## Abstract (350 words maximum)

1. Animals compete in contests over limited resources. Contestants forfeit once they ascertain that their opponent has greater resource holding potential (RHP) (mutual assessment) or once they reach a threshold of costs (self assessment). Functional scaling studies of contest behavior performance can inform how assessment signals, offensive capacity, and endurance scale with RHP and thereby elucidate the mechanisms through which each of these assessment types operates.
2. Here, we performed behavioral contest analyses to determine the assessment strategies used in snapping shrimp (*Alpheus heterochaelis*) contests. Then, we used biomechanical measurements of a common contest behavior to inform how assessment might operate. We were specifically interested in the snapping behavior during which snapping shrimp fire imploding cavitation bubbles – hereafter, "snaps" – at their opponents.
3. We showed that *A. heterochaelis* use mutual assessment early in contests. Then, when they fire snaps, they switch to cumulative assessment – a type of self assessment where contestants endure costs from their own behaviors (e.g. energy) and their opponent's (e.g. injury).
4. Because larger individuals tend to win contests, we then tested how the maximum performance and endurance of snaps scaled with size. We measured the average angular velocity of the snapping dactyl, cavitation bubble duration, and pressure of snaps as metrics of performance. We measured 10 snaps per individual (n = 76 individuals). From this series of 10 snaps, we calculated the maximum of each metric as the maximum performance and the attrition of each metric over the course of ten snaps as a measure of endurance. Maximum performance increased with size, but endurance did not.
5. This suggests that cumulative assessment in snapping shrimp is driven by opponent-imposed costs. Our results are not consistent with self-assessment based on endurance; however, the experiment could not fully replicate the quick succession of snaps fired in real contests. Future experiments should better replicate the rapid firing of snaps to test if endurance matters in a more ecologically relevant context.

6. Our framework of integrating biomechanics and behavioral ecology provides a pathway to identify precise mechanisms of contest assessment and animal behavior more broadly.

**Keywords:** weapons, performance, contests, scaling, crustaceans, endurance

## Introduction

Animal contests are disputes over ownership of limited resources such as food, territory, or mates (Andersson, 1994; Briffa and Hardy, 2013). On average, contestants with greater fighting ability, or resource holding potential (RHP), win contests. Contestants either forfeit when they ascertain that their opponent has greater RHP (i.e. by assessing signals in mutual assessment, Enquist et al., 1990), or once they reach a threshold of accrued costs (i.e. self assessment, Mesterton-Gibbons et al., 1996; Payne, 1998). In self assessment, costs can be entirely self-imposed like through energy (i.e. pure self assessment, Mesterton-Gibbons et al., 1996) or both self-imposed and imposed by the opponent like through injury (i.e. cumulative assessment, Payne, 1998). Typically, assessment strategies are determined based on empirical predictions derived from theoretical models (Arnott and Elwood, 2009). However, these empirical tests often treat the behavioral mechanisms that facilitate assessment as a black box. Nonetheless, functional studies of contest behaviors are essential because contests are grounded in functional principles, such as the link between physiological state and signal structure or intensity (Dougherty, 2021; Searcy and Nowicki, 2005). Thus, studying the performance of contest behaviors alongside the behavioral contexts in which they are used can elucidate the mechanisms of assessment (Green et al., 2021; Lailvaux and Irschick, 2006; McCullough et al., 2016).

Disparate analyses of behavior and mechanics can lead to flawed evolutionary inferences. For example, in fiddler crabs, it was long-thought that large claws are effective signals but ineffective weapons because large claws sacrifice mechanical advantage at the claw tip (Levinton and Allen, 2005); however, subsequent behavioral observations revealed that fiddler crabs compensate for this tradeoff by pinching near the pivot of the claw, diminishing the mechanical advantage tradeoff and allowing them to wield both effective signals and weapons (Dennenmoser and Christy, 2013). Because behaviors and morphologies are the evolutionary substrate on which selection acts, there is obvious value in studying behavior and biomechanics in tandem.

In this study, we paired behavioral contest experiments with biomechanical scaling studies of weapon performance to understand mechanisms of contest assessment. Performance is defined as the ability to perform a physically challenging and ecologically relevant behavior (Arnold, 1983; Byers et al., 2010). Performance has two components: maximal performance, defined as the maximum magnitude of a behavior that an individual can perform, and endurance, defined as an individual's ability to maintain maximal performance over time (Byers et al., 2010; Mowles et al., 2010). Both components can shape mating signals (e.g. Ballentine, 2009, Ballentine et al., 2004; reviewed in Byers et al., 2010), contest signals (e.g. Mowles et al., 2010; reviewed in Palaoro and Briffa, 2017), and injurious contest behaviors (Dennenmoser and Christy, 2013). The relative importance of maximal performance versus endurance depends on the behavior. In contests, for example, high RHP individuals might have greater endurance during energetic wars of attrition and cumulative assessment and therefore persist longer in contests (Lailvaux and Irschick, 2006; Mowles et al., 2010; Payne, 1998; Payne and Pagel, 1996). In injurious cumulative assessment contests, performing behaviors with greater maximum performance could increase offensive capacity — a key determinant of cumulative assessment defined as the capacity to damage an opponent (Palaoro and Briffa, 2017). In mutual assessment, performing behaviors with high endurance or high maximal performance could signal contestant RHP (Briffa and Elwood, 2002; DuBois et al., 2011). Table 1 provides examples of how maximum performance and endurance can affect contest behaviors used in each assessment type.

***Table 1:*** *Examples of how maximum performance and endurance affect contest behaviors of each assessment type.*

| Assessment Strategy | Maximum Performance Example | Endurance Example |
|---|---|---|
| Pure Self Assessment | Not applicable; pure self assessment is driven by self-imposed costs (e.g. war of attrition, Mesterton-Gibbons et al., 1996; Payne and Pagel, 1996). | Hermit crabs attempting to overtake an opponent's shell perform shell raps that require oxygen and generate lactate. Shell-rapping power |

| | | |
|---|---|---|
| | | decreases as lactate accrues, and the decision to forfeit is based on accrued lactate (Briffa and Elwood, 2000, 2001, 2002). |
| Cumulative Assessment | Fiddler crabs pinch each other using enlarged chela during escalated territorial contests (Pratt et al., 2003). Peak claw closing force increases with size (Dennenmoser and Christy, 2013). | Fiddler crabs pinch each other using enlarged chela during escalated territorial contests (Pratt et al., 2003). Fiddler crabs that are able to maintain initial pinching forces for longer (i.e. greater endurance) are more likely to overtake burrows from opponents (McLain et al., 2019). |
| Mutual Assessment | Hermit crabs defending their shells assess the acoustic power of their opponent's shell-rapping behaviors. They are more likely to forfeit shells to crabs that perform high-powered shell raps (Briffa and Elwood, 2002). | In male side-blotched lizards (*Uta stansburiana*), the duration of the push-up, head-bobbing threat display is constrained by endurance (Brandt, 2003) (but note: mutual assessment hasn't been tested explicitly in this species). |

Here, we tested how maximal weapon performance and endurance scales in the eponymous cavitation-based snap of the snapping shrimp. We then determined the assessment strategy used by snapping shrimp and interpreted our findings through the lens of assessment mechanisms. Snapping shrimp are typically found in size-assortative male-female pairs (Rahman et al., 2002). Both male and female snapping shrimp compete in sexually selected contests against same-sex conspecifics over territory and mates (Dinh et al., 2020; Nolan and Salmon, 1970). Both sexes have one enlarged claw that they use as a weapon to fire cavitation bubbles – hereafter, "snaps" – during contests (Versluis et al., 2000). In a congener snapping shrimp (*Alpheus angulosus*), snaps are used as weapons in cumulative assessment (Dinh et al., 2020). Larger shrimp have larger claws and tend to win contests; accordingly, previous work established carapace length as a convenient and reliable proxy for RHP (Dinh et al., 2020; Hughes, 2000). Furthermore, snapping shrimp fire snaps during pairing behaviors. In contrast to contests, during which snaps are used as weapons aimed directly at the contest opponent, females snap away from potential pair-mates during the pairing process (Hughes et al., 2014). While the function of pairing snaps is not yet known, researchers have speculated that this might be an acoustic signaling behavior (Hughes et al., 2014).

