

Tradeoffs and Benefits of Extreme Animal Weapons in Snapping Shrimp (*Alpheus* spp.)

by

Jason Phanliem Dinh

Department of Biology
Duke University

Date: _____

Approved:

Sheila N. Patek, Supervisor

Susan Alberts

Sönke Johnsen

T. Aran Mooney

Stephen Nowicki

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Biology in the Graduate School
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ABSTRACT

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Abstract

Animal weapons are morphologies used in contests over limited resources like food, shelter, and mates. Individuals with larger weapons tend to win contests, so evolution can favor large weaponry. Yet, the specific functional benefits that weaponry provides are often unclear. Further, the mechanisms that prevent individuals from growing arbitrarily large weapons remain hotly debated. In this thesis, I quantified the functional and competitive benefits of large weapons in snapping shrimp, *Alpheus* spp. Then, I resolved two apparent paradoxes that arise from this finding. First, if large weapons are beneficial, then what prevents individuals from growing arbitrarily large weapons? Second, if weapons are costly, then how can they scale with positive allometry? Taken in sum, my findings demonstrate that the costs and benefits of weaponry interact to explain how weapon size varies with body size, sex, and season.

In Chapter 2, I determined the competitive benefits of large weaponry. By performing behavioral experiments, I showed that weapons are used as armaments, not signals. Then, using high-speed videos with synchronous sound pressure measurements, I showed that as weapon size increases, the duration of the cavitation bubble and the pressure imposed by the snap also increase.

In Chapter 3, I showed that snapping shrimp also benefit from large weaponry by improving pairing success. Using field observations, I showed that for male snapping

shrimp, larger weapons were positively correlated with the probability of being paired and the relative body length of their pair mate. Females exhibited neither trend. That indicates a male-specific pairing benefit of large weaponry. Furthermore, using the same dataset, I showed that females exhibit sex-specific tradeoffs between egg production and weapon size. These sex-specific costs and benefits explain why snapping shrimp males have larger proportional weapon sizes than females. It can also explain why that sex difference amplifies during the breeding season.

Finally, in Chapter 4, I showed that snapping shrimp minimize their energetic maintenance costs to achieve positive allometry and weapon exaggeration. Energetic maintenance costs are the costs of maintaining homeostasis. Because tissues vary in their energetic maintenance costs, I used proportional tissue composition as a proxy. I discovered that as weapon size increased, the proportion of the claw comprised of energetically expensive soft tissue decreased. Thus, larger weapons had lower proportional energetic maintenance costs, which could facilitate positive allometry of weapon size. Additionally, exaggerated weapons, which I quantified using residuals from the weapon scaling relationship, had lower proportions of energetically expensive soft tissue compared to non-exaggerated counterparts.

Overall, the dissertation shows that the costs and benefits of weaponry underlie predictable variation in weapon size in snapping shrimp. Canonically, this logic has been used to explain honest scaling relationships based on size, condition, or quality. I

extended these classic theories to explain sex differences, seasonal oscillations, and exaggeration in animal weapons.

Dedication

To my family, for cultivating my curiosity for as long as I can remember.

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1. Introduction

Animal weapons are morphologies used in contests between conspecifics (Emlen, 2008; McCullough et al., 2016). Within a species, individuals with greater fighting ability, or resource holding potential (RHP), tend to grow larger weapons and win contests (Arnott & Elwood, 2009; Emlen, 2008; Enquist et al., 1990; Enquist & Leimar, 1983; Kodric-Brown et al., 2006; Mesterton-Gibbons et al., 1996; Payne, 1998). In this dissertation, I quantified the functional benefits of weaponry. Then, I resolved two apparent paradoxes that arise from that finding. First, if weapons are beneficial, then what prevents individuals from growing weapons to an arbitrarily large size? As detailed below, one canonical explanation is that weapons are costly (Grafen, 1990a, 1990b; Johnstone, 1997; Zahavi, 1975, 1977). Second, if weapons are costly, then how can they scale with positive allometry?

To understand the competitive advantages of large weapons, we first need to understand weapon function. Function differs depending on the type of assessment used during contests (reviewed in Arnott & Elwood, 2009; Briffa & Hardy, 2013). In mutual assessment, contestants assess their opponents to estimate their relative RHP (Enquist et al., 1990; Enquist & Leimar, 1983). Weapon size increases with RHP, so contestants might assess weapon size as a signal for competitive ability (Hughes, 1996). By contrast, in cumulative assessment, contestants impose costs on their opponents and themselves (Payne, 1998). Weapons are used as armament, not signals. In this case,

larger weapons might impose greater offensive costs or weapon size might correlate with endurance (Palaoro & Briffa, 2017; Payne, 1998). These assessment types describe the criteria that individuals use to make contest decisions; yet, they overlook the specific, functional benefits that large weaponry provides within that behavioral context. For example, they might suggest that large weapons increase offensive capacity, but they can't explain how or why. To understand the specific benefits, we need functional studies that show how weapon performance scales with RHP.

Weapons scale in predictable ways across body size, sex, and season (Clements et al., 2010; Emlen, 2008; Heuring & Hughes, 2019; Kodric-Brown et al., 2006). However, if large weaponry is beneficial, then it's natural to wonder why individuals don't grow arbitrarily large weapons. One hypothesis to explain honest scaling is called the handicap principle. This hypothesis posits that individuals produce weapons at a size that optimizes the cost-benefit difference of bearing that weapon (Grafen, 1990a, 1990b; Johnstone, 1997; Zahavi, 1975, 1977). High RHP individuals pay less, or benefit more, from a large weapon, compared to small individuals. Therefore, as RHP increases, so too does the weapon size that optimizes the cost-benefit difference (reviewed in Searcy & Nowicki, 2005). The handicap principle is now a well-accepted explanation for honest weapon scaling relationships. However, the theory's debate and acceptance rely almost entirely on theory and very little on empirical evidence (Penn & Számadó, 2020).

Acceptance of the handicap principle raises another paradox: Weapons are costly, but they still tend to scale with positive allometry (Emlen, 2008; Kodric-Brown et al., 2006; Somjee, 2021). How do large individuals bear the costs of disproportionately large weapons? To address this conundrum, a recent hypothesis called the cost-minimization hypothesis linked the handicap principle with metabolic scaling theory. It suggests that as weapon size increases, the cost of maintaining that weapon decreases (Somjee, Woods, et al., 2018; Somjee, 2021). Thus, a species can achieve positive allometry because large individuals suppress the costs they pay per unit mass of weaponry.

Snapping shrimp (*Alpheus spp.*) are an ideal species to test how weapons benefit competitors and how costs and benefits dictate weapon size. Each snapping shrimp bears one enlarged claw, hereafter called a snapping claw, that it uses as a weapon (Heuring & Hughes, 2019; Nolan & Salmon, 1970). Both male and female snapping shrimp use weapons during disputes with same-sex conspecifics (Dinh et al., 2020; Dinh & Patek, 2022; Heuring & Hughes, 2019; Nolan & Salmon, 1970). Individuals cock their snapping claws open, load them with elastic energy, and fire them shut with angular velocities approaching 5,000 radians per second (Dinh & Patek, 2022; Longo et al., under review). During claw closure, a tooth-shaped protrusion in the dactyl inserts into a socket in the propodus (Kaji et al., 2018; Versluis et al., 2000). That generates a cavitation bubble that, upon collapse, produces light, heat equivalent to the surface of the sun, and

immense pressure that, were it not for co-evolved protective helmets, would incapacitate other snapping shrimp (Anker et al., 2006; Kingston et al., 2022; Lohse et al., 2001; Versluis et al., 2000). Males have larger weapons relative to body size compared to females, and this sex difference amplifies during the breeding season (Heuring & Hughes, 2019). These three axes of variation — across body size, between sexes, and between seasons — are ideal for testing how differences in costs and benefits within a species lead to predictable variation in weapon expression.

In this thesis, I established the landscape of costs and benefits that dictate weapon scaling relationships in the snapping shrimp. I begin in Chapter 2 by performing behavioral experiments to determine contest assessment strategy. Then, I recorded over 700 high speed videos with synchronous sound pressure recordings to determine how large weaponry provides benefits in that behavioral context. I collected all the data under the guidance of Dr. Patek. This chapter is published in *Functional Ecology*. In Chapter 3, I identified a suite of tradeoffs and benefits that underlie predictable variation in weapon size based on scaling, sex, and season. I provide empirical support of the handicap hypothesis and extend its logic to explain sex and seasonal variation. I collected all the data under the guidance of Dr. Patek. This chapter is under review at *eLife*. In Chapter 4, I established that cost minimization facilitates positive allometry in snapping shrimp and fiddler crabs. Furthermore, I extended the cost-minimization hypothesis to explain weapon exaggeration, defined as weapons that

exceed the predictions made by scaling relationships. I collected all data for this chapter independently. I published this chapter in *Biology Letters*.

2. Weapon performance and contest assessment strategies of the cavitating snaps in snapping shrimp

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2.1 Introduction

Animal contests are disputes over ownership of limited resources such as food, territory, or mates (Andersson, 1994; Briffa & 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 & 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 & 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 & 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 & 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 & 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 & 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 & Irschick, 2006; Mowles et al., 2010; Payne, 1998; Payne & 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 & Briffa, 2017). In mutual assessment, performing behaviors with high endurance or high maximal performance could signal contestant RHP (Briffa & 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 & 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 & 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 & Elwood, 2002).	In male side-blotched lizards (<i>Uta stansburiana</i>), 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 & 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 & Caldwell, 2005). Interestingly, male and female mantis shrimp also use their feeding appendages to strike opponents during territorial

contests (Green & 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 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 & Briffa, 2017; Payne, 1998; Payne & 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 (following Arnott & 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.

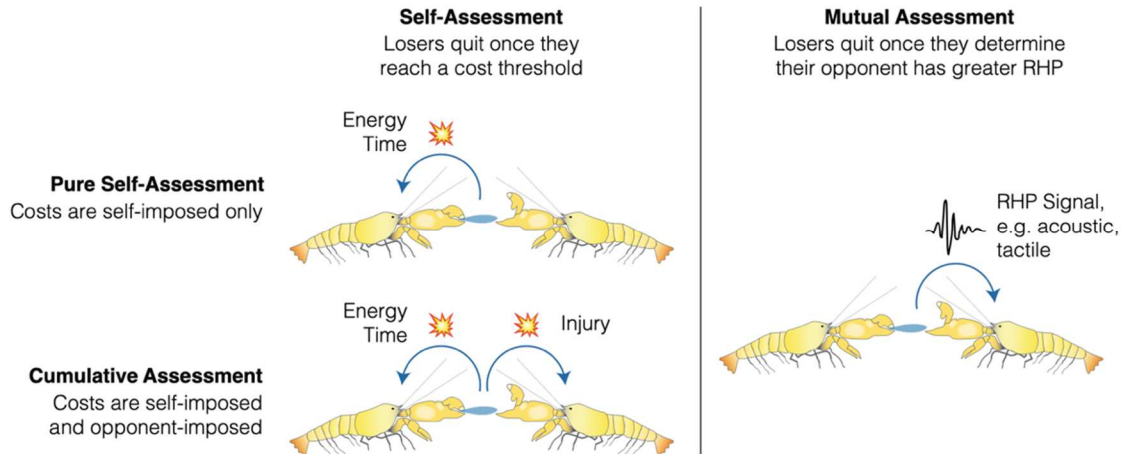


Figure 1: Schematic of assessment types. In self-assessment, snaps impose costs. Some costs, like time and energy, can be self-imposed. In cumulative assessment, costs can also be opponent-imposed like through injury. By contrast, in mutual assessment, behaviors aren't used as armament, but as signals. 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)

2.2 Materials and Methods

2.2.1 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.

2.2.2 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 & 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 mPa 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: $\pm 1 \mu\text{g}$; 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 $\log_{10}(\text{claw mass})$ as the explanatory variable and log-transformed measures of weapon performance as the response variables (Kilmer & 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 $\log_{10}(\text{pressure}) \sim \log_{10}(\text{carapace length})$ 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 & 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: $D \sim I + M$, and $M \sim I$. The average direct effect (ADE) is determined as the slope of $D \sim I$, and the average causally mediated effect (ACME) is the product of the slope of $M \sim I$ and the slope of $D \sim M$. 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 duration³ 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 duration³. 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 \sim 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.

2.2.3 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 a clear sign of dominance and subordination (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 & Nepusz, 2006; Green & Patek, 2018). First, we coded behaviors in all contests using the Behavioural Observation Research Interactive Software (Friard & Gamba, 2016). We used previously established ethograms from the snapping shrimp *Alpheus heterochaelis* (Nolan & Salmon, 1970) and *Alpheus angulosus* (Dinh et al., 2020). We also added two previously undocumented behaviors: pincer snap and clicking.

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 & Arnott, 2012; Taylor & 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 & 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 & Arnott, 2012; Taylor & 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 & Arnott, 2012; Taylor & 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	Negative correlation: Low RHP individuals only defeat other low RHP opponents. The average RHP difference between	No correlation: The absolute RHP of two equally matched competitors doesn't matter; the RHP difference does.

	<p>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.</p>	<p>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.</p>	<p>As long as the two competitors are RHP-matched, contests will be long regardless of whether they are formidable or weak.</p>
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2.3 Results

2.3.1 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]).

