Meral-Spot Reflectance Signals Weapon Performance in the Mantis Shrimp *Neogonodactylus oerstedii* (Stomatopoda)

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Abstract. During animal contests over resources, opponents often signal their fighting ability in an attempt to avoid escalating to physical attack. A reliable signal is beneficial to receivers because it allows them to avoid injuries from engaging in contests they are unlikely to win. However, a signaler could benefit from deceiving an opponent by signaling greater fighting ability or greater aggressive intent than the signaler possesses. Therefore, the reliability of agonistic signals has long intrigued researchers. We investigated whether a colored patch, the meral spot, signals weapon performance in the stomatopod *Neogonodactylus oerstedii*. During fights over possession of refuges, stomatopods can injure or even kill opponents with their ultrafast strike. We found that darker meral spots correlate with higher strike impulse, which reflects the total force integrated over time. Furthermore, we demonstrate that stomatopods that strike more often with both appendages have darker meral spots and that the first hit in a two-appendage strike has a greater mean strike impulse than that of a single-appendage strike. This indicates that stomatopods with darker meral spots tend to invest more energy in each strike. Our results provide evidence that stomatopods use total reflectance as an honest signal of weapon performance or aggressive intent. This improves our understanding of the evolution of agonistic signals.

Introduction

Animals commonly compete over resources such as food, territories, or mates. In these situations, one individual will receive a benefit from winning, and one will experience a cost from losing (Maynard Smith, 1979; Searcy and Nowicki, 2005);

but both may experience a cost if they are injured during the competition. Therefore, they each benefit from accurately assessing their opponent and resolving a contest without physical combat. This could be achieved by first signaling their fighting ability, commonly termed their "resource holding potential" (Parker, 1974) or their aggressive intent (Enquist, 1985). It might seem that the signaler would benefit from deceiving an opponent by signaling greater fighting ability or aggressive intent than it possesses. Conversely, a receiver will benefit from responding to the signal only if that signal is honest. If cheating became sufficiently common, receivers would no longer benefit from responding to the signal, and the signaling system would no longer function (Maynard Smith, 1979; Searcy and Nowicki, 2005). Thus, signaling theory predicts that these signals must be "honest on average" to persist in the population (Maynard Smith and Parker, 1976; Johnstone and Grafen, 1993; Searcy and Nowicki, 2005).

Color is commonly used as a signal of resource holding potential in agonistic encounters throughout the animal kingdom, including animals such as birds (Pryke *et al.*, 2001; Siefferman and Hill, 2005), reptiles (Whiting *et al.*, 2006; Ligon and McGraw, 2016), fish (Gerlach *et al.*, 2014; Kelley *et al.*, 2016), and cephalopods (Adamo and Hanlon, 1996; Scheel *et al.*, 2016). In these cases, the honesty of the signal is maintained because producing the color is costly, due to physiological constraints (Lozano, 2001), social costs (Ligon and McGraw, 2016), increased predation risk (Moodie, 1972), or nutritional or energetic limitations (Frischknecht, 1993). For example, many red or orange patches are produced from carotenoid pigments. These carotenoids must be ingested, and in addition to creating colored patches, they are also required for immune function or other physiological functions (Britton, 2008; Svensson and Wong, 2011). Thus, carotenoids are limited, and animals must resolve a trade-off between creating a deeply colored patch and maintaining adequate immunity. Although there are many studies investigating color signal hon-

esty in fish (Candolin, 2000; Balzarini *et al.*, 2016) and in terrestrial animals including birds (Pryke *et al.*, 2001; McGraw, 2007), reptiles (Whiting *et al.*, 2006; Ligon and McGraw, 2016), and insects (Lindstedt *et al.*, 2010; Blount *et al.*, 2012), there are few examples in aquatic invertebrates (but see Cortesi and Cheney, 2010). Such information about agonistic signals is essential to understand whether color signaling theory extends across more taxa than are currently studied.

One aquatic invertebrate group that likely uses color signals is the stomatopod group (mantis shrimps). Previous work has shown that they probably use color signals during contests for possession of refuges (Caldwell and Dingle, 1975, 1976; Franklin *et al.*, 2016, 2017). Refuges, such as holes in coral rubble or rock, are required to process food, escape predators, mate, and brood eggs (Caldwell, 1987). During contests, stomatopods often strike their opponent with their raptorial appendages. Stomatopod strikes are extremely powerful and fast, generating forces thousands of times the stomatopod's body weight (Patek *et al.*, 2004; Patek and Caldwell, 2005);

and these strikes may injure or even kill an opponent (Caldwell and Dingle, 1975; Berzins and Caldwell, 1983). Before physical blows, stomatopods often perform a threat display called a "meral spread" (Fig. 1A; Dingle, 1969). This posture shows the color of a patch, called the meral spot, which seems to indicate fighting ability or aggressive intent (Caldwell and Dingle, 1975, 1976; Franklin *et al.*, 2016, 2017).