Snaps are highly energetic; they generate temperatures that approach those at the surface of the sun, flashes of light, and extreme sound pressures close to the physical limit of underwater pressure, bested only by cetaceans 6 orders of magnitude larger in mass (Jakobsen et al., 2021; Lohse et al., 2001; Versluis et al., 2000). Cavitation collapse is intense and destructive. Mantis shrimp, for example, produce cavitation during their powerful snail-smashing strikes (Patek and Caldwell, 2005). Interestingly, male and female mantis shrimp also use their feeding appendages to strike opponents during territorial contests (Green and Patek, 2015, 2018). Patek & Caldwell (2005) demonstrated that cavitation force produced by mantis shrimp, which was measured as a proxy for pressure, can exceed the already devastatingly forceful impact of its hammer. Cavitation can even ravage human-engineered equipment. For example, cavitation bubbles form on the tips of fast-spinning boat propellers and are a common source of ship damage (Brennen, 1995). Because cavitation can impose such devastating forces, the cavitation-based weapon of snapping shrimp is an excellent system with which to test how performance scales with RHP and how performance could mediate assessment in contests.

We measured the two components of performance — maximal performance and endurance — using three metrics: (1) cavitation bubble duration; (2) cavitation sound pressure (i.e. force/area); (3) average angular velocity of the dactyl.  This third metric is relevant to performance, because greater energy invested by an individual in a snap should positively correlate with dactyl velocity.  Furthermore, given that greater dactyl velocity is achieved through greater energy use by the snapping animal, dactyl velocity should also positively correlate with cavitation bubble duration and sound pressure.  Therefore, the three performance metrics are not mutually exclusive and should be correlated with each other through the common pathway of energetic input by the individual animal in each snap. Maximal performance is measured as the maximum value for each of these metrics across ten snaps by a given individual.  Endurance is measured for each of these metrics as the slope of performance across 10 snaps: a greater reduction in performance corresponds to greater attrition in performance and, therefore, lower endurance. Note, however, that snapping shrimp in this experiment had ample rest between snaps, which is uncommon in actual contests (see methods for detailed discussion of this caveat).

These three metrics are also influenced by the claw mass of snapping shrimp (Au and Banks, 1998; Harrison et al., 2021; McHenry et al., 2016; Pereira et al., 2014; Versluis et al., 2000) (Table 2).  We predicted that maximal bubble duration and sound pressure would increase with claw mass because larger claws propel greater volumes of water, behind which the cavitation bubbles form, and likely form larger cavitation bubbles; mathematical modeling predicts that larger bubbles produce greater sound pressures (Au and Banks, 1998; Versluis et al., 2000) (Table 2). However, we predicted that shrimp with more massive claws would produce slower maximal angular velocities because angular velocities of rotating latch-mediated spring-actuated systems tend to decrease with increasing mass (Harrison et al., 2021; McHenry et al., 2016). Furthermore, we predicted that larger individuals would have greater endurance than smaller individuals. Smaller organisms tend to have higher mass-specific metabolic rates. Therefore, smaller individuals should expend proportionally more energy per snap and have lower endurance than larger individuals (Schmidt-Nielsen, 1984; but see Glazier, 2005, 2009; Kotiaho et al., 1998). Positive scaling of endurance is also a foundational assumption of self assessment models (e.g. wars of attrition and cumulative assessment (Palaoro and Briffa, 2017; Payne, 1998; Payne and Pagel, 1996)) (Table 2). We therefore expected larger individuals to show greater endurance than smaller individuals.

Finally, we performed behavioral experiments to determine assessment strategies used by snapping shrimp (Arnott and Elwood, 2009). The behavioral analysis allowed us to determine whether snaps are used as signals in mutual assessment or as cost-imposing armament in pure self assessment or cumulative assessment (Fig. 1). Integrating behavioral context with behavioral scaling allowed us to make inferences about the mechanisms of assessment used during contests.

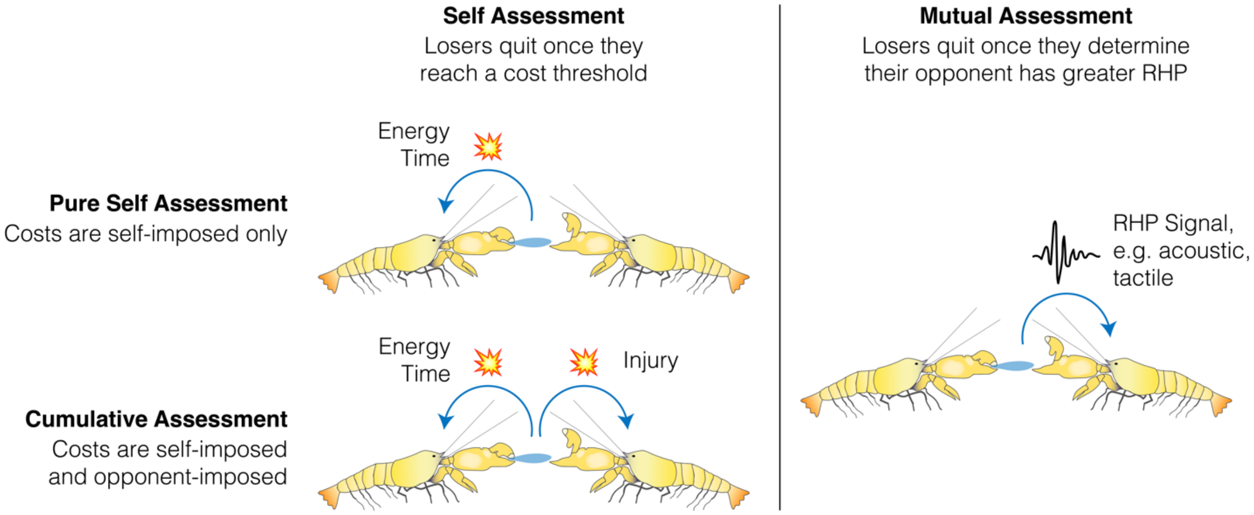

***Figure 1:*** *In self assessment, snaps impose costs. Some costs, like time and energy, can be self-imposed. In cumulative assessment, costs can also be opponent-imposed like through injury. By contrast, in mutual assessment, behaviors aren't used as armament, but as signals. For instance, snap receivers might assess the pressure or water flow from a snap as a signal of RHP and use this to estimate relative fighting ability.*

***Table 2**: Scaling predictions and justifications for each of the three maximal performance and endurance metrics. Negative signs mean that the performance metric decreases with size, whereas positive signs mean that the performance metric increases with size.*

| **Performance Metric** | **Maximal Performance Scaling** | **Maximal Performance Justification** | **Endurance Scaling** | **Endurance Justification** |
|---|---|---|---|---|
| Average Angular Velocity of Dactyl | - | Low-mass objects accelerate more quickly and reach greater average angular velocity in spring-actuated movements (Harrison et al., 2021; Ilton et al., 2018; McHenry et al., 2016) | + | Smaller individuals use more energy per gram of body mass during exercise, so they should be less able to maintain high performance over time (Glazier, 2009; Schmidt-Nielsen, 1984) |
| Bubble Duration | + | Larger claws have larger dactyls that will accelerate larger volumes of water (Pereira et al., 2014) | + | Smaller individuals use more energy per gram of body mass during exercise, so they should be less able to maintain high performance over time (Glazier, 2009; Schmidt-Nielsen, 1984) |
| Sound Pressure Level | + | Larger claws produce larger bubbles, which should produce greater pressures upon collapse (Au and Banks, 1998; Versluis et al., 2000) | + | Smaller individuals use more energy per gram of body mass during exercise, so they should be less able to maintain high performance over time (Glazier, 2009; Schmidt-Nielsen, 1984) |

## Materials and Methods

### *Animal collection and husbandry*

We collected 168 snapping shrimp (*Alpheus heterochaelis*) from Beaufort, North Carolina, USA from March – September 2020 and March – June 2021 (NCDENR Scientific and Education Permit no. 707075 to the Duke University Marine Laboratory). No ethical permit was required for experiments. Snapping shrimp can live several years in captivity, and we performed experiments within two months after capture. We used 76 individuals to determine weapon performance scaling and 92 individuals to determine assessment mechanisms. No individuals were used in both experiments to avoid confounds like motivation, prior experimentation, and excessive handling. Snapping shrimp were collected from oyster reefs surrounding Piver's Island at low tide by flipping oyster debris and excavating roughly 4 cm of mud. We transported all snapping shrimp to Duke University (Durham, North Carolina, USA) in individual tubes filled with seawater from their local environment, where they were immediately transferred into individual 0.1 x 0.1 x 0.1 m polystyrene tanks filled with lab-made seawater. Water changes and feedings of frozen krill and live brine shrimp nauplii were provided daily.

### *Weapon performance*

We measured three metrics of weapon performance: average angular velocity, cavitation bubble duration, and peak-to-peak sound pressure induced by bubble collapse. As detailed below, we measured average angular velocity of the dactyl and cavitation bubble duration using high-speed videos, and we measured peak-to-peak sound pressure using audio recordings synchronized with the high-speed videos.