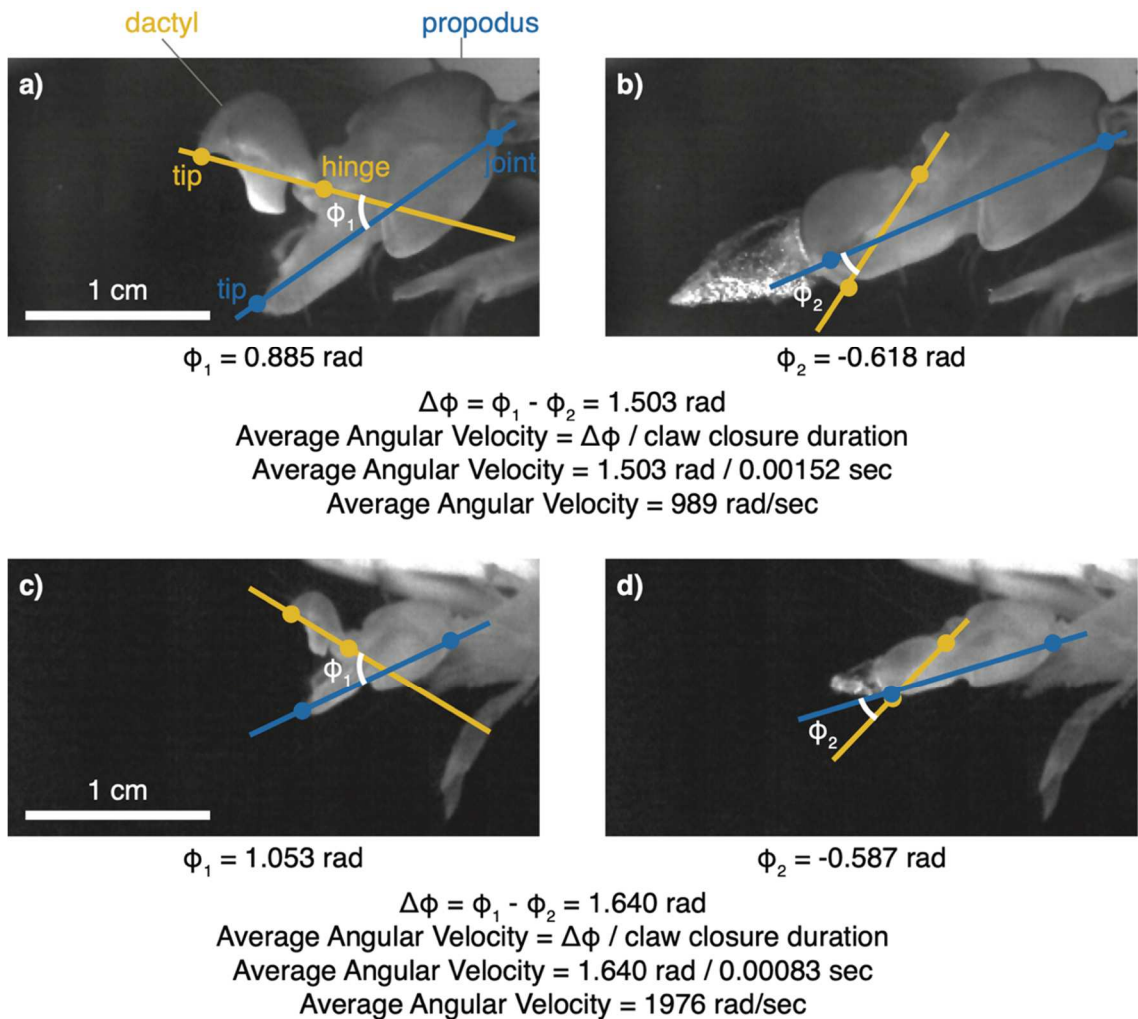


Figure 2: Larger individuals (a, b) had lower average angular velocities than smaller individuals (c, d). Two lines were traced before claw closure (a, c) and after claw closure (b, d). The yellow line tracks the dactyl tip and the dactyl hinge, whereas the blue line tracks the propodus tip and the propodus 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.

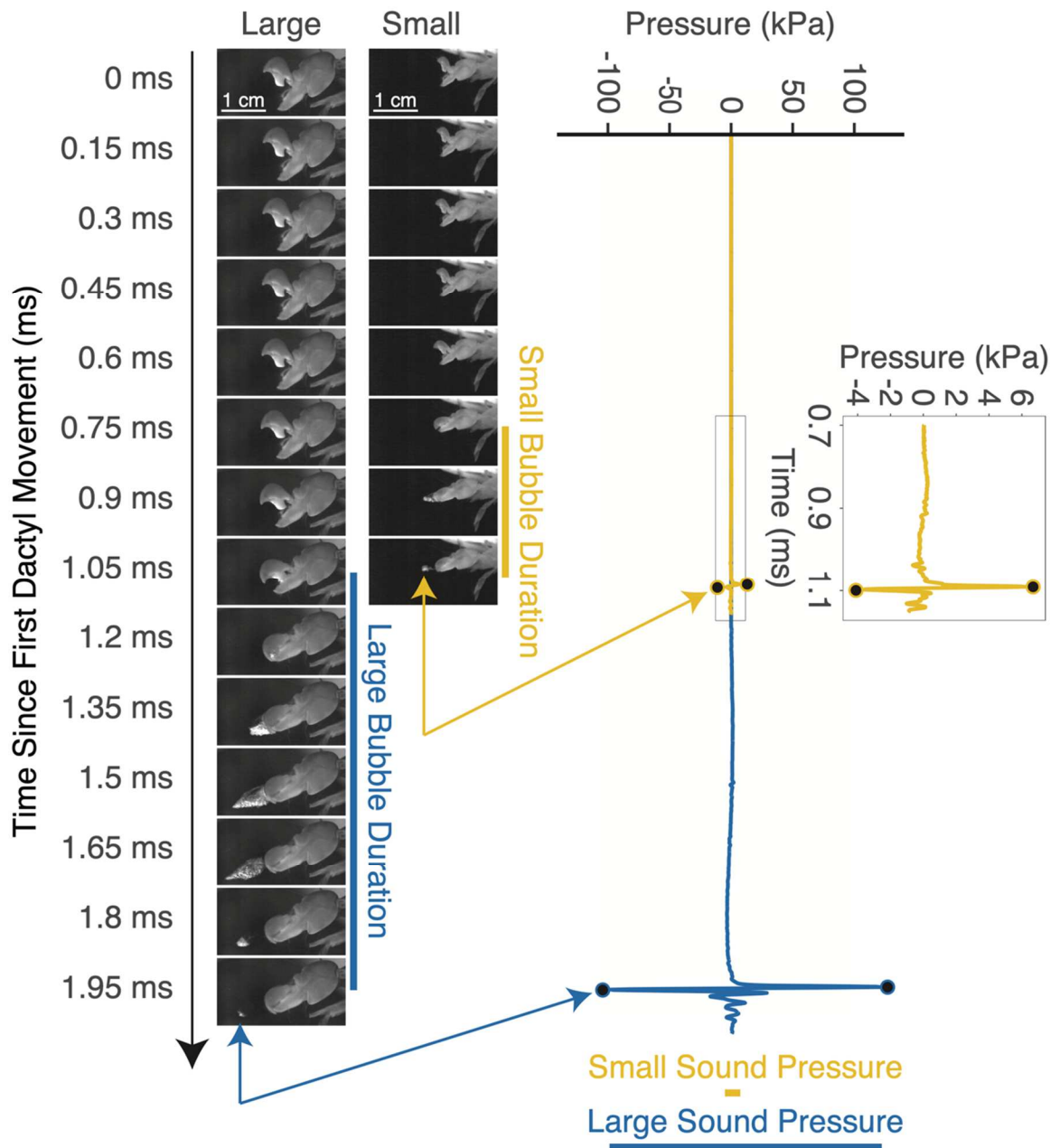


Figure 3: Large individuals take longer to fully shut their claws, generate longer lasting cavitation bubbles, and produce greater pressures than small individuals. Representative stills from high speed videos and audio recordings for a small and large individual. Frames that encompass the cavitation 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 Δ 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.

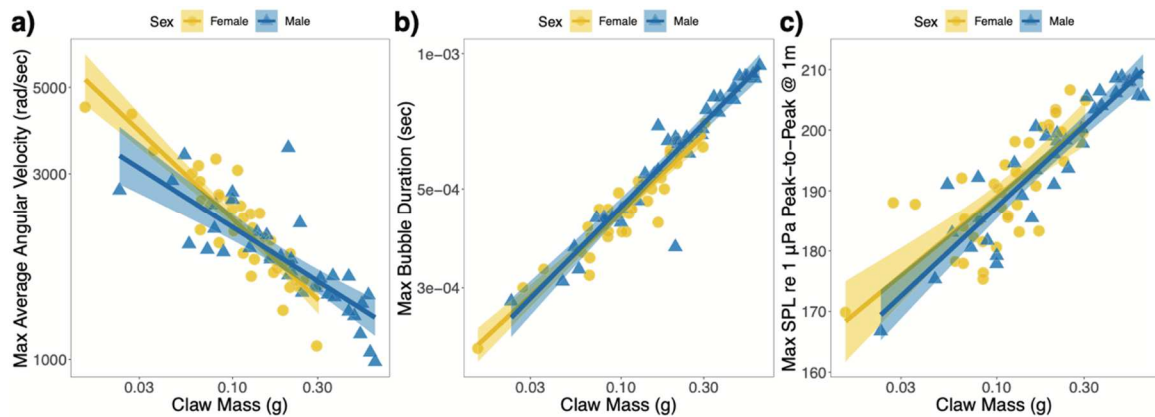


Figure 4: Correlations between claw mass, average angular velocity, bubble duration, and sound pressure level. Claw mass is a) negatively correlated with maximum average angular velocity of the dactyl during a snap, b) positively correlated with maximum bubble duration, and c) positively correlated with 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 mPa) is already a logarithmic scale. $n = 76$ individuals for each regression.

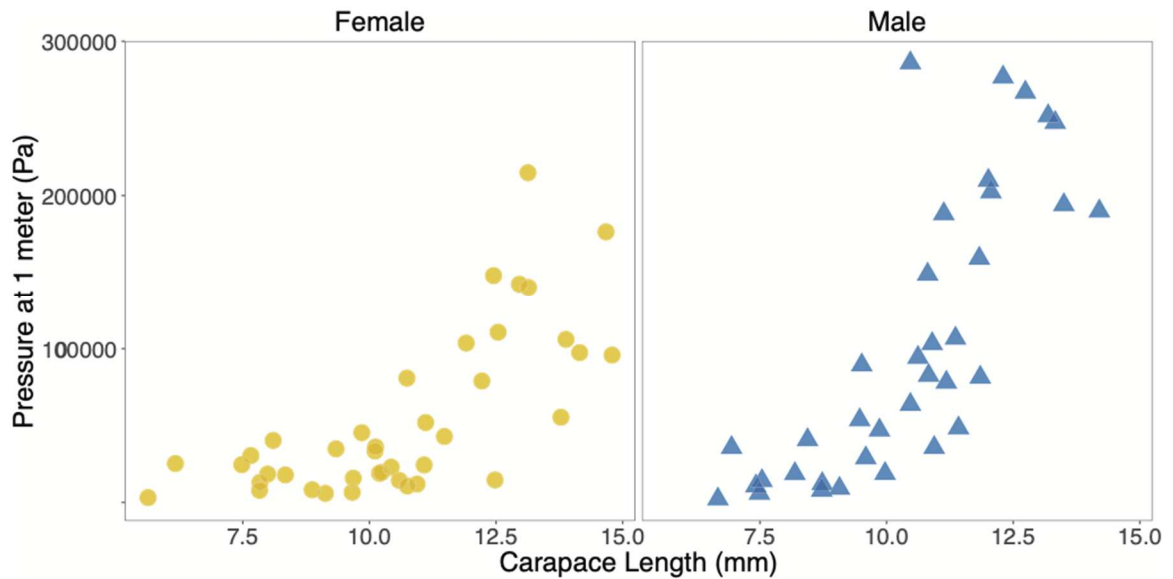
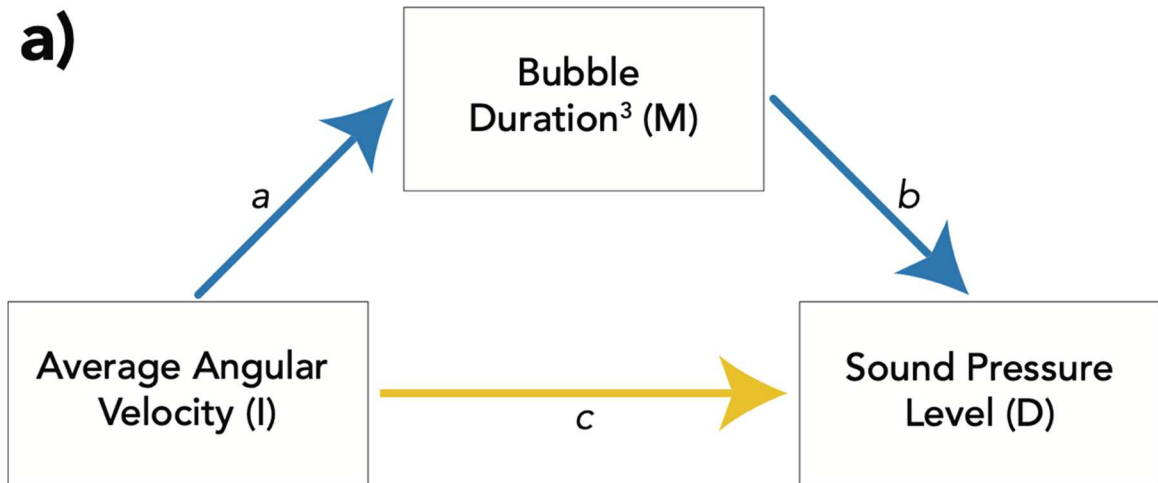