Despite the high cost of fighting, we do not know whether stomatopods first signal fighting ability to opponents. Indeed, Green and Patek (2015) found that the meral spread was not used to avoid escalation in size-matched pairs of the stomatopod *Neogonodactylus bredini*. They found that nearly all conflicts between individuals of similar size and fighting ability escalated to strikes, even after a meral spread. Moreover, the winners of a contest did not have the strongest strike; instead, they struck the loser more times (Green and Patek, 2015). However, *N. bredini* has a white meral spot, not a colored patch. Other stomatopod species, such as *Neogonodactylus oerstedii* (studied here; Hansen, 1895), have a colored meral
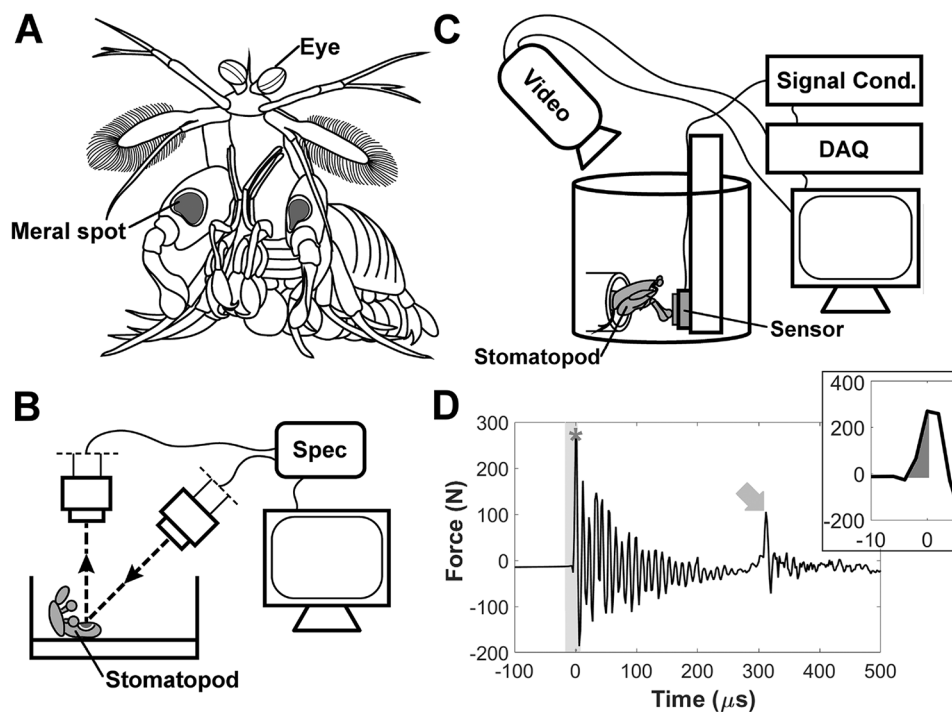
Figure 1.   Schematic images of a mantis shrimp performing the meral spread, and the experimental setup. (A) During the meral spread threat display, the raptorial appendages are pulled laterally, and the meral spots are displayed (shaded dark gray). (Adapted from A. M. Franklin *et al.,* 2017, *Behav. Ecol.* 1329–1336. By permission of Oxford University Press on behalf of the International Society for Behavioral Ecology.) (B) The spectrophotometer (Spec) was set up with the light source at 45° and the collector probe perpendicular. The light path is indicated by arrows. (C) Strike force from a stomatopod was recorded with a one-axis force sensor and filmed at 16,000 frames per second. The signal was processed through a signal conditioning box (Signal Cond.) and a data acquisition device (DAQ). (D) Typical force reading. The gray asterisk indicates the peak force from a strike, and the gray arrow indicates force from the cavitation bubble collapsing. Oscillations are due to the resonant frequency of the sensor. Light gray shading indicates inset region. Inset is the first peak recorded and shows the calculation of impulse (gray shading).

spot that may signal resource holding potential (Franklin *et al.*, 2016, 2017).

Stomatopod species with colored patches are known to use color signals during contests over refuges (Franklin *et al.*, 2016, 2017), but the information content of these signals remains a mystery. Recent research that manipulated signal color in *N. oerstedii* demonstrated that receivers increase agonistic behaviors toward opponents with lighter-colored spots (*i.e.*, increased total reflectance) or toward those with decreased ultraviolet (UV) reflectance (Franklin *et al.*, 2016, 2017). Thus, behaviorally, it appears that the meral spot color signals fighting ability or aggressive intent; but does it represent an honest signal?

To investigate signal honesty, we determined whether aspects of the signal correlate with the whole organism's performance. Whole-organism performance refers to an animal's ability to conduct an ecologically relevant task (*e.g.*, sprinting rapidly or biting forcefully), as opposed to measurements of physiological effects at lower functional levels (*e.g.*, producing enzymes; Irschick *et al.*, 2008; Lailvaux and Husak, 2014). For example, higher bite force in collared lizards is correlated with components of the gape display and with blue coloration (Lappin *et al.*, 2006; Plasman *et al.*, 2015). Many other studies across different taxa have linked whole-organism performance with components of threat signals (Lailvaux *et al.*, 2005; Lappin *et al.*, 2006; Bywater *et al.*, 2008; Henningsen and Irschick, 2012; Mowles and Briffa, 2012). Although whole-organism performance is not the same as fighting ability (*i.e.*, the animal's ability to win a contest), studies have demonstrated a link between whole-organism performance, including weapon performance, and contest outcome (*e.g.*, crayfish, Bywater *et al.*, 2008; hermit crabs, Mowles *et al.*, 2010).

To investigate the relationship between components of threat signals and performance, it is essential to consider the reliability of performance measurements. For example, recordings of lizard bite force are affected by the measuring device, where in the mouth the bite is applied, low sample size, lizard temperature, and lizard motivation (Losos *et al.*, 2002; Anderson *et al.*, 2008). We attempted to minimize these errors by using reliable equipment, strict requirements for usable measurements, a minimum number of measurements per individual, and constant experimental conditions. Despite these requirements, maximum measures of performance can still be affected by animal motivation and by variable numbers of recordings per individual (Losos *et al.*, 2002; Hagey *et al.*, 2016). To overcome these issues, we modeled each stomatopod's performance using the Weibull distribution, instead of using the maximum measurement recorded (following the procedure in Hagey *et al.*, 2016).

As our measurement of whole-organism performance, we recorded peak force (N) and impulse (N · s) from stomatopod strikes (following Patek and Caldwell, 2005). The peak force is related to the stress in the material that the stomatopod is striking, which then contributes to deformation and, potentially, failure. It is also related to the material properties of the material; the very stiff steel sensor used here records very high peak forces for a very short duration, but a softer material would have a smaller peak force absorbed over a longer duration (Patek and Caldwell, 2005). The impulse, the integral of force through time, helps to compare these two cases. Tests on circular steel plates showed that deformation and failure of the plate are linearly proportional to the applied impulse, not the peak force (Florence, 1966; Corbett *et al.*, 1996). Thus, a large force over a short time or a small force over a long time may have the same impulse and the same potential to damage the object that the stomatopod is striking.