We filmed high speed videos of snapping shrimp in a 75 x 30 x 45 cm tank filled 40 cm high with lab-made seawater (100,000 frames per second, 384 x 408 pixels, model SA-Z, Photron U.S.A., Inc., San Diego, CA, U.S.A.). Snapping shrimp were suspended in the tank and oriented towards the center of the tank.  They were positioned at 23 cm depth by adhering a toothpick to the dorsal surface of their carapace and mounting the toothpick on a custom-designed 3-D printed stand. A mirror was positioned below the animal at 45° to obtain both a ventral and lateral view. Typically, the claw was in plane in the ventral view. Snaps were stimulated by probing the tip of the claw with forceps. In nature, snapping shrimp can snap spontaneously or when aggravated by external stimuli and conspecifics; spontaneous snaps are lower in intensity than aggressive ones, and artificially provoking animals elicits intense aggressive snaps akin to those seen in contests (Rossi et al., 2016). We recorded 10 snaps for each individual except for rare instances when the animal would not snap 10 times (see Figure S1). In total, we recorded 736 videos.

We measured the average angular velocity of the dactyl following Kagaya & Patek (2016). Briefly, we tracked two lines — one on the propodus and one on the dactyl — at the beginning and the end of the strike using the Fiji distribution of ImageJ (version 2.0.0) (Schindelin et al., 2012) (Fig. 2). We calculated the angle change between the two lines from the beginning to the end of the snap, which is equivalent to the angular change between the two rotating segments of the appendage around the center of rotation (Kagaya and Patek, 2016). We divided this angle change by the strike duration (duration between the onset of dactyl rotation to the end of dactyl rotation) to determine average angular velocity. We used 603 high-speed videos for angular velocity calculations because in the remaining videos, the claws were not in the plane of recording, and angular change could not be measured reliably.

We measured bubble duration starting when the cavitation bubble formed to the time it collapsed. We did not measure bubble diameter because claw orientations varied between snaps, and minor changes in bubble directionality could introduce error in diameter measurements.

We synchronized high speed imaging with acoustic pressure recordings. We recorded audio using a B&K Type 8104 hydrophone (flat frequency range 0.1 Hz – 10 kHz; full frequency range 0.1 Hz – 80 kHz; Brüel & Kjær, Nærum, Denmark) amplified with a B&K Type 2635 charge amplifier (flat frequency range 0.1 Hz – 100 kHz; band-pass filter 1 Hz – 100 kHz Brüel & Kjær, Nærum, Denmark). Audio was synchronized with high speed video using a National Instruments data acquisition board such that for every frame of high-speed video there were ten data points from the acoustic recording (NI USB-6251; sampling frequency = 1 MHz; National Instruments, Austin, Texas, USA). The hydrophone was placed 9 cm from the recorded snapping shrimp at 23 cm depth. Because the hydrophone was placed only 9 cm from the sound source and 15 cm from the nearest tank wall, and because we measured sound pressure at the initial onset of the bubble collapse, sound arrived at the hydrophone before it could be reflected from the tank walls. Therefore, pressure measurements of the initial bubble collapse were not distorted by tank reverberations. All audio recordings were visually inspected to ensure that background noise levels were low and flat. No audio recordings oscillated at low frequencies. We calculated the peak-to-peak sound pressure level produced by the initial collapse of the cavitation bubble and calculated a source level (dB re 1 μPa at 1 m) by subtracting geometric transmission loss assuming spherical spreading from our received levels. This sound pressure level encompassed the first peak positive and negative values upon bubble collapse and did not include any heavily oscillating acoustic data following bubble collapse (Fig. 3).

We towel- and air-dried the claws and measured their mass on a microbalance (resolution: ±1 µg; XPE56, Mettler Toledo, Pleasant Prairie, WI, USA). To document scaling relationships with the three metrics of weapon maximal performance and endurance (average angular velocity, bubble duration, and acoustic source level), we constructed a series of linear models. For each of the three metrics, we constructed log-transformed ordinary least squares (OLS) linear regressions with $\log_{10}$(claw mass) as the explanatory variable and log-transformed measures of weapon performance as the response variables (Kilmer and Rodríguez, 2017). We used claw mass in this analysis because investment into growth and development of the weapon is likely the best predictor of weapon performance. It’s highly correlated with carapace length — the best known morphological proxy for RHP — but more directly tied to weapon performance than carapace length.

Then, we tested how weapon performance scaled with carapace length. We used carapace length as an RHP proxy because it has been previously established to predict contest success (Dinh et al., 2020). To visualize the non-linearity of the relationship, we regressed carapace length against the linear pressure measurement 1 meter from the source. To estimate the scaling exponent, we regressed log10(pressure) ~ log10(carapace length) for males and females.

To test if producing higher angular velocities generated longer bubble durations and greater sound pressure levels through a common energetic pathway, we conducted a causal mediation analysis with linear mixed effects models where individuals were assigned as random effects. Causal mediation analysis allows us to test the extent to which the effect of an independent variable (I) on a dependent variable (D) is mediated through a third mediating variable (M) (Agler and De Boeck, 2017; Little, 2018; Tingley et al., 2014). Indirect effects of I on D which are mediated through M are separated from direct effects of I on D using a series of linear regressions: D ~ I + M, and M ~ I. The average direct effect (ADE) is determined as the slope of D ~ I, and the average causally mediated effect (ACME) is the product of the slope of M ~ I and the slope of D ~ M. Using this analysis, we can determine how across the 10 snaps performed by a single individual, producing greater average angular velocities increases bubble duration and, in turn, increases sound pressure.

In our causal mediation analysis, we used source sound pressure as the dependent variable, average angular velocity as the independent variable, and bubble duration$^3$ as the mediator. We also used individual as a random effect. This model allowed us to test whether for any given individual, producing a greater angular velocity would produce a longer-lasting cavitation bubble and therefore a greater sound pressure. We used linear sound pressure and the cubed exponent of bubble duration because linear sound pressure increases proportionally to bubble volume (Versluis et al., 2000). Cavitation bubbles expand in all three dimensions during cavitation bubble formation, so bubble volume should scale roughly proportionally to bubble duration$^3$. Because the variables differed drastically in scale (e.g., bubble duration and source pressure varied by 13 orders of magnitude) we standardized each parameter so that the mean value was zero and each increment of 1 represented a change in 1 standard deviation. Then, we constructed mediator and outcome models as described above and built 95% confidence intervals for the average causally mediated effect (ACME), average direct effect (ADE), total effect, and proportion of effect mediated through indirect causal pathways. We performed causal mediation analysis using the mediation R package (Tingley et al., 2014).

To test if snap performance declined with repeated use, we constructed three linear mixed effects models. These models used either $\log_{10}$(average angular velocity), $\log_{10}$(cavitation bubble duration), or sound pressure level — a logarithmic pressure measurement — as the response variable. We included snap number, where 1 is the first snap and 10 is the final snap,

as the explanatory variable. We allowed random slopes and intercepts for each individual. We tested whether across all individuals, each measure of weapon performance worsened over the 10 snaps by removing snap number and its random slope from the model and performing a likelihood ratio test comparing the full and reduced models. We also calculated evidence ratios for the full and reduced models to quantify relative support for each model given the data. We constructed linear mixed effects models using the lme4 package (Bates et al., 2022).
Then, to test if the attrition of weapon performance (i.e., endurance) scaled with size, we extracted random slopes from each model and constructed the following linear model for $\log_{10}$(average angular velocity), $\log_{10}$(cavitation bubble duration), and sound pressure level: random slope ~ claw mass. In actual contests, snapping shrimp fire snaps in quick succession. Here, however, we waited 1-2 minutes between snaps to save high speed videos. Thus, our endurance metric may not be ecologically relevant.

*Assessment strategy*

We randomly paired 92 same-sex snapping shrimp and staged 46 dyadic contests. We staged contests as described in detail in Dinh et al. (2020). Contests were staged in a 0.3 x 0.2 x 0.1 m plastic tank that had the interior coated in a spray-on rubber (Plasti Dip International, Blaine, Minnesota, USA). Each tank was filled 0.07 m high with lab-made seawater and divided using an opaque 3-D printed divider. We placed a 2.5 cm piece of transparent PVC on either side of the divider as shelter. Once the divider was lifted, the two PVC pipes were nearly touching, forming one continuous and limited shelter. PVC was placed on both sides to prevent resident-effects during acclimation. We placed one individual on each side of the tank and allowed them to acclimate for 30 minutes. Then, we removed the divider and filmed the contest using a high-definition camcorder (30 frames/s, 1920 x 1080 pixel resolution, model HDR-PJ790, Sony Corp., Tokyo, Japan). Contestants were monitored until one individual made a clear and obvious retreat. Our previous work has established that initial retreat is clear sign of dominance and subordinance (Dinh et al., 2020). The loser was the individual that retreated, and the other individual was deemed the winner. We rinsed the inside of each tank with RO water and changed seawater between each contest.