Figure 5: Scaling of sound pressure with carapace length is non-linear. Carapace length is a known proxy for resource holding potential (RHP) (Dinh et al., 2020). These sound pressure data are the same as shown in Fig. 9c, except that they have been transformed to Pascals. In contrast to the non-linear 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.



$$M = i_M + aX + e_M$$

$$Y = i_Y + cX + bM + e_Y$$

$$ADE = c$$

$$ACME = ab$$

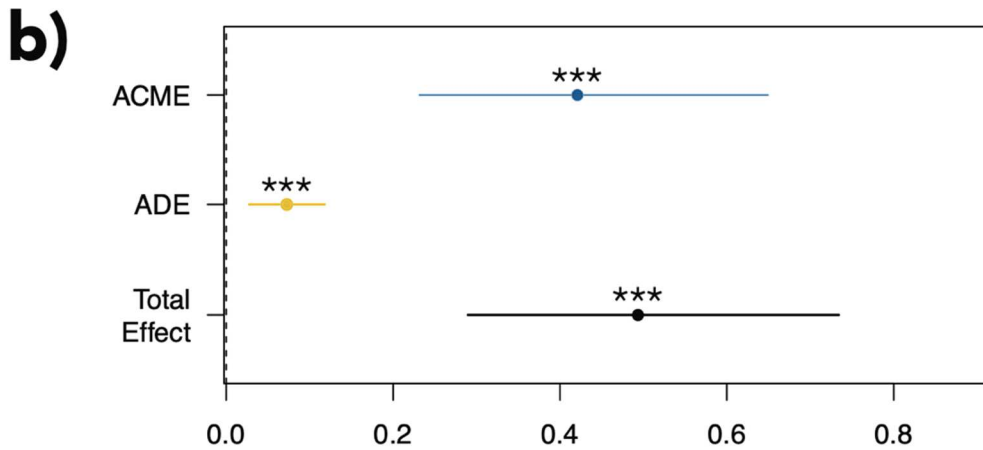


Figure 6: Mediation model results. Within individuals, greater average angular velocity of the dactyl during the snap was associated with greater sound pressure, and this effect was primarily mediated through increased bubble duration. We tested how average angular velocity influenced sound pressure level both directly and through a mediated effect of bubble duration³. 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.

2.3.2 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, $p < 0.05$). 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 (ΔAIC for initiation phase range: 2.68 – 8.24; ΔAIC 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.

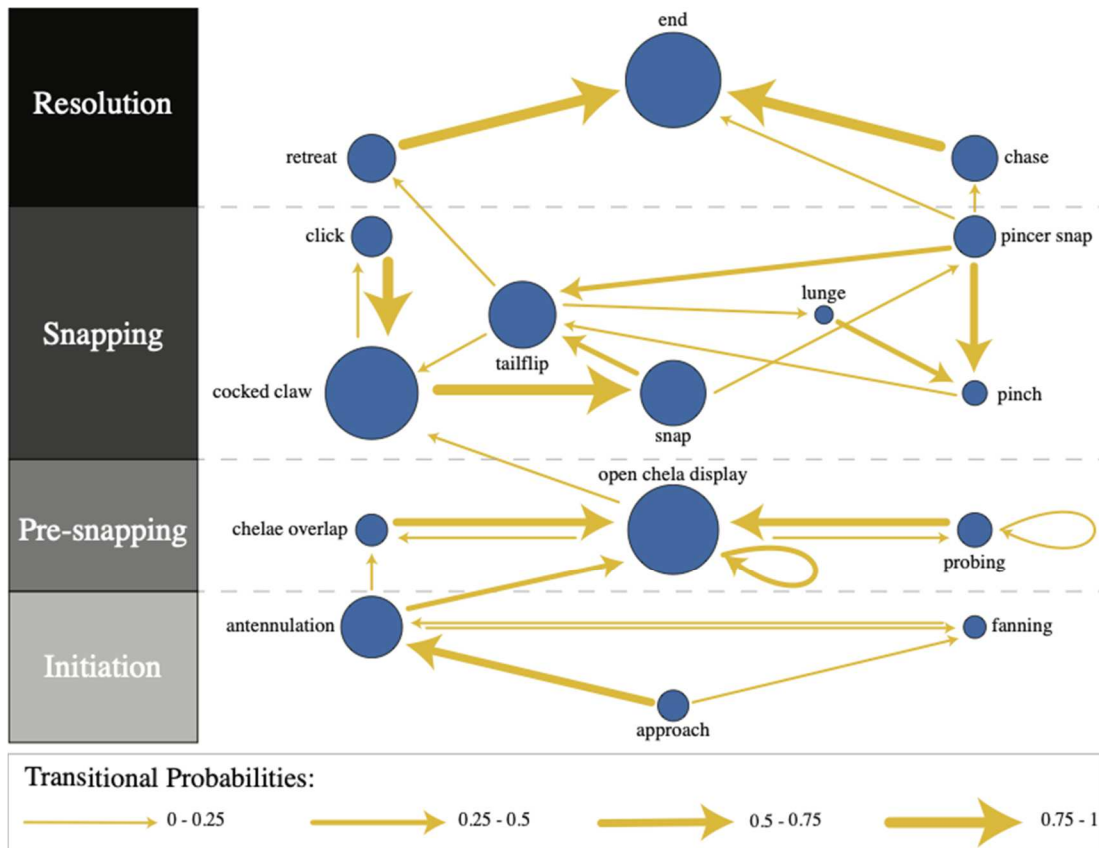


Figure 7: Contests escalated through phases, and de-escalation was uncommon. Circles represent contest behaviors, and the diameter of the circle is proportional to the frequency that the behavior was used such that larger circles represent behaviors more commonly used. Arrows represent behavioral transitions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

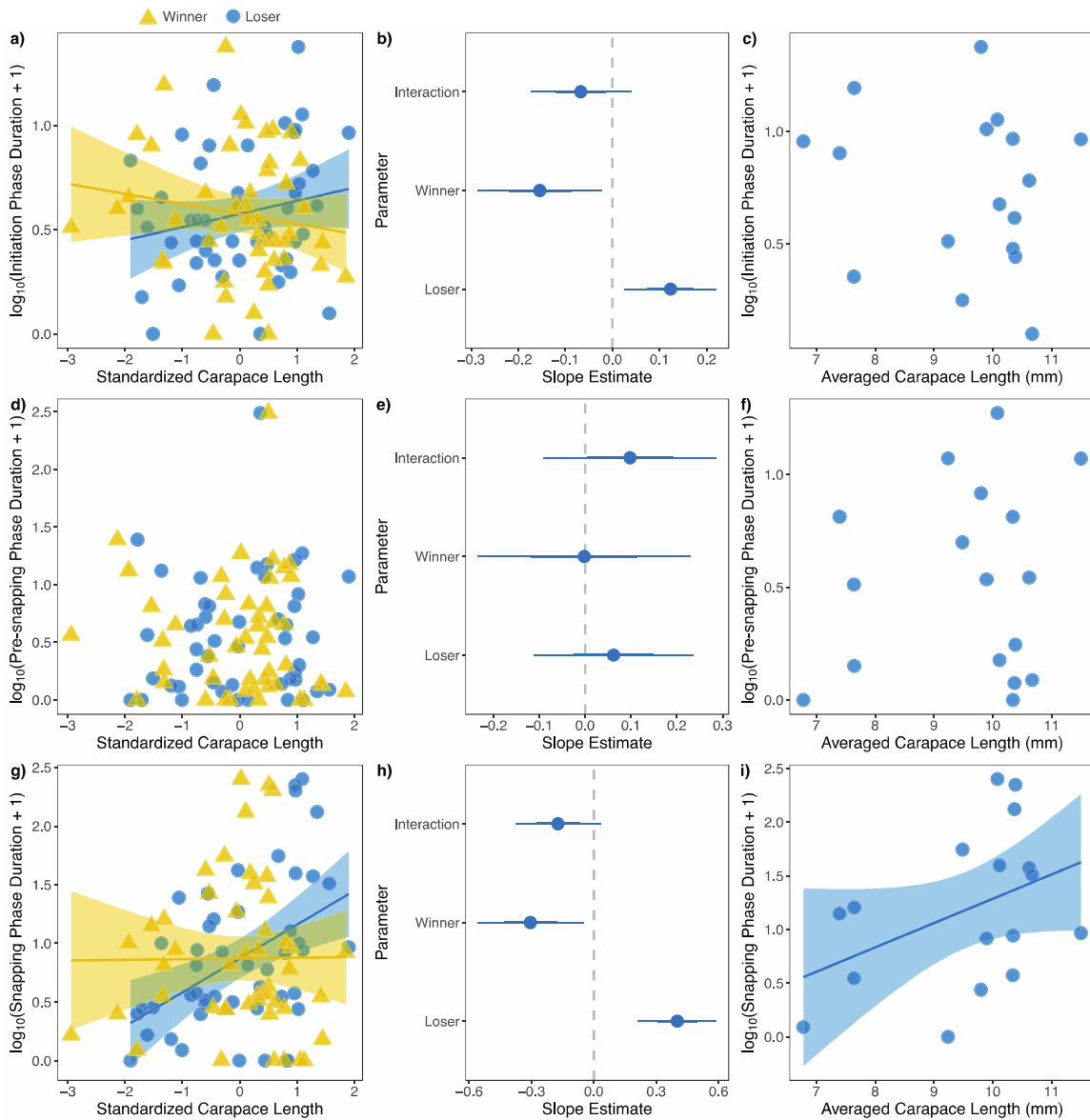


Figure 8: Assessment type determination for the initiation phase (a-c), pre-snapping phase (d-f), and snapping phase durations (g-i). In randomly matched contests, (a, d, g), the (b) initiation phase duration and (h) snapping phase durations were negatively correlated with winner carapace length and 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).

2.4 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 \pm 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 & 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 & 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 & 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 & 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 & 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 & 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 & 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 (Wytttenbach & Farris, 2004). However, snapping shrimp and underwater crustaceans detect sound as acoustic particle motion, not sound pressure (Dinh & Radford, 2021). In the acoustic near field, within the range of snapping shrimp contests and courtship, acoustic particle motion dominates acoustic sound pressure

(Larsen & 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 & 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.

3. Tradeoffs and benefits explain scaling, sex differences, and seasonal oscillations in the remarkable weapons of snapping shrimp (*Alpheus* spp.)

3.1 Introduction

Weapons, ornaments, and other secondary sexual traits often scale with the trait-bearer's quality. Larger weapons can better deter or damage competitors, and more intense ornaments can better attract mates. By first approximation, one might expect that all individuals should express these traits to arbitrarily high magnitudes because greater expression yields fitness benefits. However, fitness costs and physical limitations ensure that traits are expressed honestly instead of arbitrarily (reviewed in Searcy & Nowicki, 2005). Despite decades of research, the costs that maintain reliable scaling relationships remain hotly debated.

One hypothesis called the handicap principle suggests that sexual traits are costly, and these costs ensure that trait expression is not arbitrary. Costly traits lower fitness by reducing survival (Kotiaho et al., 1998; Møller & de Lope, 1994; Mappes et al., 1996) or reproduction (Cavender et al., 2021; Joseph et al., 2018; Moczek & Nijhout, 2004; Somjee, Miller, et al., 2018). Individuals should therefore express traits at a level that maximizes their benefits relative to their unit of cost (Grafen, 1990a, 1990b; Nur & Hasson, 1984; Zahavi, 1977). For example, the handicap principle posits that sexually selected traits scale with quality because low-quality individuals pay more for, or benefit

less from, costly traits compared to high-quality individuals. These differential costs set the optimal trait expression at a lower value for lower-quality individuals compared to higher-quality ones (Grafen, 1990a, 1990b; Nur & Hasson, 1984; Zahavi, 1977). Even though this is a widely accepted explanation for honest scaling of sexual traits, empirical evidence is scarce (Kotiaho, 2001; Penn & Számadó, 2020) .

In addition to scaling relationships, costly traits can also differ depending on sex and season. For example, some secondary sexual traits are expressed in both sexes but at greater magnitudes in males than females (Heuring & Hughes, 2019; Nolzco et al., 2022). Moreover, costly traits might be expressed more intensely during the breeding season compared to the nonbreeding season, such as the annual shedding and regeneration of deer antlers (Brookes et al., 2004; Clements et al., 2010; Price et al., 2005). Snapping shrimp offer a particularly tractable system with which to test these classic questions about scaling, sex, and seasonality in the expression of costly traits. Snapping shrimp live in size-assortative male-female pairs. Individuals of both sexes bear one enlarged claw that they use as weapons during fights with same-sex conspecifics (Nolan & Salmon, 1970). They assess weapons as visual signals (Hughes, 1996, 2000) and use them as armament to injure or damage opponents (Dinh et al., 2020; Dinh & Patek, 2022; Kingston et al., 2022). Snapping shrimp use latch-mediated spring actuation to produce powerful strikes (Kaji et al., 2018; Longo et al., 2019; Longo et al., in review; Patek & Longo, 2018). They cock their claws open and use muscles to load an elastic mechanism

comprised of flexing exoskeleton and stretching apodemes (Longo et al., *in review*). They unlatch the claw to quickly release elastic energy, driving the dactyl shut in as little time as 0.36 milliseconds (Dinh & Patek, 2022). Upon closure, a tooth-shaped protrusion in the dactyl inserts into a cavity in the propodus, which generates a high-velocity water jet that vaporizes the trailing region of water. This vapor bubble, known as a cavitation bubble, collapses and produces pressures that are audible to the human ear as a “snap” (Kaji et al., 2018; Lohse et al., 2001; Versluis et al., 2000a). Snapping shrimp fire snaps at opponents during contests (Dinh et al., 2020; Dinh & Patek, 2022; Nolan & Salmon, 1970). The pressure of the cavitation bubble collapse can cause neurotrauma to the opponent, so snapping shrimp have evolved shock-absorbing helmets called orbital hoods to dampen the blows (Kingston et al., 2022).