We used these measures of whole-organism performance to investigate meral spot signal honesty in *N. oerstedii*. Meral spot color in *N. oerstedii* is likely based on carotenoproteins (Newbigin, 1897; Zagalsky *et al.*, 1970; Bandaranayake, 2006), which are carotenoids that have formed chemical complexes with proteins. Because carotenoids must be ingested, a darker meral spot that would require more pigment may indicate a stomatopod that has had more success foraging and that is in better condition. Therefore, we predicted that strike force and strike impulse would increase as the darkness of the meral spot increases.

Materials and Methods

Stomatopod husbandry

Stomatopods (*Neogonodactylus oerstedii* (Hansen, 1895)) were ordered commercially (KB Marine Life, Big Pine Key, FL) and shipped overnight to Tufts University, Medford, Massachusetts. They were housed under a 12h : 12h light : dark cycle in artificial seawater maintained at 33–35 ppt salinity and 22–25 °C. Aquaria (75 L) were divided into 3 compartments, with 1 stomatopod housed per compartment. Stomatopods could not see other individuals. Water was circulated through a carbon filter and flowed through all three compartments. Each stomatopod was provided with a 3-inch section of 0.5-inch polyvinyl chloride tube as a refuge. Twice per week stomatopods were fed pollock, and one-third of the water was changed. When stomatopods were to be tested, they were transferred in their refuge to a 1-L bucket 3 days before force measurements were to be recorded. These buckets were maintained at 22 °C and aerated with air pumped through an air stone, and the twice weekly water changes continued. The 1-L buckets let us transfer buckets to the testing area with minimal disturbance to the stomatopods. Stomatopods were housed in captivity for at least one month to allow for acclimation and to ensure that we were testing stomatopods that had not recently molted (*i.e.*, intermolt). To avoid any physiological deterioration due to time in captivity, we only analyzed data from stomatopods that were housed in the lab for fewer than 100 days.

Force measurements

To measure strike force, we used a one-axis force sensor (model 200B02, PCB Piezotronics, Depew, NY), which was placed near the entrance to the refuge (Fig. 1C). The sensor had one layer of yellow Octavia laminating film (10 μm thick, GBC, Lake Zurich, IL) stuck to it, because this helped to elicit a strike. To further encourage a stomatopod to strike, we put shrimp paste on the sensor. If the shrimp paste did not work, we also waved a thin strip of yellow laminating film in between the sensor and the refuge. This plastic decoy was removed before the strike, so the stomatopod did not strike through the decoy. Data were recorded at 500 kHz, using LabView (ver. 15.0.1, National Instruments, Austin, TX) with a USB-6343 data acquisition system (National Instruments). From these force recordings, we first subtracted a baseline reading, averaged in the window from 500 μs to 10 μs before the strike. Then we calculated strike force (the amplitude of the first peak relative to the baseline) and impulse (the integral of force over time from 50 μs before the first peak, up to the time of the first peak), using custom MATLAB code (vR2014a, Mathworks, Natick, MA; Fig. 1D). Each recording had oscillations due to the resonant frequency of the sensor (Fig. 1D), but it was not possible to get sensors with higher resonant frequencies. All trials were conducted under bright lights and were filmed at 16,000 frames per second, 60 μs exposure time, and 320 $\times$ 240 resolution, using a Phantom Miro M120 camera (Vision Research, Wayne, NJ). From the video footage, we recorded whether the stomatopod struck with 1 or 2 appendages, whether the strike was near the center of the sensor (> ~1 mm from the edge), and whether the strike was perpendicular to the sensor (*i.e.*, did not glance across the sensor; Video 1, available online). The video footage was synchronized to the force recording to distinguish force peaks from each appendage and from cavitation. Strikes were used in subsequent analysis only if they were perpendicular, near the center of the sensor, and if we could calculate the force from one appendage only (*i.e.*, force peaks matching the video footage were discernible in the output for each appendage and/or cavitation). When stomatopods struck with two appendages, only data from the first appendage that contacted the sensor were used. Three stomatopods were excluded from analysis because we did not obtain five usable strikes. We obtained 5–11 suitable strikes from 4 males and 14 females.

Meral spot color and size

After strike measurements were recorded, we recorded the spectral reflectance and size of each of the stomatopod's meral spots. Crustacean colors can change dramatically after a molt (Wade *et al.*, 2005), and meral spot total reflectance is greater immediately after a molt (Reaka, 1975; Franklin *et al.*, 2017). Thus, to ensure that we were recording intermolt meral spot color similar to wild populations, only animals that had not molted since arriving in the laboratory (*i.e.*, for at least one month) were included in the analysis. No stomatopods molted within the week after testing procedures concluded. To record meral spot measurements, live stomatopods were anesthetized by cooling them in the freezer (-13 °C) until they stopped moving. This took about 20 min in 25 mL of seawater. Spectral measurements were recorded using a JAZ spectrophotometer (Ocean Optics, Largo, FL) with a pulsed xenon light source. Reflectance was recorded between 300 and 750 nm and was measured relative to a WS-1 white standard. The light source and collecting probes were 600 μm UV-visible fiber-optic cables (Ocean Optics) with collimating lenses attached to the end. Both were fixed 20 mm from the meral spot, in a position that mimicked natural lighting conditions (Endler, 1990), with the light source at 45° to the meral spot surface and the collecting probe perpendicular to it (Fig. 1B). The collecting probe was focused to a diameter of 1 mm, which is smaller than the diameter of meral spots of stomatopods used in this study. In a petri dish, stomatopods were placed on one side, and the lower raptorial appendage was pulled posteriorly and pinned so that the meral spot was exposed and facing up. Two measurements each were taken of both the left and right meral spot in air. Meral spot color does not vary between left and right meral spots (Franklin *et al.*, 2016); therefore, these four spectra were averaged to obtain one spectral measurement for each stomatopod. While stomatopods were in this position, we used a Dino-Lite 5.0-MP USB microscope (New Taipei City, Taiwan) to take two photos of each meral spot. Meral spots in *N. oerstedii* consist of a purple patch surrounded by a white ring (Fig. 1A). From these photos, we measured the area of the entire meral spot and just the purple patch, using Image J (https://imagej.nih.gov/ij). We then calculated the proportion of the meral spot that was pigmented and averaged to obtain one measurement for each stomatopod.