We determined whether contests progressed in phases using a behavioral network analysis with the igraph R package (Csardi and Nepusz, 2006; Green and Patek, 2018). First, we coded behaviors in all contests using the Behavioural Observation Research Interactive Software (Friard and Gamba, 2016). We used previously established ethograms from the snapping shrimp *Alpheus heterochaelis* (Nolan and Salmon, 1970) and *Alpheus angulosus* (Dinh et al., 2020). We also added two previously undocumented behaviors: pincer snap and clicking (see supplementary materials for ethogram and definitions)

We sorted behaviors by individual and ordered them in their temporal sequence. We then used a permutation procedure to identify behavioral transitions that occurred more often than would be expected if transitions were random. Details are available in Green & Patek (2018), but briefly, we determined the total number of transitions for each possible behavioral transition. Then, we resampled each behavior keeping the occurrence frequency of behaviors the same but randomizing transitions. We repeated this random resampling process 10,000 times. This set of behavioral transitions was used as a distribution of expected transitional frequencies of behavioral transitions were random. We determined that a behavioral transition was significant if it occurred more commonly than the 99.142% percentile of this distribution ($\alpha = 0.05$ plus correction for false discovery rate with 190 parallel comparisons, Benjamini and Yekutieli, 2001). Behavioral phases were points of significant transitions after which no significant transitions backwards occurred.

For each behavioural phase, we discriminated between assessment strategies using regression analyses between an RHP proxy and phase duration (Elwood and Arnott, 2012; Taylor and Elwood, 2003) (Table 3). We used carapace length as our RHP proxy since this was previously established as a convenient and reliable correlate of RHP (Dinh et al., 2020). Table 3 provides detailed rationale for each experimental prediction, which we briefly layout here. We first built a multiple linear regression with each contest phase as the response variable and winner carapace length, loser carapace length, and their interaction as explanatory variables. Pure self assessment predicts a positive correlation with loser carapace length and a near-zero positive relationship with winner carapace length, whereas mutual and cumulative assessment predict a positive correlation with loser carapace length and a negative relationship with winner carapace length (Elwood and Arnott, 2012). We also tested for sex differences by adding sex and its interaction terms to the model and comparing AIC to the model without sex. Although this analysis can differentiate pure self assessment, it cannot differentiate between mutual assessment and cumulative assessment (Elwood and Arnott, 2012; Taylor and Elwood, 2003). To differentiate between mutual and cumulative assessment, we considered only size-matched contests (n = 18) and built a linear regression between the averaged carapace length of the two contestants and phase duration for each phase (Elwood and Arnott, 2012; Taylor and Elwood, 2003). Cumulative assessment predicts a positive correlation, whereas mutual assessment predicts no correlation. We also tested for sex differences by adding sex and its interaction with averaged carapace length to the model and comparing AIC to the model without sex.

***Table 3:*** *Contest predictions and rationale based on each assessment type (reviewed in Arnott & Elwood, 2009).*

| **Assessment Strategy** | **Contest Duration ~ Loser RHP** | **Contest Duration ~ Winner RHP** | **Size Matched Contest Duration ~ Averaged RHP** |
|---|---|---|---|
| Pure Self Assessment | Positive correlation: Larger individuals can sustain greater costs and endure longer in contests. | Weak positive correlation: As RHP increases, the average RHP of possible subordinate opponents increases as well. Therefore the average duration that those opponents would persist also increases. | Positive correlation: Larger individuals can sustain greater costs and endure longer in the contests. |
| Cumulative Assessment | Positive correlation: Larger individuals can sustain greater costs and endure longer in contests. | Negative correlation: Larger individuals impose greater costs and push losers past cost thresholds more quickly. | Positive correlation: Larger individuals can sustain greater costs and endure longer in contests. |
| Mutual Assessment | Positive correlation: High RHP individuals only lose to other formidable opponents. The average RHP difference between the two is usually small, so contests tend to be long. By contrast, low RHP individuals can lose to a wide range of opponents. When they lose to opponents much stronger than them, contests are short. Therefore, contests with high RHP losers tend to be longer on average than contests with low RHP losers. | Negative correlation: Low RHP individuals only defeat other low RHP opponents. The average RHP difference between the two is usually small, so contests tend to be long. By contrast, high RHP individuals can defeat to a wide range of opponents. When they defeat opponents much weaker than them, contests are short. Therefore, contests with low RHP winners tend to be longer than contests with high RHP winners. | No correlation: The absolute RHP of two equally matched competitors doesn’t matter; the RHP difference does. As long as the two competitors are RHP-matched, contests will be long regardless of whether they are formidable or weak. |

## Results

### *Weapon performance*

Snapping shrimp weapon performance increased as claw mass increased. As predicted, larger claws produced lower average angular velocities, longer lasting cavitation bubbles, and higher sound pressure levels (Figs 2 — 4). Furthermore, the pressure generated by a snap increased supralinearly with carapace length (Fig. 5). Log-log relationships between pressure and carapace length had a scaling exponent of 3.212 for females (95% confidence interval [2.160 – 4.263]) and 5.536 for males (95% confidence interval [4.370 – 6.702]).

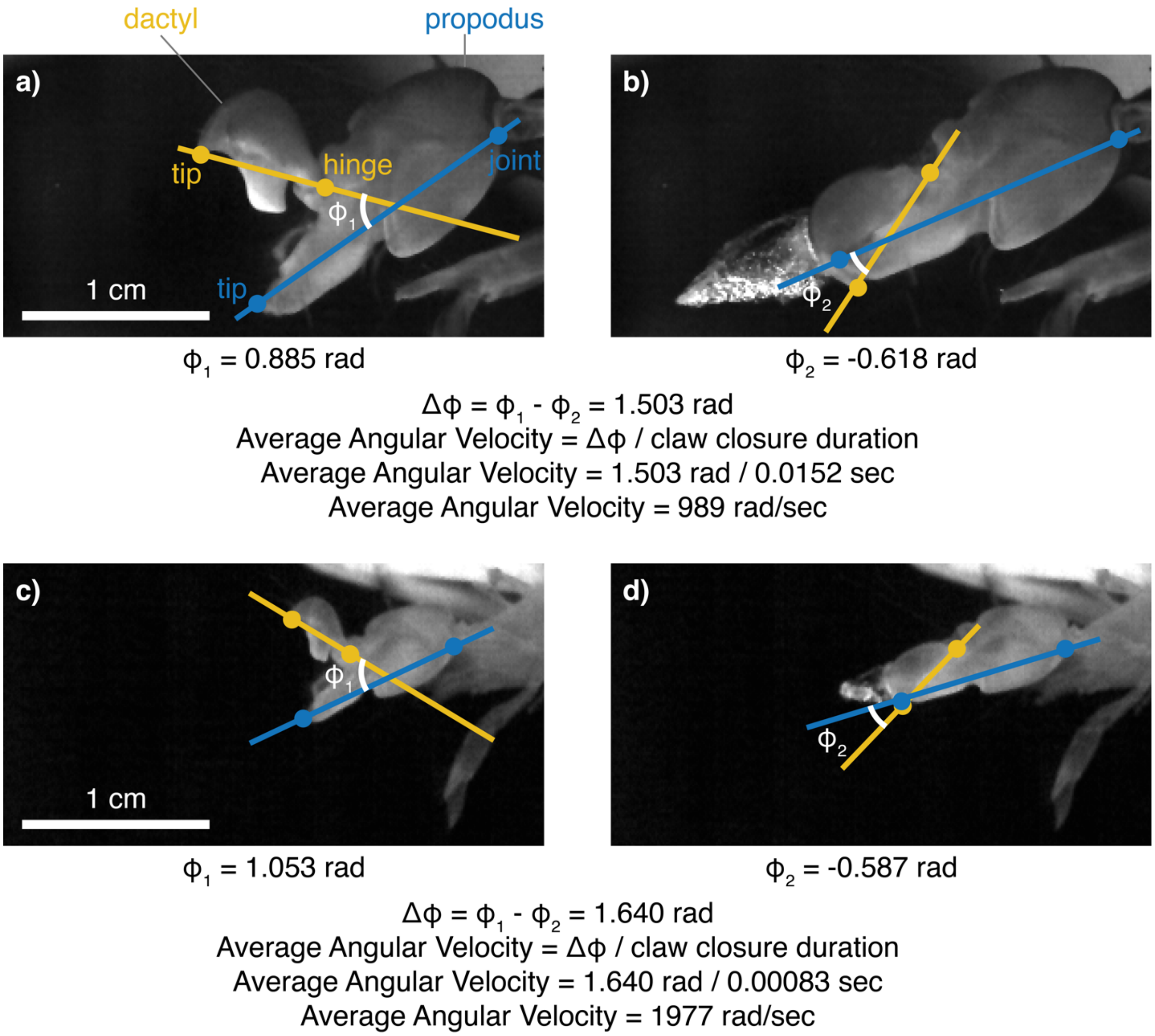

***Figure 2:*** *Larger individuals (a, b) had lower average angular velocities than smaller individuals (c, d)). Two lines were traced before claw closure (a, c) and after claw closure (b, d). The yellow line tracks the dactyl tip and the dactyl hinge, whereas the blue line tracks the propodus tip and the propodus joint. The change in angle between these two lines was divided by the duration of claw closure to calculate average angular velocity. For these two exemplars, the small individual had an average angular velocity two times greater than the large individual.*