Individuals with larger weapons produce longer-lasting cavitation bubbles, greater pressures, and have greater offensive capacity (Dinh & Patek 2022). They also tend to win contests (Dinh et al., 2020; Dinh & Patek, 2022). Yet, snapping shrimp don't grow weapons to arbitrary sizes. Instead, they vary along three axes: 1) larger individuals have larger weapons, 2) at any given body size, males have larger weapons than females, and 3) the sex difference amplifies during the summer breeding season (Heuring & Hughes, 2019). Therefore, costs and benefits of weapon size can be examined across these three axes: body size, sex, and breeding season.

We test if snapping shrimp face tradeoffs that scale with condition as predicted by the handicap principle. Then, we test the hypothesis that sex and seasonal differences in weaponry arise from sex-specific costs and benefits in alpheid snapping shrimp. We did not measure fitness and therefore refrain from using the term “costs”. Instead, we use the term expenditure to represent tradeoffs that could cascade to fitness costs (Kotiaho, 2001). To identify weapon expenditures that vary with size as predicted by the handicap principle, we tested if snapping shrimp individuals bearing large weapons sacrificed resources from the abdomen (the muscular segmented region of the body used for swimming) (S. Arnott et al., 1998; Hunyadi et al., 2020). Reduced abdomen size could lower fitness through reduced survival, given that abdomen length is positively correlated with predator escape velocity in other benthic decapod crustaceans (Hunyadi et al., 2020). Snapping shrimp with smaller abdomens could therefore be more vulnerable to predation. Furthermore, female snapping shrimp hold eggs underneath their abdomen, and reduced abdomen size could constrain maximum egg clutch volume. Thus, we tested whether snapping claws exhibit a morphological tradeoff with abdomen size, and whether this expenditure increases as body size decreases.

Next, we tested if growing weapons larger than predicted by the weapon size scaling relationships reduced the average angular velocity of the snapping claw, cavitation bubble duration, or pressure of the snap. Larger weapons produce longer-lasting cavitation bubbles and greater pressures (Dinh & Patek, 2022). However,

individuals that grow larger weapons than predicted by snapping claw scaling relationships do so using less muscle and more exoskeleton (Dinh, 2022). Reducing the amount of muscle in the claw may hinder elastic loading and snap production. We predicted that this tradeoff would be steepest in the smallest males as predicted by the handicap principle.

Then, to determine if female-specific expenditures explain why females have lower proportional weapon sizes than males, we tested for tradeoffs between female weaponry and egg production. In snapping shrimp, females bear the entire burden of egg production (Knowlton, 1980). Therefore, resources allocated to costly traits like weaponry should reduce the allotment invested in primary reproduction. Indeed, analogous tradeoffs between primary and secondary sexual characteristics arise for males in taxa as diverse as narwhals and dobsonflies (Dines et al., 2015; Liu et al., 2015; Simmons et al., 2017). To our knowledge though, weapon-egg tradeoffs in females have only been identified once, in leaf-footed cactus bugs (*Narnia femorata*) (Miller et al., 2019).

Finally, if males benefit more from large weaponry than females, then that could also contribute to the sex differences in weaponry. Therefore, we tested if males with large weaponry benefited through improved pairing success. Snapping shrimp form size-assortative pairs (Mathews, 2002; Nolan & Salmon, 1970). We tested whether large weapons improved the likelihood of pairing and whether individuals with large weapons paired with relatively larger mates. If either of these pairing advantages

disproportionately benefits males, then this could explain why males have larger weapons than females.

3.2 Materials and Methods

3.2.1 Animal Collection

In total, we collected 677 *Alpheus heterochaelis* snapping shrimp from Beaufort, North Carolina, USA (NCDENR Scientific and Education permit # 707075 to Duke University Marine Laboratory). We measured each individual and tested for a tradeoff between abdomen and snapping claw size (see *Morphological Tradeoff* and *Seasonal Trends* sections below). Subsets of these same *Alpheus heterochaelis* individuals were used in the remaining analyses: we used 76 individuals to test for kinematic costs (see *Kinematics* section), 37 egg-bearing females to test for reproductive tradeoffs (see *Reproductive Tradeoffs* section), and 486 individuals to test for pairing benefits (see *Pairing* section). Finally, we captured 45 *Alpheus estuariensis* individuals from the same site and 53 *Alpheus angulosus* individuals from Beaufort, South Carolina, USA, and we tested whether morphological tradeoffs also arose in these species. No ethical permits were required.

We collected *A. heterochaelis* and *A. estuariensis* once per month during the spring tide from July to October 2020 and February to August 2021. We collected *A. angulosus* during one trip in March 2019. We found snapping shrimp in oyster reefs at low tide by

flipping oyster clusters and excavating several centimeters of mud. We located individuals through turbid waters by scanning for antennae sweeping the water surface. We designated two shrimp as a male-female pair if they occupied the same tidepool underneath an oyster clump, and we acquired pairing data for 486 *Alpheus heterochaelis* individuals. We also noted whether individuals were caught during the breeding season. We considered breeding season as a binary variable. If any female was found holding eggs, it was considered the breeding season. The breeding season occurred between April and October, and no eggs were found during February and March collections. The months of breeding resemble those seen in *A. angulosus* populations in Charleston, South Carolina, USA (Heuring & Hughes, 2019). Temperatures in nearby waters were colder during the non-breeding season, fluctuating between 8 and 14 degrees Celsius, whereas breeding season temperatures fluctuated between 18 to 30 degrees Celsius (NOAA Station 8656483, Beaufort, Duke Marine Lab, North Carolina, USA).

For all three species, we measured each individual's carapace length, abdomen length, rostrum-to-telson length, and snapping claw length using digital calipers (resolution +/- 0.02 mm, Husky Tools, Atlanta, Georgia, USA). We built log-log scaling relationships for snapping claws, and abdomen length as a function of rostrum-to-telson length, sex, and their interaction.

3.2.2 Statistical Analysis

All statistical analyses were conducted using, R version 4.1.1, RStudio version 1.4.1717, and the tidyverse suite of R packages (R Core Team, 2018; RStudio Team, 2021; Wickham et al., 2019).

3.2.3 Morphological Tradeoffs

For each species, we hypothesized that growing a larger snapping claw would coincide with reduced abdomen size. We tested this relationship by calculating the residuals from the log-log abdomen and snapping claw scaling relationships defined above, where positive residuals indicate a larger abdomen or snapping claw than predicted by the scaling relationship. To test for a morphological tradeoff, we built regressions using abdomen residuals as the response variable and snapping claw residuals, sex, and their interaction as the explanatory variables. We repeated this analysis for *A. heterochaelis*, *A. angulosus*, and *A. estuariensis*.

Then, we tested whether slopes of the tradeoff depended on quality. Here and throughout the rest of the paper, we used carapace length as a measure of quality because it's the best known proxy for resource holding potential, the best-known predictor for female fecundity, and a reliable predictor of dominance and subordination in dyadic contests (Dinh et al., 2020). We hypothesized that the slope of the tradeoff would increase as carapace length decreased. To test this, we standardized carapace

length so that the mean was zero and each increment of one represents an increase of one standard deviation. We built a regression with abdomen residual as the response variable and snapping claw residual, standardized carapace length, and their interaction as the explanatory variable. We performed this analysis only for *Alpheus heterochaelis*, the species for which we had the greatest sample size and statistical power. We predicted a negative coefficient for the interaction, meaning that the tradeoff slope would approach zero as carapace length increased.

3.2.4 Kinematics

We reanalyzed data from Dinh & Patek (2022) to test if exaggerated weapons reduced weapon performance. We recorded high speed videos with synchronous pressure measurements from 10 snaps each in 76 individuals. We measured the average angular velocity, cavitation bubble duration, and peak-to-peak sound pressure level of each snap. Details about recording setup, equipment, and performance metrics are provided in Dinh & Patek (2022). In brief, we calculated average angular velocity as the angle change between the dactyl and the propodus during closure divided by the duration of closure (Kagaya & Patek, 2016). Then, we calculated cavitation bubble duration as the duration between the initiation of cavitation to the onset of initial bubble implosion. Finally, we calculated the peak-to-peak sound pressure level coincident with cavitation bubble collapse.

In previous research, we showed that average angular velocity decreased as claw mass increased, whereas cavitation bubble duration and sound pressure level increased as claw mass increased (Dinh & Patek, 2022). Here, we tested if these relationships also depended on weapon residuals. We built three linear models that used either $\log_{10}(\text{average angular velocity})$, $\log_{10}(\text{bubble duration})$, or sound pressure level (a logarithmic measure of pressure) as the response variable. In each model, we used $\log_{10}(\text{claw mass})$ and weapon residual as explanatory variables. We built separate models for males and females. For each performance metric, we hypothesized that performance would decrease with high-residual snapping claws, and we therefore predicted a negative coefficient for snapping claw residuals.

3.2.5 Reproductive Tradeoffs

We collected 37 ovigerous *A. heterochaelis* females. We removed each egg clutch and photographed them. We only included eggs in the early stage of development when the egg yolk was barely consumed and oblong deformation by the embryo was minimal. We counted the total number of eggs in each egg clutch and measured the estimated average egg volume using the Fiji distribution of ImageJ (version 2.0.0) (Schindelin et al., 2012). For each egg clutch, we measured the egg volume for 20 randomly selected eggs and calculated their mean as the average egg volume $V_{egg} = \frac{1}{6}\pi d_{min}^2 d_{max}$, where V_{egg} represents egg volume, d_{min} represents the minimum egg diameter, and d_{max} represents

the maximum egg diameter (Kuris, 1990). Finally, we calculated total egg mass volume (EMV) as the egg count multiplied by the average egg volume.

Egg count and EMV increased as carapace length increased. Therefore, we regressed egg count and EMV against carapace length and calculated egg count residuals and EMV residuals from the scaling relationship. These residuals reflect investment into eggs, where more positive residuals indicate greater investment and more negative residuals indicate less investment. We did not use residual analysis for average egg volume because it did not scale with carapace length. To test for reproductive tradeoffs between eggs and weapons, we built three linear regressions that used either egg count residual, average egg volume, or EMV residual as the response variable. All models included snapping claw residual as the sole explanatory variable. We predicted a negative relationship that reflected a reproductive tradeoff.

Then, to test if female snapping shrimp with smaller carapace lengths faced steeper tradeoffs, we added carapace length and its interaction with snapping claw residual to each of the models. If smaller individuals pay steeper expenditures, then the interaction should be positive: the negative relationship between egg properties and snapping claw residuals would taper to zero as carapace length increases.

3.2.6 Pairing

We used t-tests to determine if paired individuals had greater weapon residuals than unpaired individuals. The response variable was weapon residual, and the

explanatory variable was a binary variable of paired status, where one represents a paired individual and zero represents an unpaired individual. We performed separate tests for each sex.

Similarly, to test if greater snapping claw residuals increased the probability of pairing, we built a binomial generalized linear model with pairing status (1 = paired, 0 = unpaired) as the response variable. The explanatory variables were carapace length and snapping claw residual. We built models for each sex separately.

Then, we tested if individuals with greater weapon residuals paired with larger mates. We calculated the relative size of pair mates as $1 - \frac{\text{rostrum-to-telson length}_{\text{focal}}}{\text{rostrum-to-telson length}_{\text{pairmate}}}$ such that more positive values mean that pair mates are larger than focal individuals, and 0 means that individuals are equally sized. We used rostrum-to-telson length here because males and females form size-assortative pairs based on body length (Mathews, 2002; Nolan & Salmon, 1970). We built a linear model with the relative size of pairmates as the response variable and snapping claw residual of the focal individual as the explanatory variable. We repeated this analysis using either males or females as the focal individuals and the opposite sex as the pairmate. We predicted a positive relationship if individuals with greater weapon residuals attracted or maintained relatively larger pairmates.

3.2.6 Seasonal Trends

We tested if reproductive costs manifested in seasonal fluctuations in morphology between breeding and non-breeding seasons in *Alpheus heterochaelis*. We performed t-tests to compare 1) abdomen residuals and 2) snapping claw residuals using breeding season as the explanatory variable (1 = breeding season, 0 = non-breeding season). The breeding season lasted from April to October when we found ovigerous female snapping shrimp. February and March collections were considered the nonbreeding season because we collected no ovigerous females. We performed separate t-tests for each sex in *Alpheus heterochaelis*. We predicted that snapping claw residuals would be elevated during the breeding season for males but not females, and that shift would coincide with a reduction in abdomen residuals. Then, to test if the scaling slope of the snapping claw changed between seasons, we built a linear model for each sex with $\log_{10}(\text{snapping claw length})$ as the response variable and $\log_{10}(\text{rostrum-to-telson-length})$, breeding season, and their interaction as the predictor variables. A significant interaction term would indicate a seasonal allometric shift. If the interaction term was nonsignificant, we removed it from the model to test if there was an overall shift in weapon investment without a change in slope across breeding and non-breeding seasons.

