Data accessibility. Supplementary materials, results and videos are available in the electronic supplementary material. Datasets and high-quality supplementary videos are available on Dryad (<http://dx.doi.org/10.5061/dryad.pd256>).

Authors' contributions. P.A.G. collected and analysed the data. P.A.G. and S.N.P. wrote the paper. Both authors gave final approval for publication.

Competing interests. We have no competing interests.

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