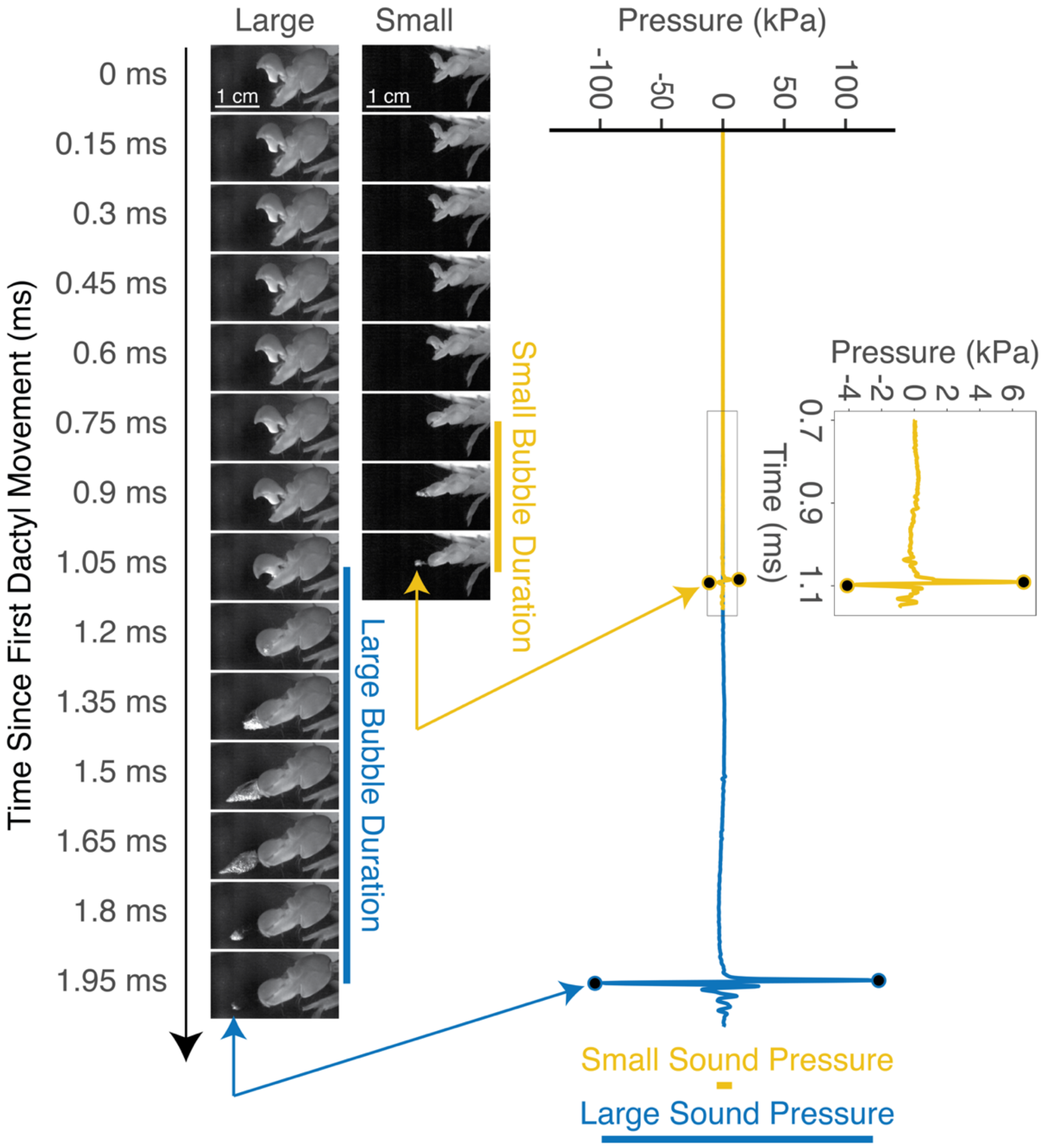

***Figure 3:*** *Large individuals take longer to fully shut their claws, generate longer lasting cavitation bubbles, and produce greater pressures than small individuals. Representative stills from high speed videos and audio recordings for a small and large individual. Frames that encompass the cavitation bubble duration are marked with vertical lines to the right of high speed video stills. Peak-to-peak sound pressure is marked with horizontal lines below the pressure trace. Inset pressure trace shows the small individual's pressure trace with a zoomed-in y-axis to better note the pressure scale. Arrows mark the initial collapse of the cavitation bubble and the corresponding time point in the pressure trace. Black points on the pressure trace mark the maximum and minimum sound pressures produced during initial bubble collapse that were used to calculate peak-to-peak sound pressure levels. In these two examples, the large shrimp produced a peak-to-peak pressure of 103.4 kPa, whereas the small snapping shrimp produced a peak-to-peak pressure at 9.8 kPa — 10.5 times lower than the pressure produced by the large individual. Reported pressures are received levels from the hydrophone 9 cm from the shrimp.*

Within individuals, greater angular velocities were associated with greater sound pressure levels, and this effect was mediated predominantly through producing longer-lasting cavitation bubbles (Fig. 6). The average causally mediated effect of the bubble duration accounted for 88.8% of the total effect (average causal mediation effect = 0.4889; total effect = 0.5500).

Across a series of 10 snaps, as snapping shrimp produced more snaps, they generated lower average angular velocities, smaller cavitation bubbles and lower sound pressure levels (range of $\Delta$AIC after removing snap number as predictor = 17 – 62.1; likelihood-ratio test $p < 0.005$ for all three metrics; see Tables S7 and S8). By calculating evidence ratios between full and reduced models, we found that the empirical support for the full model was $5.40*10^5$ times that of the reduced model for average angular velocity, $9.79*10^{17}$ times that of the reduced model for bubble duration, and $1.08*10^9$ that of the reduced model for sound pressure level. This suggests that on average, individuals produce snaps with lower average angular velocity, lower bubble duration, and lower sound pressure level as they produce more snaps. Contrary to our predictions, there was no relationship between random slopes and claw mass for $\log_{10}$(average angular velocity), $\log_{10}$(bubble duration), or sound pressure level (F-test $p > 0.05$), suggesting that there was no relationship between size and endurance as measured here.

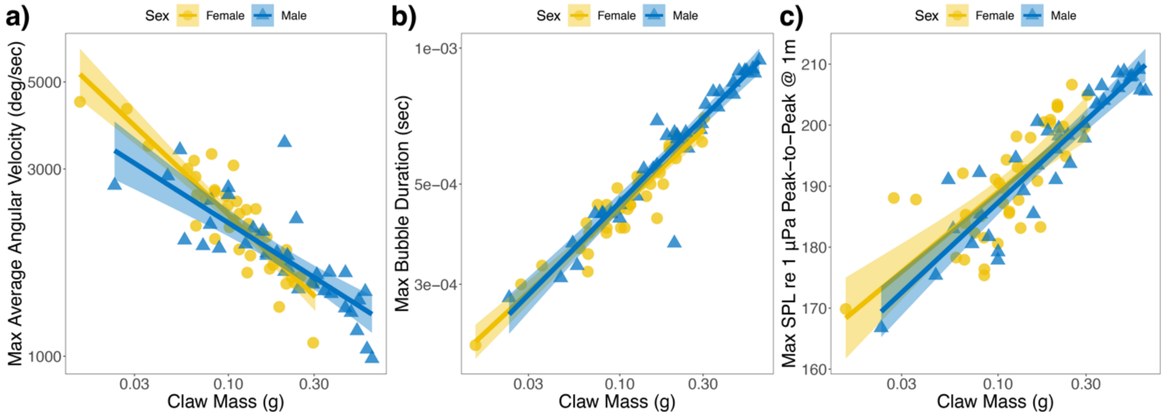

***Figure 4:** Claw mass is a) negatively correlated with maximum average angular velocity of the dactyl during a snap, b) positively correlated with maximum bubble duration, c) positively correlated with maximum sound pressure level. All x-axes are shown on log scales. Maximum average angular velocity (a) and maximum bubble duration (b) y -axes are on log scales, but maximum sound pressure level (c) is not because the unit (dB re 1 $\mu$Pa) is already a logarithmic scale. n = 76 individuals for each regression.*