3.3 Results

3.3.1 Morphology

The allometric slope of snapping claw scaling differed significantly between sexes for *Alpheus heterochaelis* and *Alpheus angulosus* but not for *Alpheus estuariensis* (Fig. 9).

Weapons with greater snapping claw residuals exhibited tradeoffs with body size. Snapping claw residuals and abdomen residuals were negatively correlated in both sexes and for all three species (Fig. 9). We tested if this tradeoff was size-dependent in *A. heterochaelis* — the species for which we had the largest sample size and greatest statistical power. For males, as predicted, individuals with smaller carapace lengths had steeper tradeoff slopes compared to those with larger carapace lengths (interaction p-value = 0.002). By contrast, we found no evidence of size-dependent slopes for female weapons (interaction p-value = 0.93).

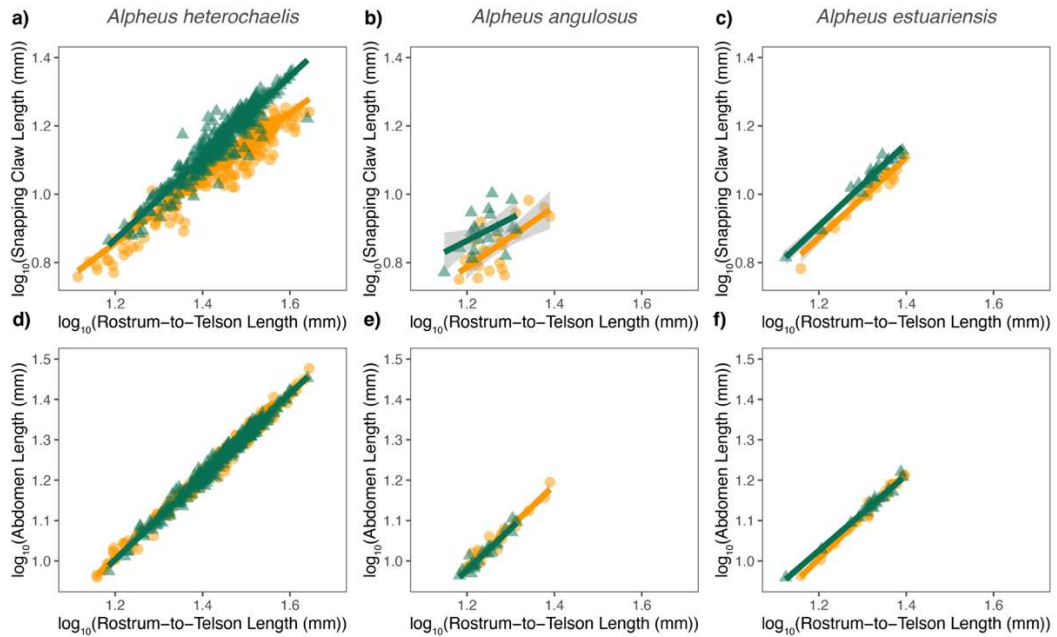


Figure 9: Snapping claw length and abdomen length increased with rostrum-to-telson length across the three alpheid species. Residuals from these lines were used to test for weapon expenditures and tradeoffs in subsequent analyses. In all panels, males are shown as green triangles, and females are shown as orange circles. Shaded regions represent 95% confidence intervals for linear regressions.

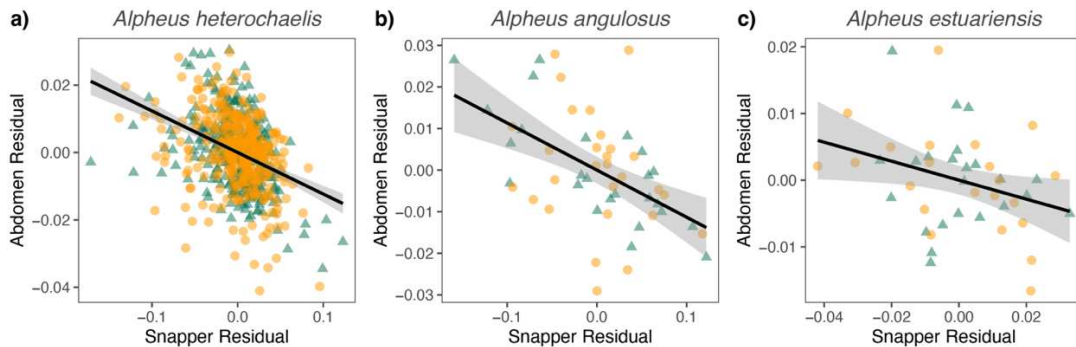


Figure 10: In all three analyzed species, there was a tradeoff between snapping claw residuals and abdomen residuals. Individuals with greater snapping claw residuals had lower abdomen residuals in a) *Alpheus heterochaelis*, b) *Alpheus angulosus*, and c) *Alpheus estuariensis*. Green triangles are males and orange circles are females. Regressions were calculated from both sexes because sex and the sex*snapping claw

residual interaction were not significant predictors in any model. Shaded regions represent 95% confidence intervals for linear regressions.

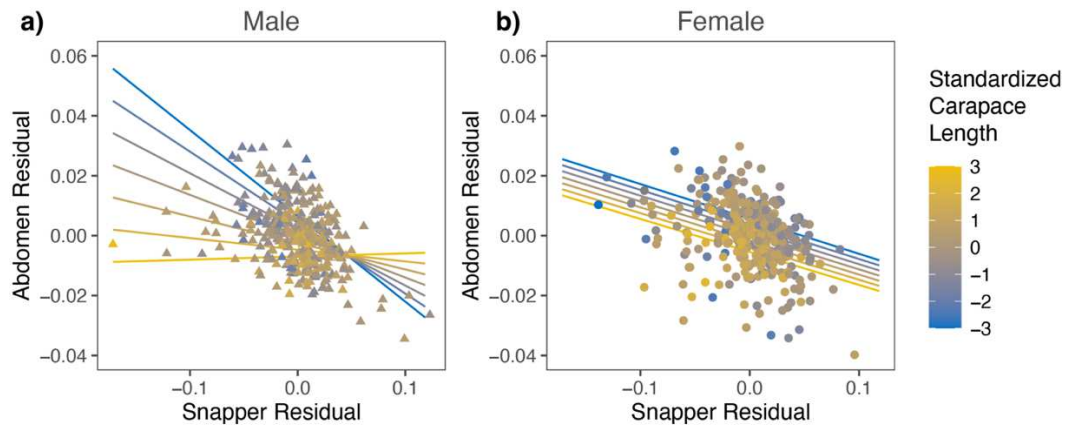


Figure 11: The tradeoff between snapping claw residuals and abdomen residuals was steepest for the smallest individuals in *Alpheus heterochaelis* males (a) but not females (b). Lines represent model predictions for standardized carapace lengths of -3, -2, -1, 0, 1, 2, and 3. A standardized carapace length of 0 represents an individual with the mean carapace length, and each increment of 1 represents one standard deviation.

3.3.2 Kinematics

Exaggerating weapons did not affect snap performance in *A. heterochaelis* males or females. Neither weapon residuals nor its interaction with claw mass were significant predictors of \log_{10} (average angular velocity), \log_{10} (bubble duration), or sound pressure level

3.3.3 Reproductive Tradeoffs

For female *A. heterochaelis*, weapon residuals had egg production tradeoffs.

Weapon residuals were negatively correlated with egg mass volume (EMV) residuals, average egg volume, and egg count residuals (Fig. 12). Tradeoffs for egg count residuals and EMV residuals were not size-dependent ($p_{\text{interaction}} = 0.223$ and $p_{\text{interaction}} = 0.483$, respectively). However, average egg volume tradeoffs were steeper for females with smaller carapace lengths compared to those with larger carapace lengths (interaction term t-test: $b = 1.241$, $se = 0.538$, $t = 2.306$, $p = 0.028$) (Fig. 13).

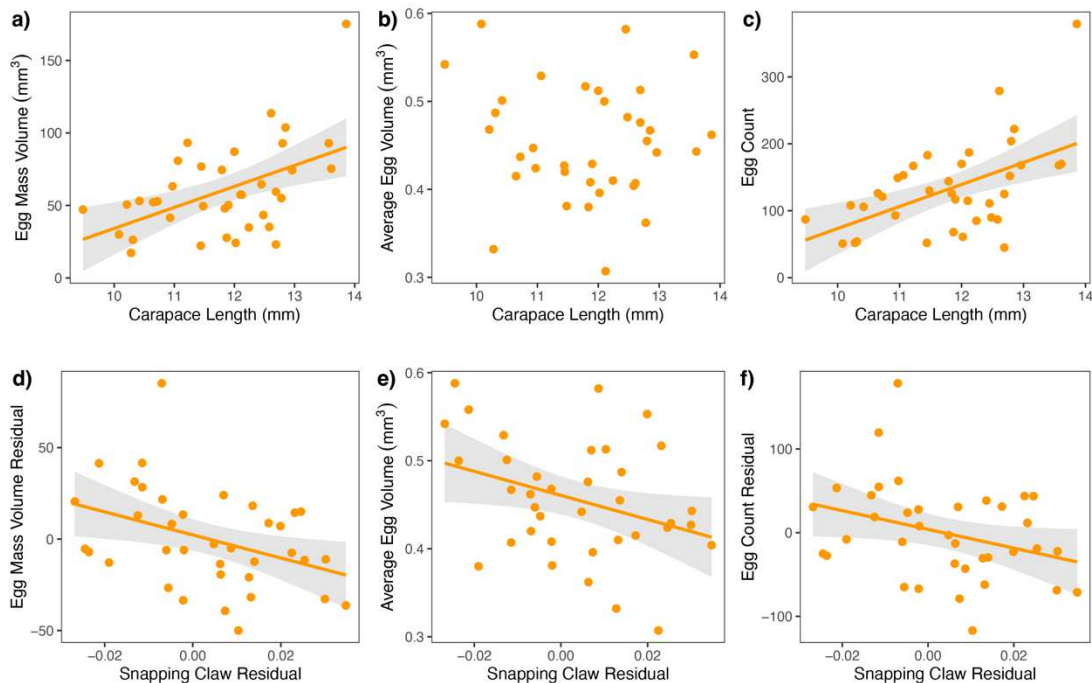


Figure 12: *Alpheus heterochaelis* females exhibit tradeoffs between weapon size and egg mass volume, average egg volume, and egg count. As carapace length increased, a) egg mass volume increased, b) average egg volume remained constant, and c) egg

count increased. As snapping claw residuals increased, d) egg mass volume residuals decreased, e) average egg volume decreased, and f) egg count residual decreased.

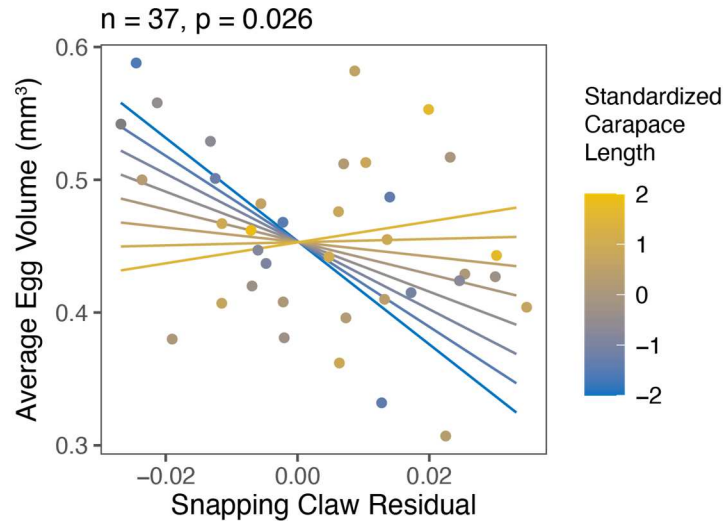


Figure 13: Smaller *Alpheus heterochaelis* females exhibited steeper tradeoffs between snapping claw residuals and average egg volume compared to larger females. Lines represent model predictions for standardized carapace lengths of -2, -1.5, -1, -0.5, 0, 0.5, 1, and 1.5. A standardized carapace length of 0 represents an individual with the mean carapace length, and each increment of 1 represents one standard deviation.

3.3.4 Pairing

In *A. heterochaelis*, paired males had significantly greater weapon residuals compared to unpaired males (t-test: n = 233, p = 0.000299), but there was no significant difference for females (t-test: n = 253, p = 0.56) (Fig. 14).

For males, the probability of being paired increased as snapping claw residual increased (n = 233, b = 16.879, SE = 5.652, z = 2.986, p = 0.00345), but there was no

significant relationship with carapace length ($p = 0.104$). By contrast, for females, the probability of being paired increased as carapace length increased ($n = 253$, $b = 0.574$, $SE = 0.142$, $z = 4.034$, $p = 3.72 \times 10^{-5}$) but there was no significant relationship with snapping claw residual ($p = 0.487$) (Fig. 15).

For paired males, as weapon residuals increased, the relative rostrum-to-telson lengths of their pair mates also increased (linear model F-test, $n = 111$, $p = 0.00467$). However, there was no significant trend in females (linear model F-test, $n = 111$, $p = 0.0649$) (Fig. 14).