Statistical analysis

To analyze the force data, we first investigated variation in strike force and strike impulse. We determined whether these parameters were correlated by using Pearson's moment correlation coefficient. Then, for both strike force and strike impulse, we investigated whether there was a difference between experimental days (*i.e.*, duration in lab), between strikes within days, or between one-appendage and two-appendage strikes. Linear mixed models were used, with day number, strike number (within day), and appendage number as predictor variables and stomatopod ID as a random effect. The response variable was either strike force (N) or impulse (N $\cdot$ s), and both were log transformed to meet the homoscedasticity assumption of a linear model. To investigate whether the force or impulse of one strike influenced the subsequent strike, we plotted autocorrelation function estimates. Marginal hypothesis tests

using the chi-square statistic were conducted to assess the significance of each term.

We then used a Weibull distribution to estimate peak force and impulse from all strikes recorded from an individual stomatopod (Hagey *et al.*, 2016). Because we did not obtain the same number of strikes for every stomatopod, using the maximum force or the maximum impulse recorded for each stomatopod was a biased estimate (Head *et al.*, 2012). The Weibull method allowed us to account for unequal sample sizes and downweighted any extreme values that might influence estimates (Hagey *et al.*, 2016). For each individual, we fitted a Weibull distribution to its strike force recordings and used the scale parameter of this distribution as an estimate of peak force (Hagey *et al.*, 2016). We followed the same procedure to estimate impulse for each stomatopod. From here on, we will refer to these Weibull estimates as peak force or impulse.
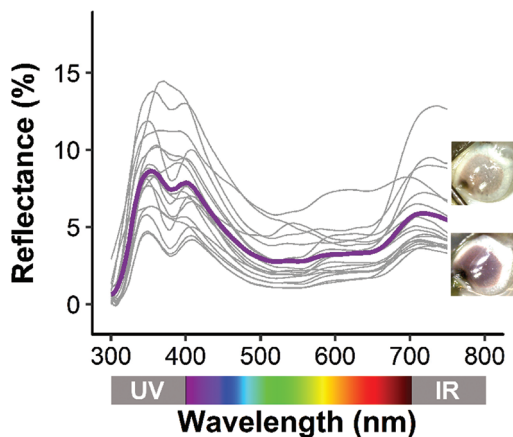
From the raw spectral reflectance data (Fig. 2), we obtained traditional measures of total reflectance and chroma. Total reflectance (%) was calculated as the mean reflectance for the interval 300–750 nm (R_{avg}; Delhey *et al.*, 2003), and chroma was calculated as $(R_{300-\lambda(R_{50})} - R_{\lambda(R_{50})-750})/R_{300-750}$, where $\lambda(R_{50})$ is the wavelength at which the reflectance is halfway between the maximum and minimum reflectances (Andersson *et al.*, 2002; Whiting *et al.*, 2006). The spectral range of 300–750 nm corresponds to the visual sensitivity of *N. oerstedii* (Marshall and Oberwinkler, 1999; Franklin *et al.*, 2016). Hue (wavelength of peak reflectance) is also commonly measured in studies investigating color signals. However, our previous research suggests that total reflectance and/or chroma are more likely to be used as a signal (Franklin *et al.*, 2017). Thus, we did not include hue, because we did not want to overparameterize the statistical model. There was no correlation between time in captivity and meral spot total reflectance or chroma (total reflectance: $F_{1, 16} = 3.8$, $P = 0.070$; chroma:

Figure 2. Spectral reflectance of *Neogonodactylus oerstedii* meral spots. Gray lines indicate spectral reflectance from individual stomatopods (averaged across both meral spots; $N = 18$), and the purple line indicates the mean spectral reflectance from stomatopods in this study. Insets indicate the visual difference between meral spots with higher than average (top) and lower than average (bottom) total reflectance. IR, infrared; UV, ultraviolet.

$F_{1, 16} = 2.0$, $P = 0.18$). Total reflectance and chroma also did not vary significantly between the sexes (total reflectance: $F_{1, 16} = 0.65$, $P = 0.43$; chroma: $F_{1, 16} = 0.06$, $P = 0.81$). Therefore, we did not include sex in any subsequent analyses, because of the small number of males in the sample (4 of 18).
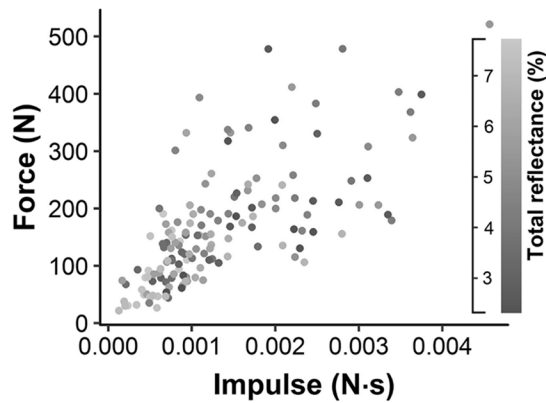
Linear models were used to investigate the relationship between performance estimates (peak force and impulse), meral spot total reflectance or chroma, body length, and duration of captivity. The proportion of the meral spot that was pigmented was also initially included as a predictor; however, this parameter negatively correlated with total reflectance ($F_{1, 16} = 5.2$, $P = 0.037$, $r^2 = 0.25$) and was not correlated with peak force ($\chi^2 = 0.05$, df $= 1$, $P = 0.81$) or impulse ($\chi^2 = 0.04$, df $= 1$, $P = 0.85$), and so it was removed to avoid multicollinearity. We calculated variance inflation factors for the remaining predictor variables, and all were less than 2, indicating no further collinearity issues (Zuur *et al.*, 2010). Strike force in stomatopods has been shown to increase with overall body size as well as with measurements of raptorial appendage size (Patek and Caldwell, 2005; Zack *et al.*, 2009; Claverie *et al.*, 2011). Following Claverie *et al.* (2011), we elected to include body length as a predictor in our models, rather than scale our peak force or impulse measurements. We used a lognormal probability error distribution for both peak force and impulse models because quantile-quantile plots, residual plots, and the Akaike information criterion suggested that this distribution fitted the data best. To investigate the influence of each term, marginal hypothesis tests were conducted using the chi-squared statistic to compare the fit of the full model with that of the nested model (without one term). For significant terms, we also calculated a pseudo-R^2 as $R^2 = 1 - (D_\alpha/D_0)$, where D_0 is the deviance of the null model and D_α is the deviance of the model including the parameter of interest (Cameron and Windmeijer, 1997; Coxe *et al.*, 2013). The coefficient of determination (r^2) is not calculated because generalized linear models use a maximum likelihood estimator rather than ordinary least squares regression. Pseudo-R^2 is a measure of improvement in model fit, with the addition of the parameter of interest, and it is not directly comparable to r^2. Following this, we conducted a *post hoc* test investigating whether total reflectance values differed between stomatopods that strike primarily with one or two appendages. All analyses were conducted in R 3.3.1 (R Core Team, 2014). The survival package (Therneau and Grambsch, 2000) was used to fit Weibull distributions, the lme4 package (Bates *et al.*, 2015) to fit the linear mixed models, and the *Anova* function in the car package for marginal hypothesis tests (Fox and Weisberg, 2011).