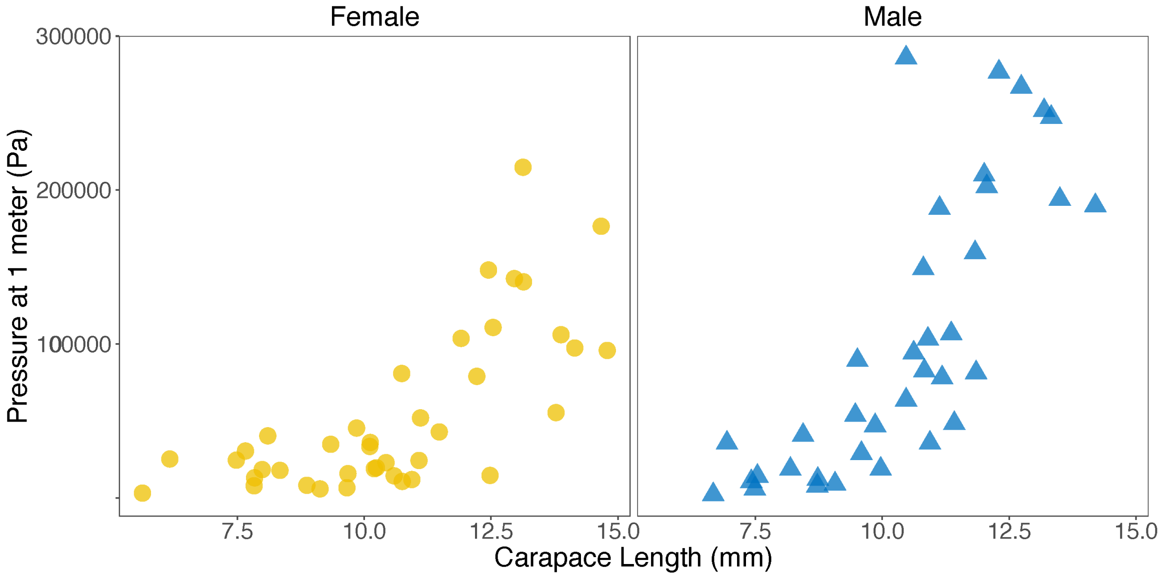

***Figure 5**: Scaling of sound pressure with carapace length is non-linear. Carapace length is a known proxy for resource holding potential (RHP) (Dinh et al., 2020). These sound pressure data are the same as shown in Figure 4c, except that they have been transformed to Pascals. In contrast to the non-linear relationship shown here, when these data are log-transformed, they indicate a scaling exponent of 3.212 (95% confidence interval [2.160 – 4.263]) for females and 5.536 (95% confidence interval [4.370 – 6.702]) for males. n = 40 for females and n = 36 for males.*

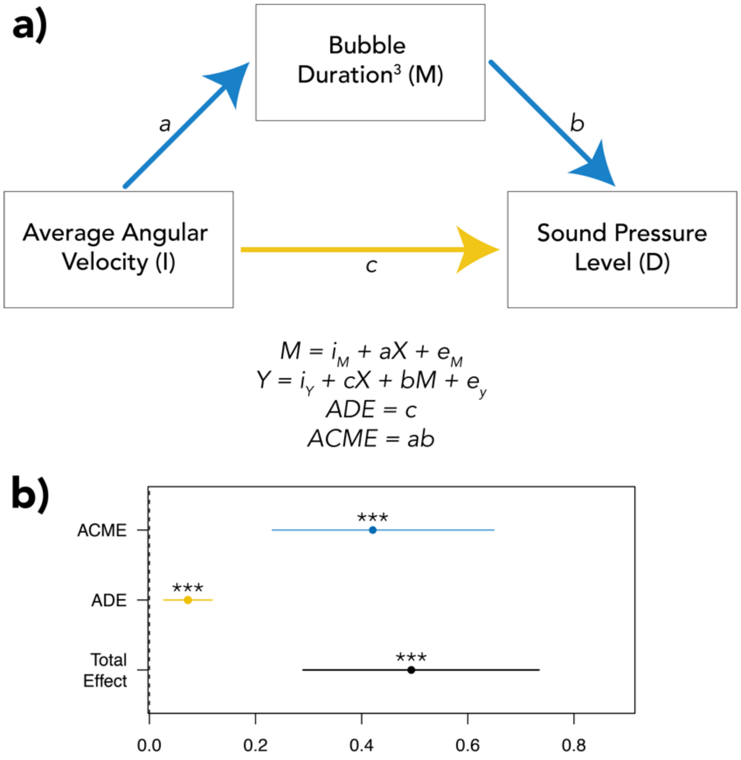

***Figure 6:** Within individuals, greater average angular velocity of the dactyl during the snap was associated with greater sound pressure, and this effect was primarily mediated through increased bubble duration. a) We tested how average angular velocity influenced sound pressure level both directly and through a mediated effect of bubble duration$^3$. b) The averaged cumulative mediated effect (ACME) was 88% of the total effect, whereas the averaged direct effect (ADE) was only 12% of the total effect. Points represent mean estimates, and bars represent 95% confidence intervals. $^{***}p < 0.0005$.*

*Assessment strategies*

Snapping shrimp contests progressed through escalating phases, and de-escalation was uncommon (Fig. 7). This is consistent with mutual assessment or a switching assessment strategy.

For both the initiation and snapping phases, winner carapace length was negatively correlated with phase duration, and loser carapace length was positively with phase duration (t-test, $p < 0.05$; see Tables S2 and S4). The pre-snapping phase regression was highly zero-inflated and difficult to interpret. We therefore refrain from presenting further analyses of this phase.

The same trends arose in information AIC model analysis. In both the initiation and snapping phases, a model containing winner carapace length and loser carapace length was the most supported model. In the snapping phase, the full model with winner carapace length, loser carapace length, and their interaction was the best-fitting model, and in the initiation phase, the model with winner carapace length and loser carapace length without the interaction was the best-fitting model. In both cases, the slope for loser carapace length was positive and the slope for winner carapace length was negative (Fig. 8). This is consistent with cumulative assessment or mutual assessment, but it is not consistent with pure-self assessment. In both the initiation phase and snapping phase, adding sex and any interaction terms increased model AIC, suggesting no sex difference ($\Delta$AIC for initiation phase range: 2.68 – 8.24; $\Delta$AIC for snapping phase range: 1.09 – 9.67). AIC importance for each predictor is presented in Tables S2 – S5.

To differentiate between mutual assessment and cumulative assessment, we considered only size-matched contests and tested correlations between the phase durations and the averaged carapace lengths of the contestants. The initiation phase durations and pre-snapping phase durations were not correlated with the averaged carapace length of contestants (Fig. 8). This is consistent with mutual assessment. However, the snapping phase durations were positively correlated with the averaged carapace length of contestants, consistent with cumulative assessment (F-test, $F_{1,16} = 5.402$, $p = 0.03$, $R^2 = 0.2524$) (Fig. 4).

Adding sex and its interaction with averaged carapace length to the model increased AIC, suggesting no sex difference. Taken together, snapping shrimp switch assessment strategies from mutual assessment during the initiation and pre-snapping phases to cumulative assessment during the snapping phase.