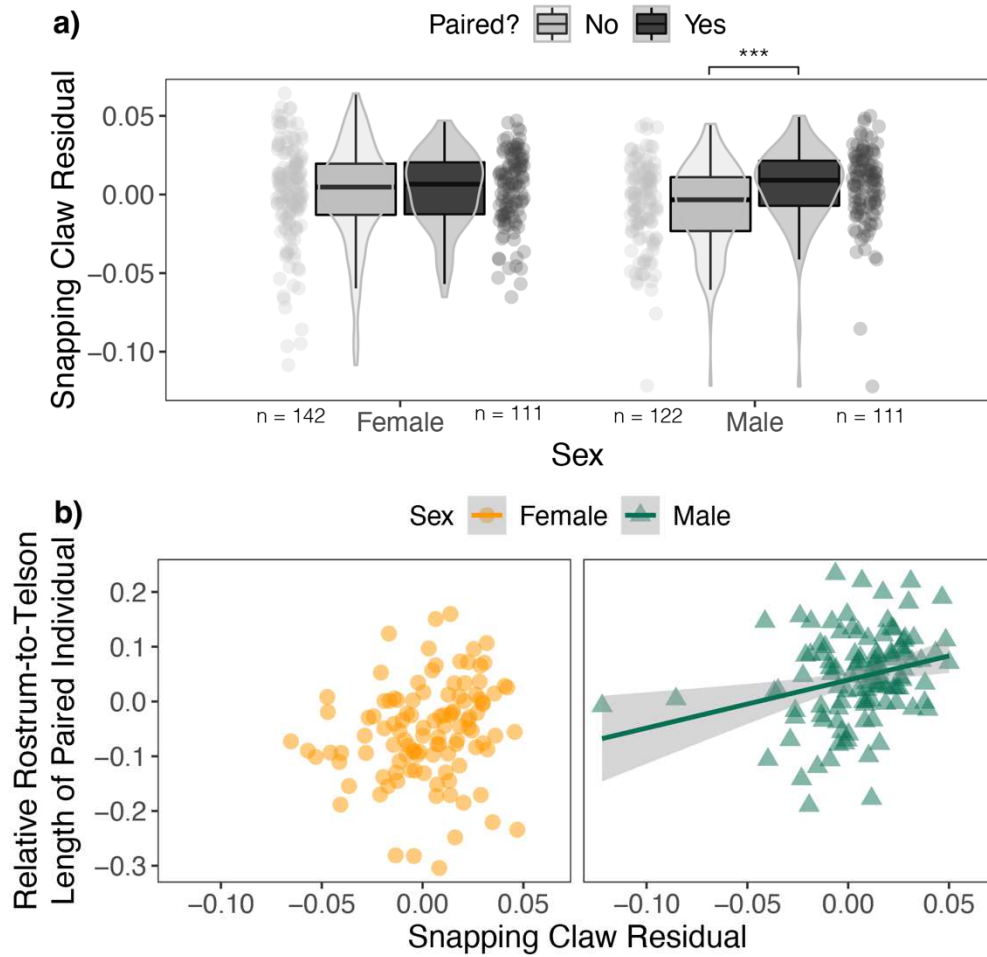


Figure 14: Males *Alpheus heterochaelis* benefited from more positive snapper residuals in a way that females did not. a) Paired *Alpheus heterochaelis* males had greater snapping claw residuals than unpaired males, but there was no such trend in females. b) Males with more positive residuals paired with relatively larger pairmates, but there was no such trend in females. The shaded region is the 95% confidence interval.

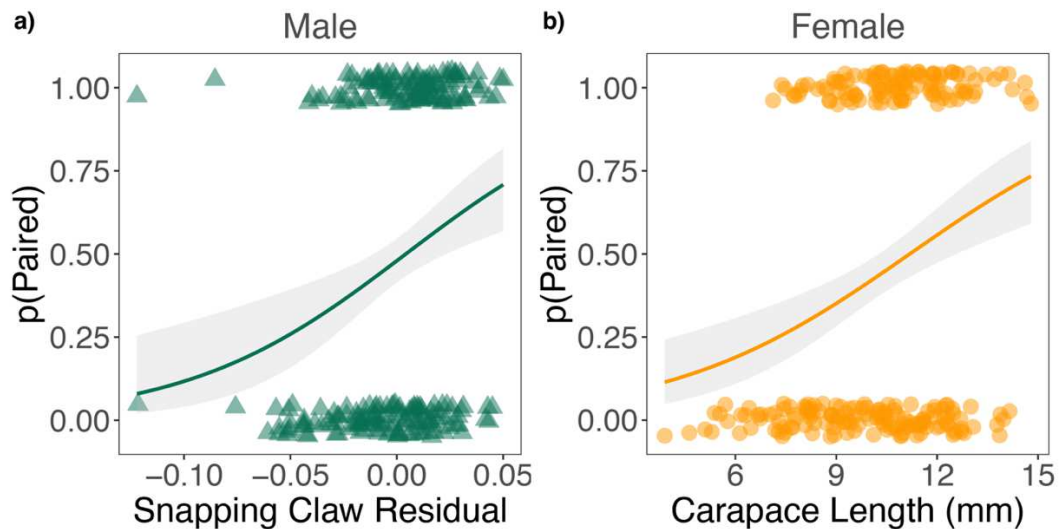


Figure 15: Snapping claw residuals predicted the probability of being paired for *Alpheus heterochaelis* males but not females. a) The probability of being paired was positively correlated with snapping claw residuals (but not carapace length) for males. b) Meanwhile, the same probability was correlated with carapace length (but not snapping claw residuals) for females. Each point represents one individual, and the shaded region is the 95% confidence interval. 1 indicates paired individuals, and 0 indicates unpaired individuals. Points are jittered vertically around these values for visual clarity.

3.3.5 Seasonal Trends

Abdomen residuals were reduced in male *A. heterochaelis* during the breeding season compared to the non-breeding season, whereas female exhibited no significant seasonal shift (Fig. 16a). By contrast, snapping claw residuals were elevated in males during the breeding season compared to the non-breeding season, whereas females exhibited no significant seasonal shift (Fig. 16b).

Furthermore, the scaling slope for female snapping claws became more shallow during the breeding season (interaction term t-test: $n = 348$, $b = -0.183$, $p = 0.000838$). There was no such seasonal shift in allometry for males (interaction term t-test: $n = 329$, $p = 0.233$). After the nonsignificant interaction term was removed from the male model, there was a significant increase in snapping claw lengths across all rostrum-to-telson lengths (t-test, $n = 329$, $b = 0.023$, $p = 5.62 \cdot 10^{-6}$) (Fig. 17).

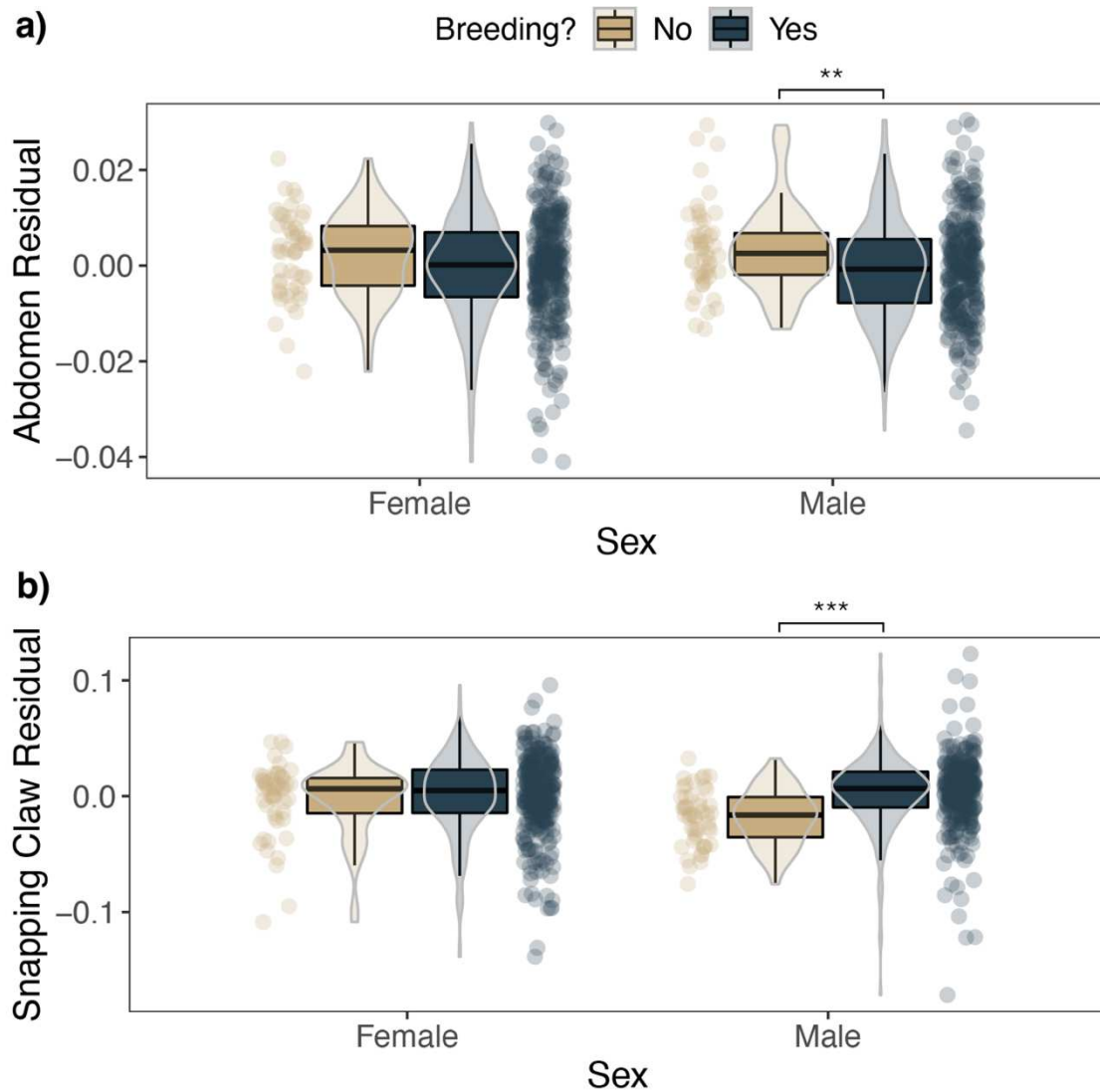


Figure 16: Male *Alpheus heterochaelis* shifted investment from their abdomen to their snapping claws during the breeding season, but no such shift was evident in females.

During the breeding season, males had a) reduced abdomen residuals and b) increased snapping claw residuals. Females did not exhibit significant morphological shifts. **p < 0.01 *p < 0.001**

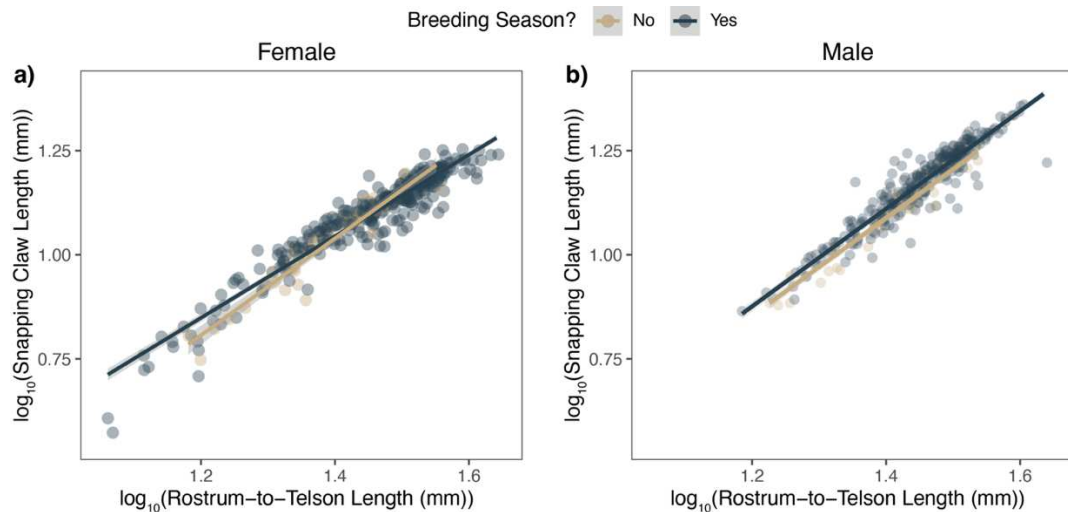


Figure 17: Scaling slopes shifted during the breeding season. Female *Alpheus heterochaelis* scaling slopes were significantly shallower during the breeding season compared to the nonbreeding season. Male scaling slopes did not significantly change seasonally, but during the breeding season, there was an upward shift in snapping claw lengths across all rostrum-to-telson lengths. Shaded regions are 95 percent confidence intervals.

3.4. Discussion

Evolutionary theory suggests that individuals express costly traits like weapons and ornaments at an optimal magnitude that maximizes the cost-benefit ratio. Because individuals differ in the costs they pay and the benefits they reap, trait expression varies in systematic and predictable ways across the population (Grafen, 1990a, 1990b; Nur & Hasson, 1984; Zahavi, 1977). We found empirical evidence for size-dependent expenditures that could explain reliable scaling of trait expression: the smallest snapping shrimp exhibited the steepest morphological tradeoffs and reproductive costs. Moreover, we applied the same logic — that costs and benefits differ between

individuals and lead to different optimal trait expression — to explain sex differences in weaponry. Large weaponry is especially costly to females which suffer reproductive tradeoffs. Meanwhile, large weaponry benefits males by increasing the probability of being paired and the relative rostrum-to-telson length of their pair mate. These sex-specific implications of weapon investment on reproduction and pairing are vital to fitness because female egg production is the primary determinant of fecundity (Knowlton, 1980). Males can boost fitness by pairing with larger females, and females sacrifice fitness by reducing investment into eggs. These sex-specific tradeoffs and benefits can therefore explain why females have smaller proportional weapon sizes compared to males, why this sex difference amplifies during the breeding season, and why female weapon scaling slopes become more shallow during the breeding season when egg production and pairing is at a premium.