Results

We found a strong correlation between strike force and strike impulse ($t = 12.3$, df $= 162$, $P < 0.001$, $r^2 = 0.48$; Fig. 3). However, the variation within this correlation was large (Fig. 3), so

Figure 3. Strike force and strike impulse of *Neogonodactylus oerstedii* individuals are positively correlated with each other and with the darkness of the meral spot ($r^2 = 0.48$). Each dot is one strike. Shading indicates the mean total reflectance value for the meral spot of the striking stomatopod ($N = 18$), where darker shading indicates darker meral spots.

we elected to conduct all analyses on both strike impulse and strike force. Neither parameter was affected by experimental day number (strike impulse: $\chi^2 = 1.71$, df = 1, $P = 0.19$; strike force: $\chi^2 = 2.69$, df = 1, $P = 0.10$) or strike number within day (strike impulse: $\chi^2 = 0.01$, df = 1, $P = 0.93$; strike force: $\chi^2 = 0.68$, df = 1, $P = 0.41$; Table 1). Furthermore, there was no autocorrelation in the residuals, indicating that the force or impulse of one strike did not influence the next strike. Strike force was not influenced by whether the stomatopod struck with one or two appendages ($\chi^2 = 0.37$, df = 1, $P = 0.54$); but one-appendage strikes had lower strike impulse than two-appendage strikes, even for strikes from the same individual ($\chi^2 = 10.91$, df = 1, $P < 0.001$; Table 1).

Stomatopods with darker meral spots struck with a greater impulse, and there was a trend toward these individuals also striking with greater peak force (Fig. 4; impulse: $\chi^2 = 5.44$, df = 1, $P = 0.020$, pseudo-$R^2 = 0.17$; peak force: $\chi^2 = 3.75$, df = 1, $P = 0.053$, pseudo-$R^2 = 0.20$; Fig. 4; Table 2). Impulse and peak force were also positively correlated with stomatopod body length (impulse: $\chi^2 = 10.28$, df = 1, $P = 0.001$, pseudo-$R^2 = 0.20$; peak force: $\chi^2 = 5.36$, df = 1, $P = 0.021$, pseudo-$R^2 = 0.10$; Table 2; Fig. A1). Peak force also negatively correlated with duration of captivity ($\chi^2 = 4.01$, df = 1, $P = 0.045$, pseudo-$R^2 = 0.30$; Fig. A2), whereas impulse did not correlate with duration of captivity ($\chi^2 = 2.32$, df = 1, $P = 0.13$). Neither impulse nor peak force correlated with chroma (impulse: $\chi^2 = 0.015$, df = 1, $P = 0.90$; peak force: $\chi^2 = 0.002$, df = 1, $P = 0.96$; Table 2). Stomatopod length had the largest effect in our model, accounting for a change of 120.1 N and 2.1 mN · s across the range of stomatopods we measured (37.4–53.6 mm). Meral spot total reflectance had the second-largest effect, accounting for a change of 106.3 N force and 1.4 mN · s over the range of spectral intensities measured. On average, strike force also decreased by 101.2 N over the testing period, but impulse did not change significantly.

When stomatopods struck with both appendages, the appendages usually did not contact the sensor simultaneously. The results reported above indicated that for two-appendage strikes, the first appendage produced a larger strike impulse than that from a one-appendage strike. Therefore, we conducted a *post hoc* analysis to investigate whether mean total reflectance correlated with the number of appendages used in the strike. Stomatopods that struck with two appendages more often had darker meral spots than those that struck with one appendage more often ($F_{1, 143} = 5.59$, df = 1, $P = 0.019$).

Discussion

Here we demonstrate for the first time that stomatopod weapon performance correlates with the total reflectance of stomatopods' meral spots. Stomatopods with darker meral spots had higher strike impulse, and there was a trend toward higher strike force. If strike impulse or force predicts competitive success, these differences suggest that meral spot total reflectance signals fighting ability during agonistic encounters. Moreover, stomatopods with darker spots tended to strike more often with both appendages; and the strike impulse of the first appendage in a two-appendage strike tended to be higher than the strike impulse of a single-appendage strike, even for strikes from the same individual. Thus, stomatopods with darker meral spots tend to invest more metabolic energy in each strike than do stomatopods with lighter meral spots. Together, these results suggest that the total reflectance of the meral spot provides an honest signal of opponent weapon performance.