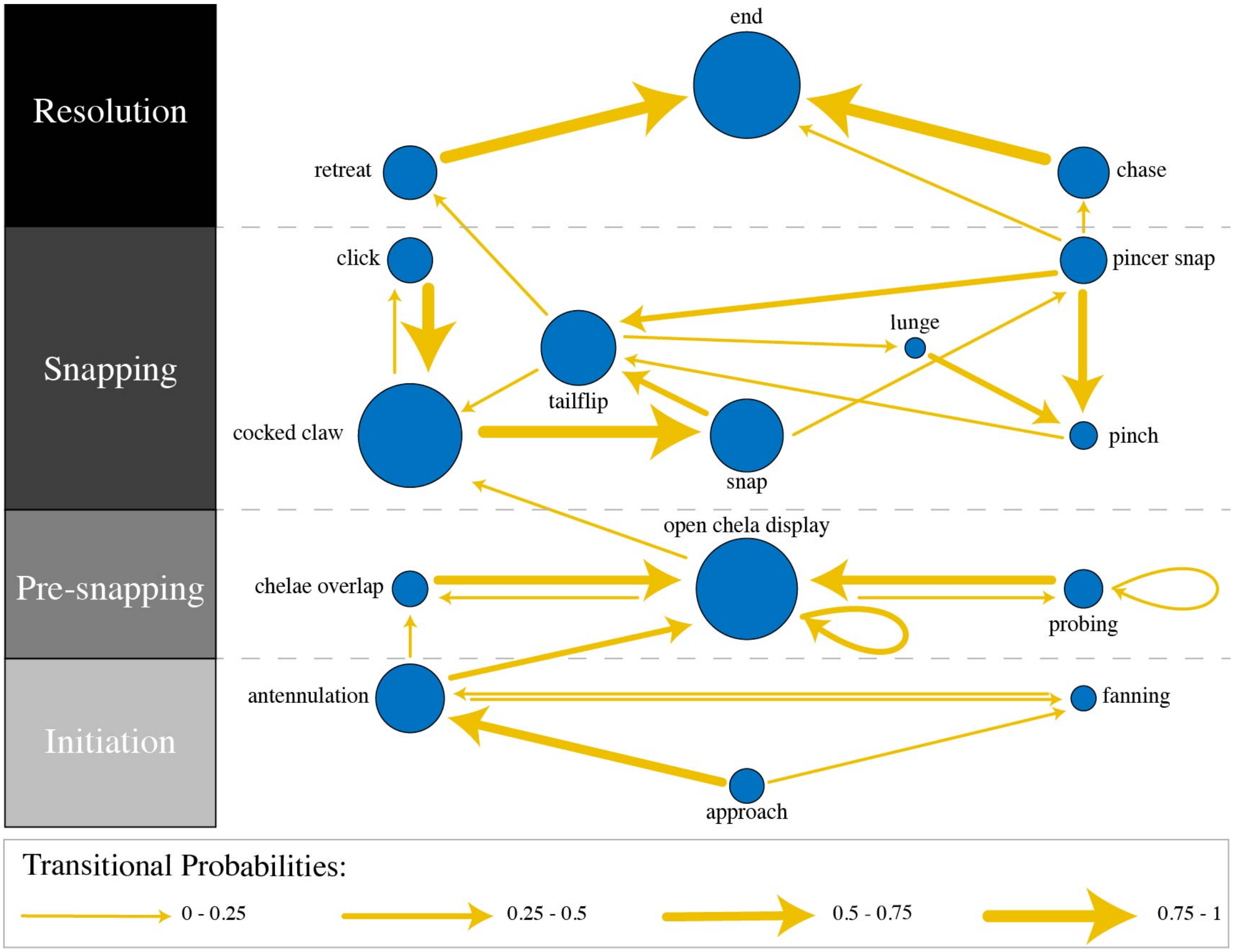

***Figure 7:*** *Contests escalated through phases, and de-escalation was uncommon. Circles represent contest behaviors, and the diameter of the circle is proportional to the frequency that the behavior was used such that larger circles represent behaviors more commonly used. Arrows represent behavioral transitions that occur more often than predicted if transitions were random, and arrow width represents transitional probabilities.*

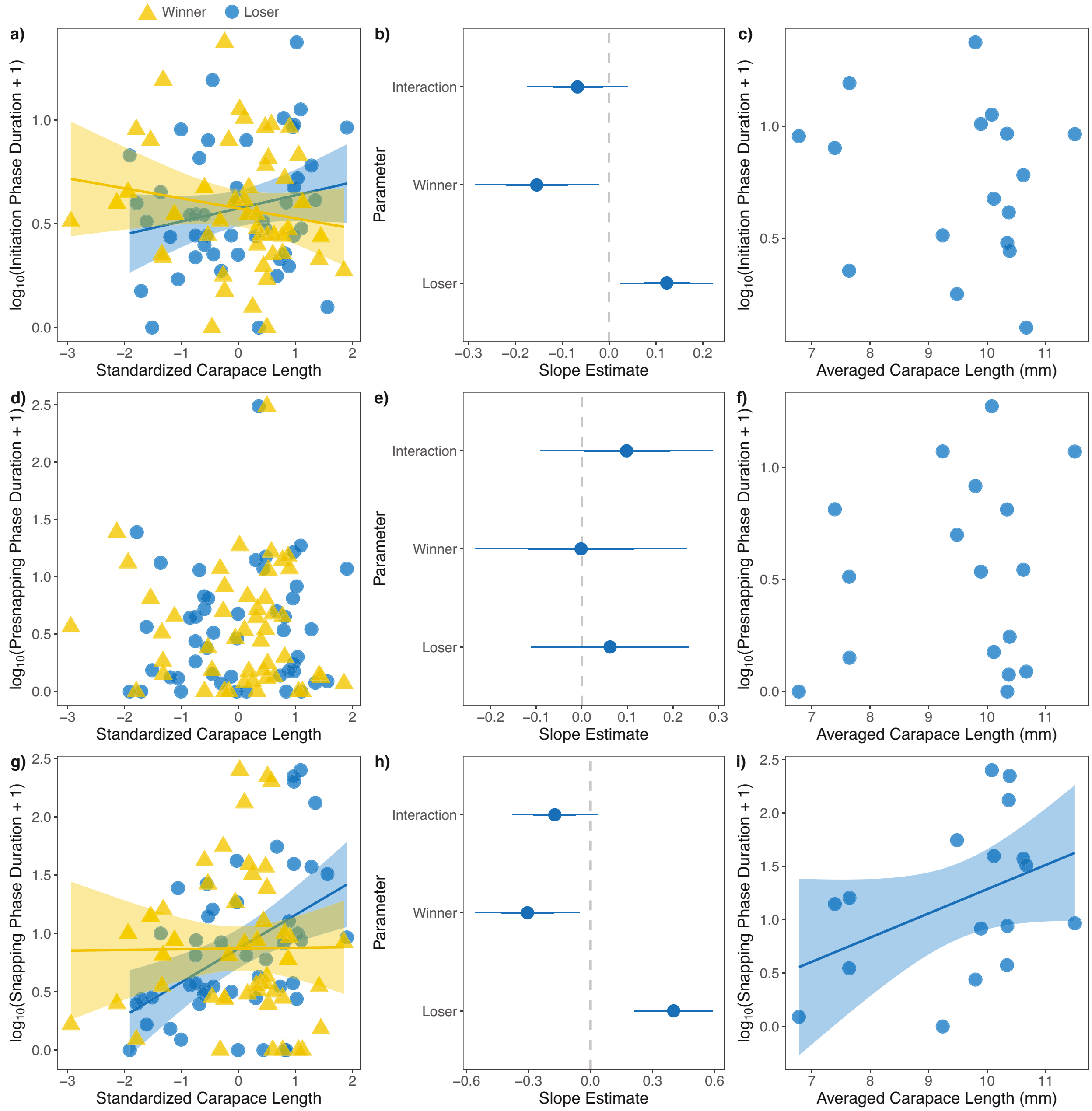

***Figure 8:*** *Assessment type determination for the initiation phase (a-c), pre-snapping phase (d-f), and snapping phase durations (g-i). In randomly matched contests, (a, d, g), the b) initiation phase duration and h) snapping phase durations were negatively correlated with winner carapace length and positively correlated with loser carapace length. No trends were evident in the pre-snapping phase. In size-matched contests, the averaged carapace length of contestants was not correlated with c) initiation and f) pre-snapping phase duration but i) positively correlated with snapping phase duration (F-test, p = 0.03). These results suggest that snapping*

*shrimp use mutual assessment in the initiation and pre-snapping phase but switch to cumulative assessment in the snapping phase. In the middle column, points show slope estimates, thick lines show the estimate ± 1 standard error, thin lines show the estimate ± 2 standard errors. Note that panels a, d, and g show single linear regressions between phase duration and either winner carapace length and loser carapace length, not the slopes calculated in the multiple regression used to determine contest assessment type (b, e, h).*

## Discussion

The correlation between RHP and performance can mediate assessment in animal contests. For example, performing behaviors with high maximal performance can signal RHP in mutual assessment or impose greater damage in cumulative assessment. Furthermore, in pure self assessment and cumulative assessment, individuals with greater endurance can persist longer in a contest. We determined assessment strategies and measured weapon performance of a high-acceleration cavitation-inducing snapping behavior in the snapping shrimp. Snapping shrimp switch assessment strategies from mutual assessment in the initiation and pre-snapping phases to cumulative assessment during the snapping phase. This switching assessment strategy is identical to another species of snapping shrimp, *Alpheus angulosus* (Dinh et al., 2020). Maximal performance of snaps scaled positively with carapace length — a convenient proxy for RHP — but endurance did not. In cumulative assessment, performing snaps with greater maximal performance could increase offensive capacity by imposing greater pressure on contest opponents. This suggests that in snapping shrimp, the mechanism of cumulative assessment likely derives at least partially from positive scaling of offensive capacity. By contrast, our results are not consistent with cumulative assessment mediated by scaling of endurance. However, because our metric for endurance may not have been ecologically germane, we cannot reject the possibility entirely.

Between individuals, the maximal cavitation bubble duration and sound pressure level increased with claw mass (Fig. 4). By contrast, maximum average angular velocity decreased with claw mass (Fig. 4a). Although seemingly counterintuitive, this matches expectations for spring-actuated systems and comparative analyses of spring-actuated movements (Harrison et al., 2021; Ilton et al., 2018; Longo et al., 2019; McHenry et al., 2016).