We tested for size-dependent weapon expenditures using morphological tradeoffs. For both males and females, individuals with larger weapons had smaller abdomens (Fig. 10). This was true in all three species of snapping shrimp that we tested. Additionally, in male *Alpheus heterochaelis*, smaller males exhibited a steeper tradeoff than larger males, indicating a size-dependent expenditure of weaponry (Fig. 11).

The proportion of the claw made of muscle decreases as weapon residual increases (Dinh, 2022). Therefore, we tested whether weapon residuals were negatively correlated with average angular velocity in the snapping claw, cavitation bubble

duration, and snap pressure. Surprisingly, weapon residuals were not correlated with any of these metrics.

The expenditures and benefits of growing a large weapon also differed by sex. For ovigerous *A. heterochaelis* females, greater weapon size led to lower egg counts, smaller average egg volume, and lower egg clutch volume (Fig. 12). Reproductive expenditures were also size-dependent: the tradeoff between weapons and average egg volume was steepest for females with the smallest carapace lengths. Sex-specific costs could explain why females have smaller proportional weapon sizes than males.

In addition, we showed that male *A. heterochaelis* benefited by investing in weaponry through pairing, whereas females did not. In males, weapon residuals were positively correlated with the probability of being paired and the relative body length of their pair mates (Fig. 14 – 15). Females did not exhibit either of these benefits. Male-specific benefits could therefore contribute to sex differences in weapon investment.

Egg production is particularly salient to female snapping shrimp because they bear the entire energetic burden of egg production (Knowlton, 1980). Likewise, there is incentive for males to pair with large and fecund females. Therefore, growing a large weapon is particularly burdensome to females and particularly beneficial for males. These reproductive expenditures and benefits could therefore explain why males have larger proportional weapon sizes than females.

The sex-specific expenditures and benefits are also consistent with seasonal oscillations in weaponry. *A. heterochaelis* males had greater weapon residuals during the breeding season compared to the non-breeding season, whereas female weapon residuals remained consistent throughout the year (Fig. 16). Furthermore, the scaling slope of the snapping claw became more shallow during the breeding season for females. By contrast, males did not show a significant seasonal change in scaling slope, but across the range of body sizes, snapping claw lengths increased during the breeding season (Fig. 17). Concurrently, males had significantly lower abdomen residuals during the breeding season, whereas females exhibited a slight but nonsignificant decrease in abdomen residuals. Similar trends have been reported in *A. angulosus*, although in that species, females significantly reduce proportional abdomen sizes during the breeding season (Heuring & Hughes, 2019). We speculate that males shift investment from their abdomens into weapons during the breeding season because it increases their likelihood of being paired. Female snapping shrimp shift investment from abdomens to eggs, and they don't increase weapon size because they face tradeoffs between eggs and weapons.

Female weapon-egg tradeoffs are analogous to classic examples of male weapon-testes tradeoffs (Simmons et al., 2017; Simmons & Emlen, 2006). Our findings are the second example of reproductive tradeoffs in female weapons (Miller et al., 2019). Most likely, the dearth of findings is simply due to insufficient studies of female weaponry. Sex biases in research, such as the misconception that only males fight and only females

choose, are common (Haines et al., 2020; Pollo & Kasumovic, 2022; Tang-Martínez, 2016). For example, it's now accepted that female birdsong is widespread, but for centuries, historical research focused almost entirely on males that were presumed to be the only sex to compete for mates (Odom et al., 2014; Odom & Benedict, 2018; Riebel et al., 2019). Like birdsong, female secondary sexual traits, weapons, and competition are not uncommon, and they often serve signaling functions just as they do in males (Amundsen & Forsgren, 2001; LeBas, 2006; Miller et al., 2019; Nolzco et al., 2022; Nordeide, 2002; Watson & Simmons, 2010). Sex-inclusive research on the costs and benefits of these traits would not only redress long-standing omissions from the scientific literature, but comparisons between males and females would also provide empirical tools to understand how costs and benefits govern trait expression within a single species.

Ideally, we would be able to link each of the expenditures and benefits we identified here to a fitness cost (Kotiaho, 2001). However, this bar is infeasibly high in snapping shrimp. They are prolific breeders, cryptic, and difficult to mark and recapture because they molt each month. The egg production tradeoffs are as close to a direct fitness cost as we could identify. Morphological tradeoffs, on the other hand, are more distant to fitness costs. However, it is a reasonable possibility that abdomen tradeoffs impact survival. For example, the primary mode of predator escape in many decapod crustaceans is the tailflip, during which individuals contract their abdomen to propel

themselves backwards (Wiersma, 1947). Tailflip velocity and acceleration in crayfish increases with abdomen length (Hunyadi et al., 2020). If the same holds in snapping shrimp, then the abdomen tradeoff that we found here could influence survival.

However, future work is required to reach a definitive answer.

Some expenditures we documented did not differ with size; however, the overall fitness cost might still be size-dependent. For example, smaller females did not exhibit a weapon size tradeoff with the total number of eggs they produced. Even though the scaling slopes were invariant across the size range, small individuals might suffer a greater relative reduction in eggs and therefore a greater cost in relative fitness. For example, reducing a 100-egg clutch by 10 would incur a 10 percent decrease, but reducing a 200-egg clutch by 10 would incur a 5 percent decrease. Compared to large and fecund individuals, then, smaller individuals might suffer a greater relative fitness cost than larger individuals despite a similar absolute tradeoff in egg production.

Empirical evidence of fitness costs is elusive because fitness manifests from a mosaic of subtle expenditures. Some of these expenditures, like reproduction, are obviously correlated to fitness, while others might have subtle yet meaningful effects. There is likely a smorgasbord of expenditures that we didn't test for here, some of which are undetectable in purely observational work. For example, in other crustaceans, weapons hinder locomotion and reduce survival during predator escape (Hunyadi et al., 2020). These expenditures need to be identified through future experiments. Other

expenditures might not be tractable through morphology, but through social interactions. In the paper wasp *Polistes dominulus*, for example, body size is correlated with pigment deposition in facial masks. Poor-condition wasps with facemasks manipulated to appear formidable experienced social costs via conspecific aggression (Tibbetts & Dale, 2004). The observational work we present here is a starting point to identify the fitness consequences of large weaponry. We encourage observations of behavior in naturalistic conditions and experiments that manipulate sexual traits to paint the entire mosaic of fitness-relevant expenditures of weaponry.

The handicap principle suggests that individuals are plastic in their ability to signal at different levels, and they signal at the level that optimizes their cost-benefit difference (Grafen, 1990a, 1990b; Nur & Hasson, 1984; Zahavi, 1977). This hypothesis requires costs or benefits that differ between individuals. However, the debate and acceptance of this principle has relied more on theory and less on empirical evidence (Penn & Számadó, 2020). We showed through field observations that size-dependent expenditures can ensure signal reliability through morphological and reproductive tradeoffs. Furthermore, we co-opted the same logic of differential costs and benefits to show that large weapons are particularly beneficial to males and particularly burdensome to females. These sex-specific implications of weaponry on reproduction could underlie sex and seasonal differences in costly trait expression.

4. Large and exaggerated sexually selected weapons comprise high proportions of metabolically inexpensive exoskeleton

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4.1 Introduction

Sexually selected weapons are morphologies used in intrasexual contests (McCullough et al., 2016). Oftentimes, proportional weapon size increases with body size (Emlen, 2008; Kodric-Brown et al., 2006). This phenomenon is called positive allometry, which is characterized by log-log scaling relationships with slopes greater than 1 (Kodric-Brown et al., 2006; Schmidt-Nielsen, 1984).

Weapon size is constrained by costs that decrease a weapon-bearer's fitness (Kotiaho, 2001). For example, large weapons can increase predation risk (Metz et al., 2018) and impose tradeoffs with primary sexual characteristics (Simmons et al., 2017; Simmons & Emlen, 2006). Weapons can also impose energetic costs that reduce viability and fitness (Mappes et al., 1996). Most studies of energetic costs focus on signaling and growth, which can be ephemeral if weapon growth is episodic (Moczek & Nijhout,

2004). However, they overlook an energetic sink that is omnipresent and interminable – energetic maintenance costs.

Energetic maintenance costs are constant energy sinks that arise from the body's homeostatic biochemical reactions (Hulbert & Else, 2000). They represent the “cost of living while doing nothing” (Hulbert & Else, 2000) and are distinct from more ephemeral energetic costs of growth (Moczek & Nijhout, 2004) and signaling (Allen & Levinton, 2007). For sexually selected traits, maintenance costs are massive. For example, in leaf-footed bugs, weapon autotomy reduces resting metabolic rates by 23.5% (Somjee, Woods, et al., 2018). How can individuals grow large weapons if they are energetically expensive to maintain?

A recent hypothesis, the cost-minimization hypothesis, proposes that if maintenance costs are high and energy is limiting, then selection should favor structures that minimize energetic maintenance costs. Because tissues vary in their metabolic rate, this hypothesis predicts that as sexually selected structures grow, they should comprise proportionally more metabolically inactive tissue (e.g. cuticle 18,19) and proportionally less metabolically active tissue (e.g. muscle, 11,17) (Somjee, 2021). For example, in New Zealand giraffe weevils (*Lasiorrhyncus barbicornis*), the largest males invest 60% less in metabolically active soft tissue in their weapons and have lower resting metabolic rates compared to the smallest males (Somjee et al., 2021).

At a finer size scale, conspecifics of the same size often vary in their weapon size. Some individuals have exaggerated weapons, defined as weapons that are larger than predicted by scaling relationships. In the same way that differential tissue allocation facilitates large weapon sizes, it could also facilitate weapon exaggeration: individuals might exaggerate weapons by investing more in metabolically inactive tissues compared to metabolically active tissues. However, the cost-minimization hypothesis has never been extended to weapon exaggeration.

Here, I test and extend the cost-minimization hypothesis using proportional tissue allocation as a proxy for energetic maintenance costs in three species of crustaceans: snapping shrimp (*Alpheus heterochaelis* and *Alpheus angulosus*) and fiddler crabs (*Uca pugilator*). All three species have one enlarged claw that is used as a weapon. Snapping shrimp use enlarged claws to fire cavitation bubbles during contests (Dinh et al., 2020), and both males and females wield weapons. Male fiddler crabs use claws as pinching weapons (Pratt et al., 2003) and as visual signals during contests (Backwell & Passmore, 1996). For each species and sex, I determined the scaling relationship of metabolically active soft tissues and metabolically inexpensive exoskeleton. I predicted that exoskeleton would exhibit positive allometry but soft tissue would exhibit negative allometry. Therefore, soft tissue proportions would be greatest in the smallest individuals. Then, I tested if cost-minimizing strategies facilitated weapon exaggeration.

I predicted that claw exoskeleton proportions would decrease as weapon exaggeration increased.

4.2 Materials and Methods

4.2.1 Animal Collection

I collected snapping shrimp (*Alpheus heterochaelis* and *Alpheus estuariensis*) and fiddler crabs (*Uca pugilator*) at Piver's Island (Beaufort, North Carolina, USA) (NCDENR Scientific and Education Permit #707075 to the Duke University Marine Laboratory). I collected snapping shrimp from underneath oyster clumps and fiddler crabs in salt marshes at low tide. Within 24 hours, I froze animals in seawater to prevent osmotic shock. Cold euthanasia quickly dispatched animals within an hour.

4.2.2 Mass Measurements

I removed the enlarged claw (hereafter, weapon) from each individual at a natural breakpoint in the carpus-propodus joint. I dried all bodies and weapons in a drying oven at 70°C for 72 hours, after which a stable mass was reached. I massed bodies and weapons using a microbalance (resolution: $\pm 1 \mu\text{g}$; XPE56, Mettler Toledo, Pleasant Prairie, Wisconsin, USA). I calculated total mass as dry body mass + dry weapon mass.

4.2.3 Soft Tissue Digestion

After obtaining dry masses, I digested the soft tissue of the weapon using papain – a protease that digests soft tissue but not exoskeleton (O'Brien et al., 2019; Somjee et al., 2021). I sliced a hole into each propodus, placed claws into tubes filled with papain solution (18.5 U papain per mL 0.1 M Tris-HCl buffer, pH = 7.0), and digested them for 72 hours. Then, I washed claws with 70% ethanol, dried them in the drying oven at 70°C for 72 hours, and massed them again using a microbalance. I calculated soft tissue mass as the difference in dry mass before and after papain treatment and soft tissue proportion as soft tissue mass divided by the claw mass measured before digestion.