There is evidence that stomatopods may use this information to assess opponents in contests. They are known to assess total reflectance of the meral spot during territorial contests (Franklin *et al.*, 2017). Franklin and colleagues experimentally increased total reflectance of the meral spot by using an ultrafast laser. The range in meral spot total reflectance of both treatment and control stomatopods was similar to the range reported here (current study: 2.3%–7.8%; 2017 study control: 1.8%–

Table 1

Results of marginal hypothesis tests for the effects of day number, punch number within day, and arm number on Neogonodactylus oerstedii *strike force and strike impulse*

Variable	χ^2	df	P
Strike force			
Day number	3.30	1	0.069
Punch number within day	0.68	1	0.41
Arm number	0.40	1	0.53
Strike impulse			
Day number	2.70	1	0.10
Punch number within day	0.01	1	0.92
Arm number	11.23	1	**<0.001**

Bold indicates $P < 0.05$.
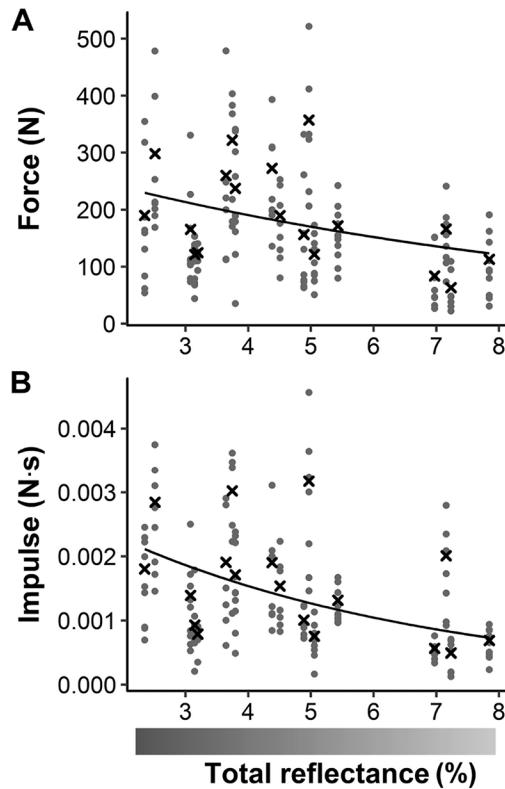
Figure 4. *Neogonodactylus oerstedii* with darker meral spots (lower total reflectance) show a trend toward having higher peak force (A; *P* = 0.053) and have significantly greater impulse (B; *P* = 0.020). Dots indicate individual strikes, and crosses indicate the Weibull estimates for each stomatopod (*N* = 18). The line shows the relationship predicted from the Gaussian generalized linear model, with a log link function. The shaded bar indicates the approximate total reflectance of the meral spot. Total reflectance is calculated as the mean reflectance for the interval 300–750 nm.

4.6%; 2017 study treatment: 3.7%–5.8%, AMF, unpubl. data), suggesting that stomatopods can perceive this variation. Together, these results suggest that total reflectance signals weapon performance to an opponent, which may be an indicator of resource holding potential. This is likely to be valuable information to a stomatopod during a contest over possession of a refuge. During these contests, one stomatopod is partially concealed within the refuge, and it may be difficult for a challenger stomatopod to assess the resident's size. Meral spot total reflectance could provide an honest signal of resource holding potential, thus allowing stomatopods to avoid injuries from contests escalating to physical combat (Berzins and Caldwell, 1983) when opponents are not equally matched. To complete the link between strike force or impulse and resource holding potential, further studies of *Neogonodactylus oerstedii* should investigate whether stomatopods that win contests have greater strike force or strike impulse.

In the group of stomatopods studied here, it might appear that reflectance is separated into two groups (those with reflectance less than 5.5% and those with reflectance greater than 6.9%, in Fig. 4). Previous research has demonstrated that bi-

modal distributions can be biologically important (*e.g.*, Nelson and Marler, 1989). However, the division was not related to any group within the data set, including sex or size class, and previous research with larger samples sizes has not detected two groups (Franklin *et al.*, 2016). This suggests that the pattern is not biologically relevant but rather is a characteristic of our sample.

Moreover, meral spot chroma did not correlate with peak force or impulse, suggesting that chroma does not indicate performance. It is possible that other measures of color, such as hue or UV chroma, may correlate with performance. These measures were not included in the final statistical model because of the low sample size. However, behavioral wavelength discrimination tests in the laboratory suggest that stomatopods have relatively coarse color vision in the visible spectrum (Thoen *et al.*, 2014). This result led Thoen and colleagues to suggest that stomatopods do not process color similarly to other organisms. While we do not know much about how stomatopods process chromatic information, this coarse spectral discrimination could indicate that stomatopods have a poor ability to detect small variations in chroma among meral spots. Although it is possible that stomatopods have greater spectral discrimination in different behavioral contexts (Jacobs, 1981; Neumeyer, 1991) or in other regions of the spectrum (*e.g.*, UV vision), the results we present here do not provide any reliable evidence that meral spot chroma is an agonistic signal.

Both impulse and peak force increased with stomatopod body length. Muscle force and power are proportional to cross-sectional area and volume, respectively, both of which are generally larger in larger animals (Schmidt-Nielsen, 1984). By these simple scaling relations, larger stomatopods should produce more powerful strikes. Indeed, previous research into scaling in stomatopod strikes has shown that force increases with increasing muscle cross-sectional area (Mendoza Blanco and

Table 2

Results of marginal hypothesis tests for the effects of total reflectance, chroma, length, and duration of captivity on Neogonodactylus oerstedii *peak force and peak impulse*

Variable	χ^2	df	*P*	Pseudo-R^2
Peak force				
Total reflectance	3.75	1	*0.053*	0.20
Chroma	0.003	1	0.96	
Length	5.36	1	**0.021**	0.10
Days in lab	4.01	1	**0.045**	0.30
Peak impulse				
Total reflectance	5.44	1	**0.020**	0.17
Chroma	0.015	1	0.90	
Length	10.28	1	**0.001**	0.20
Days in lab	2.32	1	0.13	

Pseudo-R^2 is calculated as $R^2 = 1 - (D_\alpha/D_0)$, where D_0 is the deviance of the null model and D_{α} is the deviance of the model including the parameter of interest. Bold indicates *P* < 0.05; italics indicate *P* < 0.06.