For any given individual, producing snaps with greater average angular velocity led to increased pressure, and this effect was mediated primarily through increasing cavitation bubble duration. Across a series of 10 snaps, individuals produced slower velocities, briefer cavitation bubbles, and lower sound pressure levels. Surprisingly, however, endurance as quantified as the slopes of attrition did not scale with carapace length or claw mass. Because shrimp with larger carapaces tend to win contests, our results are not consistent with cumulative assessment driven by endurance.

It is entirely plausible that our quantification of endurance is not the most relevant measure of endurance for snapping shrimp. We measured 10 snaps in our biomechanical analysis, but in our sample of contests, individuals rarely snapped 10 times (mean ± SD = 2.675 ± 2.2117; range = 0 – 12). Furthermore, snapping shrimp typically snap in quick succession, whereas in our measurements, we waited 1-2 minutes between snaps to save videos files. A more ecologically relevant measure of endurance would be the attrition of several snaps in quick succession, but limitations in our recording system precluded this experimental design. In future studies, measuring the sound pressure level of snapping shrimp that are directly competing with a conspecific could better inform whether endurance in a naturalistic context could be correlated with RHP.

Interestingly, in another crustacean that uses latch-mediated spring-actuated strikes, the mantis shrimp (*Neogonodactylus oerstedii*), strikes did not decrease in peak force after repeated use (Franklin et al., 2019). Mantis shrimp contests are strikingly similar to snapping shrimp contests in that both sexes compete in contests, they progress through escalating phases, and in escalated contests, strikes are exchanged in sparring bouts (Green and Patek, 2018). However, in mantis shrimp, sparring bouts are used in mutual assessment. One purported benefit of mutual assessment compared to self assessment and cumulative assessment is that contestants need not reach a threshold of costs before forfeiting a contest. This could mean that mantis shrimp using mutual assessment do not strike until exhaustion, whereas snapping shrimp using cumulative assessment do.

In addition to maximal offensive capacity and endurance, as measured in terms of performance, cumulative assessment contests are also influenced by damage endurance, defined as the amount of damage an individual can endure (Palaoro and Briffa, 2017). Thickening a defensive exoskeleton could increase damage endurance. For example, mantis shrimp exchange strikes to the telson in ritualized fighting. Large mantis shrimp have thicker telsons, dissipate more energy, and can withstand greater forces than small mantis shrimp (Taylor and Patek, 2010). In snapping shrimp, the exoskeleton of the weapon scales with positive allometry (Dinh, 2022). Previous work has suggested that snapping shrimp shield their body from incoming snaps using their snapping claw, so positive allometry of claw exoskeleton could reflect scaling of defensive capacity (Herberholz and Schmitz, 1998).

Additionally, snapping shrimp have orbital hoods that protect their eyes from barotraumatic damage from cavitation bubbles (Anker et al., 2006; Kingston et al., 2021, 2022). Without these protective structures, snapping shrimp suffer severe neurotrauma from snaps, losing sense of balance and direction (Kingston et al., 2022). Not only does a snapping shrimp's hood protect it from incoming fire — but it also dampens shockwaves returning from its own snaps. Because larger individuals produce greater pressures, they might also require more efficient shock dissipation to reduce the risk of injuring themselves. Future studies should therefore test how the shock dissipation of orbital hoods scales to protect the snapping shrimp from self-imposed friendly fire and incoming enemy snaps.

Finally, in addition to morphological defenses, snapping shrimp defend themselves by evading cavitation bubbles. They tailflip immediately after snapping to create distance prior to their retaliating opponent's snaps (Fig. 7). In crayfish, larger individuals can perform faster tailflips (Hunyadi et al., 2020). If snapping shrimp tailflip kinematics also scales positively, then higher RHP individuals might be better equipped to evade incoming cavitation bubbles than smaller ones.

In addition to elucidating mechanisms of assessment, functional scaling studies of contest behavior can refine theoretical models. The theoretical contest models used to generate empirical predictions about assessment types often assume linear scaling of RHP-associated traits. However, non-linear scaling can alter or even upend the predictions that models make (Palaoro and Briffa, 2017). We demonstrated that maximum offensive capacity, as measured by the pressure produced by snaps, increases supralinearly with carapace length — a known proxy for RHP (Fig. 5). This supralinear trendline is likely commonplace in animal contests because offensive weapons often scale with positive allometry (Eberhard et al., 2018). By determining how RHP-related traits scale, we can accurately parameterize the assumptions of contest models and generate empirically grounded predictions for future studies.

Although pressure scaled supralinearly with size, it is unclear how supralinear scaling of pressure is sensed in snapping shrimp and in marine invertebrates more broadly. The ability for sensory systems to discriminate between two stimuli often depends on their proportional difference rather than their absolute difference (i.e. Weber's law, reviewed in Akre and Johnsen, 2014). This means that high-magnitude stimuli require greater absolute differences in magnitude to be distinguishable. However, most studies of proportional processing focus on humans or other vertebrates which have entirely different sensory architecture and environments compared to marine invertebrates (Akre and Johnsen, 2014). For snapping shrimp, the relevant stimulus of a snap during contests could be water flow that deflects tactile mechanosensory surface hairs (Mellon, 1963). However, there has not been any research on the proportional processing of flow information. Additionally, snaps could be detected through pressure detectors in the cuticle (Laverack, 1962). In humans, pressure-based touch is sensed proportionally, but again, there is no comparative research in invertebrates (Akre and Johnsen, 2014; Weber, 1978).

Although snapping shrimp do not signal using the sound of snaps during contests, they may do so during mate choice. Female snapping shrimp fire snaps during pairing interactions with males that are directed away from the males. It’s possible that these snaps are acoustic signals (Hughes et al., 2014). In insects, sound pressure is processed proportionally (Wyttenbach and Farris, 2004). However, snapping shrimp and underwater crustaceans detect sound as acoustic particle motion, not sound pressure (Dinh and Radford, 2021). In the acoustic near field, within the range of snapping shrimp contests and courtship, acoustic particle motion dominates acoustic sound pressure (Larsen and Radford, 2018). The supralinear scaling of snap pressure could therefore be amplified in the particle motion regime. Still, it is not clear if snapping shrimp discriminate acoustic particle motion proportionally. We encourage future work to move beyond sensory detection thresholds and into sensory discrimination thresholds, choosing measurement devices that carefully consider the sensory modality relevant to the animals in their behavioral context (e.g., flow versus pressure) to better elucidate the role of non-linear scaling of performance during contests and signaling.

The scaling of behaviors is essential to assessment, contests, and sexual selection. For example, during mate choice, signal receivers are often incentivized to mate with large, high-quality mates. For female snapping shrimp who snap during pairing, for example, the snap is probably a signal of quality rather than injurious armament. Nonetheless, higher RHP females would still benefit from producing longer-lasting cavitation bubbles and greater pressures if potential mates tune into these metrics to discriminate between suitors. Similarly, during mutual assessment contests, signal receivers are incentivized to avoid fighting formidable opponents. Signal receivers might be able to assess these RHP differences based on signal scaling. Even in self assessment and cumulative assessment contests, offensive behaviors that impose costs on opponents should scale such that high-RHP individuals impose greater costs than low-RHP ones. Moreover, an individual’s ability to endure costs could scale such that high-RHP individuals are better able to endure costs than low-RHP ones.

We showed that in snapping shrimp contests, snapping bouts operate under cumulative assessment, during which individuals are not signaling but using high-pressure snaps as armament. The decision to leave a contest is based on self-imposed costs and injurious opponent-imposed costs. Maximum offensive capacity, as measured by the cavitation bubble duration and the pressure produced upon bubble collapse, scaled positively and supralinearly with claw mass. However, endurance, a proxy for self-imposed energetic costs, did not scale as predicted. Our findings are not consistent with endurance-mediated cumulative assessment contests, but importantly, our experimental design didn’t fully replicate how these snapping shrimp rapidly fire snaps during contests. Taken together, the behavioral and biomechanical analyses suggest that cumulative assessment in this species is driven at least partially by scaling of offensive capacity, but we could not rule out the role of endurance entirely.

Functional studies of contest behaviors not only inform the mechanisms of assessment in a single taxon, but they can also refine the general predictions made by theoretical contest models. Non-linear scaling of offensive capacity generates nonlinear relationships between body size and contest duration — the key predictive metric of contest assessment. These predictive relationships depend on the scaling exponents of RHP-associated traits (Palaoro and Briffa, 2017). We showed here that maximum pressure increases supralinearly with carapace length. By integrating this finding with future work identifying the scaling relationship of defensive capacity, we can test and refine the assumptions made by theoretical models to improve the empirical predictions made by different assessment strategies.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article

Figure S1 Sample size breakdown of high-speed videos

Figure S2 Correlations between total contest duration and contestant carapace length