Patek, 2014), size of the raptorial appendage (striking appendage), and overall body size (Patek and Caldwell, 2005; Zack *et al.*, 2009; Claverie *et al.*, 2011). Our size range is smaller than the size range in Claverie *et al.* (2011) (this study: 37.4–53.6 mm; Claverie *et al.*: 20–60 mm), but we detected a greater range of peak force measurements (63.1–357.2 N). This may indicate that these scaling relationships differ across species or with different morphologies.

For any given individual, strike force and impulse did not appear to be influenced by our experimental schedule. We did not find any evidence that striking with greater force or impulse influences subsequent strikes or that stomatopod strikes become weaker within or across testing days. This suggests that stomatopods can recover quickly from a strike. However, in contests stomatopods can strike in faster succession than the lag between strike recordings here. On a shorter timescale, a greater investment in one strike may influence subsequent strike force, strike impulse, or strike frequency. This could result in a trade-off between investment in the current strike and investment in future strikes.

However, the duration of time an individual was held in captivity did influence peak force and meral spot total reflectance, but there was no correlation between duration of captivity and impulse. In particular, stomatopods held in the lab for longer durations had lower peak force estimates and lower meral spot total reflectance. Because of this, we excluded stomatopods from our analysis that were in the lab for more than 100 days. The magnitude of this effect was similar to the decrease in peak force associated with increased meral spot total reflectance. This suggests that lab housing may result in a mismatch between weapon performance conveyed through meral spot total reflectance and actual weapon performance. This change in total reflectance may indicate that stomatopods in the lab are lacking dietary nutrients required for color formation (Bandaranayake, 2006). Thus, prolonged housing in the laboratory may disrupt stomatopod color signaling systems and should be a consideration for behavioral experiments. Although these results indicate that stomatopods may have deteriorated during laboratory housing, when these changes are controlled for in the statistical analyses, impulse is still correlated with meral spot total reflectance, and peak force shows a negative trend ($P = 0.053$). This suggests that the results relating to meral spot total reflectance are robust.

The mechanism that maintains the honesty of meral spot total reflectance as a signal of weapon performance may be due to the pigments that give the meral spot its color. The spot's color probably comes from carotenoproteins, a set of proteins that make many purples and blues in crustaceans (Newbigin, 1897; Zagalsky *et al.*, 1970; Bandaranayake, 2006). These chemical complexes require carotenoids, which the animals cannot synthesize themselves but must ingest. The animals probably face a trade-off, because carotenoids are also required for immune and other physiological functions (Britton, 2008; Svensson and Wong, 2011). Allocating caroten-

oids for coloration means that they cannot be used for other physiological requirements. It follows that only individuals in good condition would invest heavily in ornamentation because only for them will the benefit of a stronger signal outweigh the costs (Lozano, 2001; Getty, 2006). Diet supplementation or pigment extraction coupled with high-performance liquid chromatography experiments could be conducted to determine whether this trade-off is the mechanism behind signal reliability in *Neogonodactylus oerstedii*. Such experiments could also provide insight into whether stomatopods can modify meral spot total reflectance within a molt cycle, and into the relationship between pigment density, body condition, and meral spot total reflectance.

Our results here may be generalizable to other stomatopod species with colored meral spots. Many stomatopod species have colored meral spots that they display during agonistic encounters (Caldwell and Dingle, 1975). Research suggests that colored meral spots can be assessed reliably across a range of depths, despite the reduction in short and long wavelengths associated with increasing depth (Cheroske and Cronin, 2005). Colored meral spots tend to be purple, orange, or red (to human eyes), colors that are likely created by carotenoproteins (Newbigin, 1897; Zagalsky *et al.*, 1970; Bandaranayake, 2006). Immediately after molting, when the exoskeleton is soft and stomatopods are unable to strike, these meral spots are much lighter in color (Reaka, 1975; Franklin *et al.*, 2017). Consequently, stomatopods with colored meral spots may not be able to bluff fighting ability after a molt, as has been observed in a species with a white meral spot (Adams and Caldwell, 1990). Thus, in these species meral spot total reflectance may be a reliable signal of weapon performance by indicating strike impulse (as demonstrated here) and by indicating a recent molt.

Species that have white meral spots are unlikely to signal weapon performance by using meral spot total reflectance. This is supported by observations that species with white meral spots tend to perform the meral spread less often during contests than species with colorful meral spots (Caldwell and Dingle, 1975, 1976). Furthermore, recent research in *Neogonodactylus bredini*, a species with a white meral spot, demonstrated that the meral spread is not used to resolve size-matched contests (Green and Patek, 2015). The mechanism of signal honesty we proposed above is based on pigments, which may not be present in white meral spots. White meral spots could potentially provide a signal in the UV, which has not been measured. However, the apparent lack of pigments, along with the behavioral evidence (Caldwell and Dingle, 1975, 1976; Green and Patek, 2015), suggests that white meral spots do not act as a signal of weapon performance. Instead, they may help amplify the size of the raptorial appendage, similar to markings that amplify the size of the abdomen in jumping spiders (Taylor *et al.*, 2000). Alternatively, the bright white and UV reflectance of the meral spot may improve detection of the meral spread by a receiver. Greater contrast in spectral intensity between a signal and the background can improve signal detec-

tion (*e.g.*, anoline lizards, Persons *et al.*, 1999). Further research is needed into the reflectance variability of white meral spots and into stomatopod behavioral responses to any variability present.

Green and Patek (2015) also found that strike force did not predict contest outcome; rather, the stomatopod that delivered more strikes tended to win contests. However, strike force and strike impulse likely play a role in stomatopod conflict resolution in different conditions. Green and Patek staged contests between size-matched stomatopods (all pairs <4% difference in body length). Within these pairs, the strike force differed by only 2.48 N. However, if stomatopods compete with larger or smaller opponents, the difference between opponents in strike force and strike impulse is likely to be much larger. Here, we report differences of almost 300 N in peak strike force (range: 63.2–357.2 N) and 2.7 mN · s in peak strike impulse (range: 0.5–3.2 mN · s). Stomatopod size is known to influence contest outcome in several stomatopod species (Caldwell and Dingle, 1979; reviewed in Caldwell, 1987), and studies suggest that stomatopods are more likely to escalate contests if their opponent has a weak strike (Caldwell, 1979; Berzins and Caldwell, 1983). Thus, strike impulse and force may play a role in resolving contests when contestants are not so evenly matched. Interestingly, Green and Patek (2015) also did not find a strong correlation between size of striking appendage components and strike force, suggesting that the meral spread does not indicate fighting ability. However, studies with other species of stomatopods have found strong correlations ($r^2 > 0.55$) between components of the striking appendage (*e.g.*, merus length, propodus and dactylus size) and strike force (Claverie *et al.*, 2010) or spring force (Zack *et al.*, 2009; Claverie *et al.*, 2011). Thus, the function of the meral spread during territorial contests may vary across species. Future studies should investigate the role of colored meral spots, strike impulse, and strike force in asymmetric contests, as well as compare contest behaviors between stomatopod species.

Meral spots may also play additional roles in stomatopod ecology, including in courtship rituals, species recognition, and interactions with predators. Stomatopods perform the meral spread during courtship (Hatziolos and Caldwell, 1983), and it is possible that females assess the meral spot of potential mates. We have also previously noted that females tend to have lighter meral spots than males (Franklin *et al.*, 2016). In the current study, we did not detect a difference between males and females in total reflectance; however, we had data from only four male stomatopods. Thus, more research will be required to determine whether the meral spot plays a role in sex identification. The meral spot probably also plays a role in species recognition among different stomatopod species. Meral spot color varies across stomatopod species, and stomatopods that overlap in range tend to have differently colored meral spots (Caldwell and Dingle, 1976). Lastly, the meral spot may also act as a diematic or startle display against predators (Stevens, 2005; Umbers *et al.*, 2015). Visual models investigating how a tri-

chromatic fish predator perceives *N. oerstedii* meral spots suggest that the meral spots contrast chromatically with seagrass and rubble backgrounds (AMF, unpubl. data). Thus, fish predators can likely distinguish the meral spots; but whether stomatopods use the meral spread and meral spots as a startle display has not been investigated. Consequently, further research will likely demonstrate that the meral spot is a signal that has different functions across different contexts (*i.e.*, a pluripotent signal, Hebets *et al.*, 2016).

Our research contributes to the growing literature documenting signals that advertise performance (*e.g.*, Lailvaux *et al.*, 2005; Lappin *et al.*, 2006; Bywater *et al.*, 2008; Henningsen and Irschick, 2012; Mowles and Briffa, 2012). Further research into stomatopods may identify a link between signal, performance, and ability, similar to several other studies that have demonstrated a link between performance and contest outcome (Robson and Miles, 2001; Lailvaux and Irschick, 2007; Bywater *et al.*, 2008; Mowles *et al.*, 2010). Such studies provide support for current theory that signals should be honest on average if signals are to persist in the population (Maynard Smith and Parker, 1976; Johnstone and Grafen, 1993; Searcy and Nowicki, 2005).

Acknowledgments

Data Accessibility

Data are available at the ZMAPortal (http://zmaportal.org /zmaportal/), under study ZMA14.

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Appendix
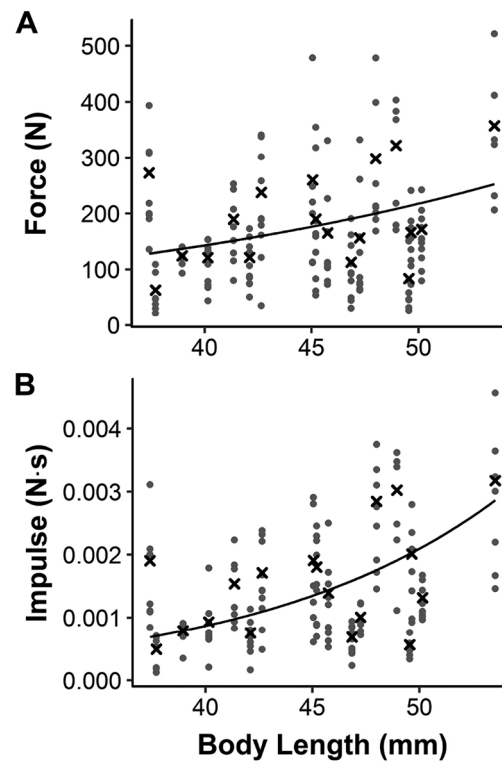
Figure A1. Larger *Neogonodactylus oerstedii* stomatopods strike with greater (A) peak force and (B) peak impulse. Dots indicate individual strikes, and crosses indicate the Weibull estimates for each stomatopod. The line shows the relationship predicted from the generalized linear model.
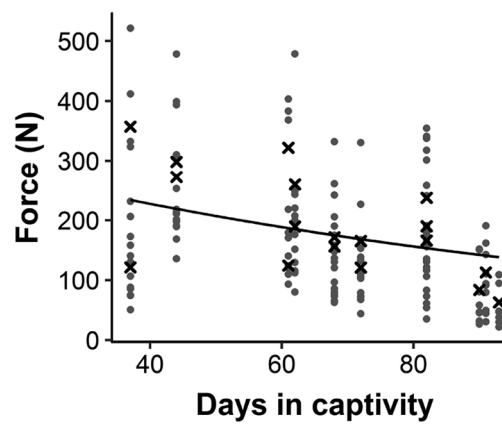
Figure A2. *Neogonodactylus oerstedii* stomatopods in captivity for longer durations have weaker peak force. Dots indicate individual strikes, and crosses indicate the Weibull estimates for each stomatopod. The line shows the relationship predicted from the generalized linear model.