I performed two control experiments to ensure that papain digested soft tissues. First, to confirm that papain was the primary proteolytic agent, I performed the same experimental procedure but did not digest in papain (i.e. claws were only ethanol washed between drying sessions). Second, to confirm that papain did not digest the cuticular exoskeleton, I manually dissected soft tissues before experimental treatment. In both cases, I predicted that experimental treatment would not affect mass. I calculated percent change in mass as $\frac{\text{mass after 2nd dry} - \text{mass after 1st dry}}{\text{mass after 1st dry}}$. I used 5 *A. heterochaelis* males per experiment. When papain was not used, claws did not change mass (percent change range = -0.58 – 0.45%) (paired t-test: $t = 0.06915$, $df = 4$, $p = 0.5273$). When soft tissues were manually dissected, there was a small loss of mass likely due to imperfect muscle dissection (percent change range = -4.2 - -1.3%) (paired t-test: $t = 3.5357$, $df = 4$, p

= 0.024). This percent change is an order of magnitude smaller than the experimental group (percent change range = -14 – -67%; mean = -35%). These results verified that, as intended, papain digestion targeted soft tissue.

4.2.4 Statistical Analysis

To determine scaling relationships between total mass and claw mass, I constructed linear regressions for each group: *Alpheus estuariensis* males, *Alpheus estuariensis* females, *Alpheus heterochaelis* males, *Alpheus heterochaelis* females, and *Uca pugnator* males. I regressed $\log_{10}(\text{claw mass})$ against $\log_{10}(\text{total mass})$ and assessed the slopes to determine allometric scaling relationships. Part-whole correlations were not an issue because in all species, claw mass was also highly correlated with mass of the rest of the body ($r^2 > 0.81$, $p < 0.0005$) (Christians, 1999). To test if muscles and exoskeleton scaled with different slopes, I built a multiple regression model with $\log_{10}(\text{tissue mass})$ as the response variable, and $\log_{10}(\text{total mass})$, tissue type (dummy coded so soft tissue = 1 and exoskeleton = 0), and their interaction as explanatory variables (Somjee et al., 2021). Positive interaction terms indicate that soft tissue scales with more positive allometry, whereas negative interaction terms indicate that soft tissues scale with more negative allometry than exoskeleton. I tested whether the interaction was a good predictor by removing it from the model and comparing AICc to the full model (Burnham & Anderson, 2002). I considered any model within 2 AICc of the best-fitting model to have substantial support (Burnham et al., 2011; Burnham & Anderson, 2002).

To test if larger individuals invested proportionally more in inexpensive exoskeleton and if exaggerated claws are built primarily with exoskeleton, I built the following beta regression: soft tissue proportion $\sim \log_{10}(\text{claw mass}) + \text{weapon residual}$. I calculated weapon residuals as the residual from the following scaling regression: $\log_{10}(\text{claw mass}) \sim \log_{10}(\text{total mass})$. This model tested whether weapon residuals influenced soft tissue proportion after controlling for claw mass. To test if weapon residual was a good predictor of soft tissue proportion, I removed it from the model and compared its AICc to the full model.

4.3 Results

Claw mass scaled positively allometrically in all groups except for *Alpheus heterochaelis* females (Fig. 17). For all groups, tissue mass was best predicted by $\log_{10}(\text{total mass})$, tissue type, and their interaction (range of ΔAICc : 9.03 – 42.44). Interaction terms always indicated more negatively allometric slopes for soft tissue. Claw exoskeleton generally exhibited positive allometry (except for *A. heterochaelis* females), and claw soft tissue generally exhibited negative allometry (except for *A. estuariensis* males).

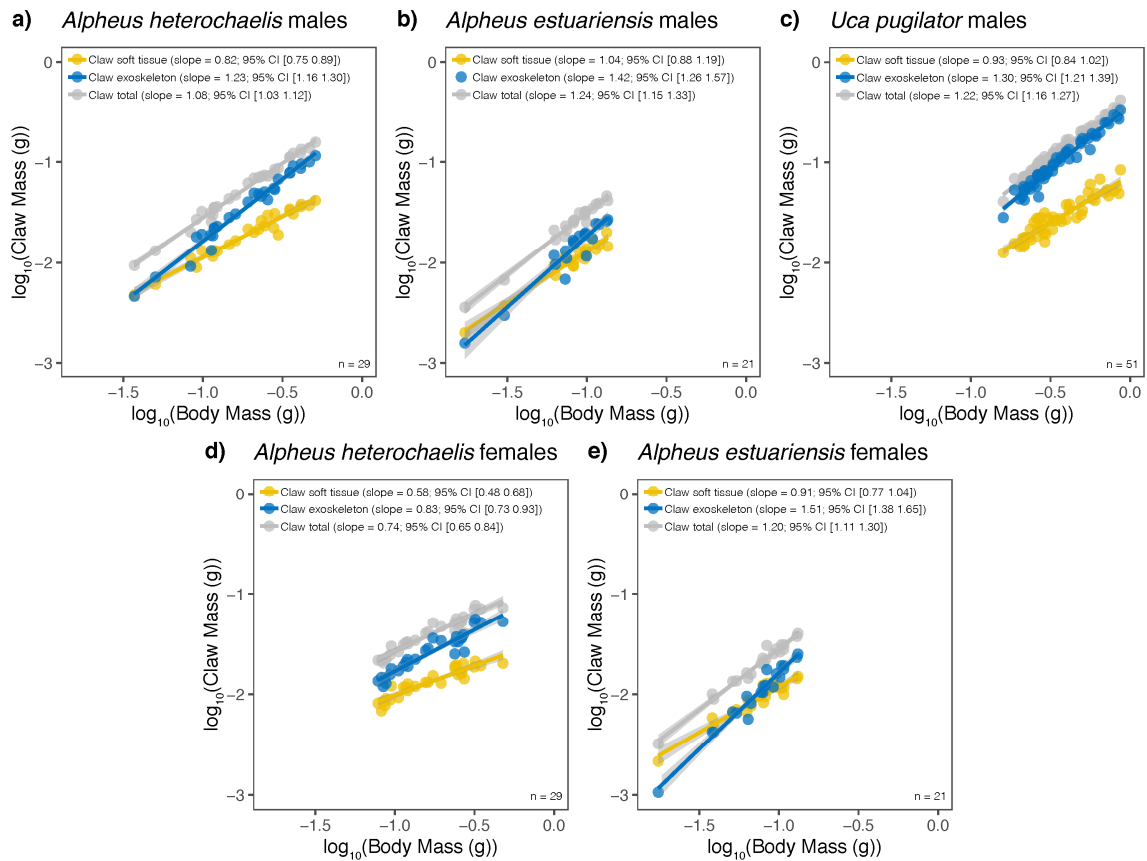


Figure 18: Allometric scaling relationships indicate more positive allometry of exoskeleton than soft tissue. Scaling exponents are shown in the legends.

Soft tissue proportions decreased as weapon size increased, and there was a ~2-fold difference between weapons with the greatest and lowest proportional soft tissue mass (1.79x in *A. estuariensis* males, 1.86x in *A. estuariensis* females, 2.50x in *A. heterochaelis* males, 1.59x in *A. heterochaelis* females, and 2.57x in *Uca pugilator* males) (Fig. 18). Furthermore, after controlling for claw size, soft tissue proportions decreased as weapon residuals increased (ΔAICc of full model < 2; all groups except for *A. estuariensis* females).

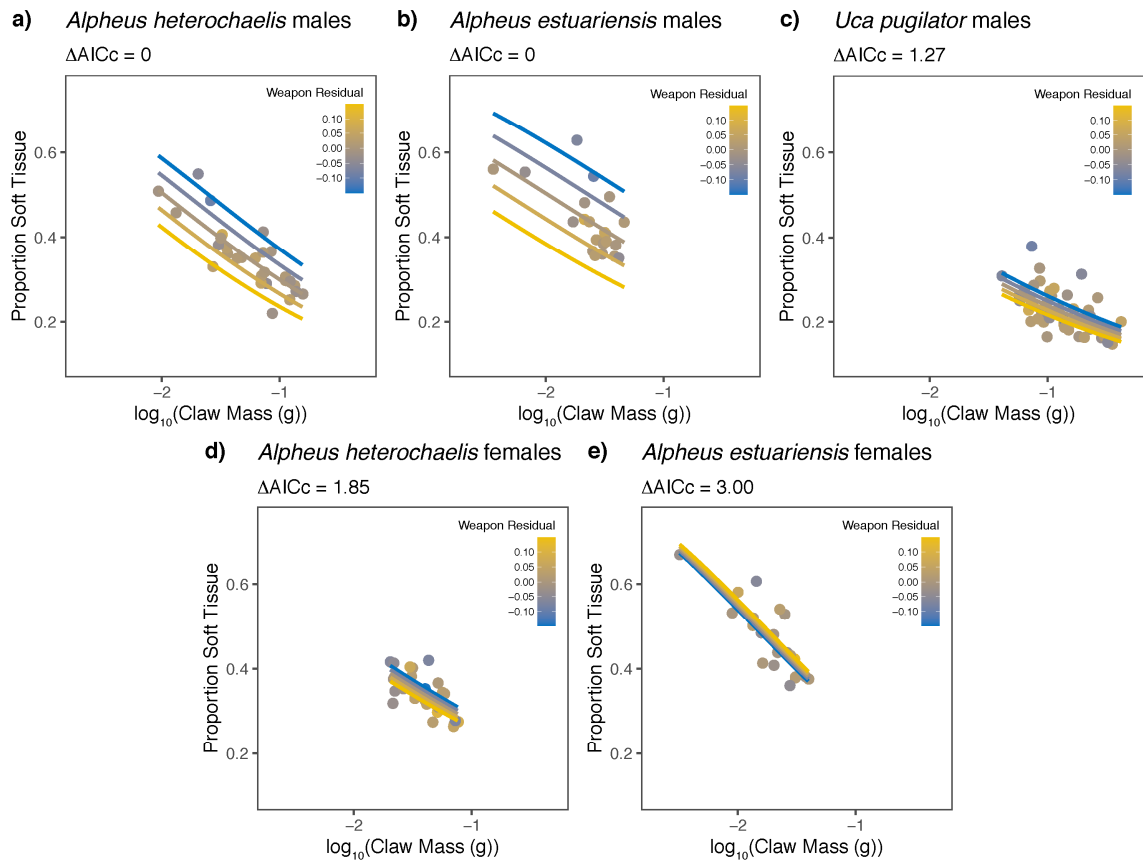


Figure 19: Larger claws had proportionally less soft tissue. In all groups except *Alpheus estuariensis* females, high-residual exaggerated claws (yellow) had proportionally less soft tissue than unexaggerated claws (blue). $\Delta AICc$ is the difference between the full model and the best-fitting model.

4.4 Discussion

In all three species and for both sexes, larger weapons comprised proportionally less soft tissue than smaller weapons (Fig. 18). The difference in proportional soft tissue composition was substantial: the largest individuals invested up to 62% less soft tissue compared to the smallest individuals in *Uca pugilator* males, 58% less in *Alpheus heterochaelis* females, 45% in *A. heterochaelis* males, 33% less in *Alpheus estuariensis*

females, and 38% less in *A. estuariensis* males (Fig. 18). Furthermore, after controlling for claw size, more exaggerated weapons comprised proportionally less soft tissue (except for *Alpheus estuariensis* females) (Fig. 18). In snapping shrimp, weapon exaggeration can deceive rivals in contests (Hughes, 2000), and in fiddler crabs, exaggeration can increase force production (Lailvaux et al., 2009). Therefore cost-minimization could provide an energetically frugal mechanism to gain a behavioral advantage in intrasexual contests. My findings support the cost-minimization hypothesis and extend its logic to weapon exaggeration: reductions in metabolically active tissues facilitate positive allometry and exaggeration of sexually selected weapons.

One might anticipate that reducing investment in muscles would only work if muscle force is not important. However, cost-minimization is widespread despite variation in behavioral contexts and musculoskeletal mechanisms. Behaviorally, giraffe weevils use elongated rostra primarily to assess rivals in mutual assessment (Painting & Holwell, 2014), snapping shrimp use snapping claws primarily as armament to impose costs in cumulative assessment (Dinh et al., 2020), and fiddler crabs use claws both to assess rivals and to impose costs (McCullough et al., 2016; Pratt et al., 2003).

Mechanistically, these species use muscles differently. Giraffe weevils use raking motions to dislodge rivals, and muscle force, which scales with muscular cross-sectional area, might be less important than the length of the rostral lever (Painting & Holwell, 2014). Snapping shrimp likely use a combination of elastic recoil and latches to power

their ultrafast strikes (Kaji et al., 2018; Patek & Longo, 2018) They have a large “loading” muscle which, like mantis shrimp that also use latch-mediated spring actuation (Blanco & Patek, 2014), must produce substantial force (Ritzmann, 1973; Ritzmann, 1974). Fiddler crab weapons also require high-force muscles, but muscle contractions must be prolonged rather than intermittent, enduring through long pinching bouts (McLain et al., 2019; Pratt et al., 2003). Despite variation in musculoskeletal mechanisms and behavioral contexts, cost-minimization is widespread. As more data come to light, meta-analyses comparing the tissue-specific allometric slopes could reveal interesting interactions with fitness costs, whereby muscle reduction is strongest in passively held weapons and weakest in high-force weapons.

Conversely, for some weapons, investing more in metabolically inexpensive hard structures could be beneficial if it improves structural integrity and resistance to injury. Injury during contests is common. For example, crustaceans often suffer punctures in their enlarged claws. In the fiddler crab (*Uca burgersi*), up to 25% of males have punctured enlarged claws (Jones, 1980), and in river shrimp (*Cryphiops caementarius*), up to 50% of males have punctured enlarged claws (Rojas et al., 2012). Resistance to puncture depends on investment in the exoskeleton’s growth and structure (Woodman et al., 2021), so differential tissue allocation from cost-minimization might impact structural integrity. Future work should therefore integrate biomechanical and energetic

approaches to reveal strategies that minimize fitness costs while improving structural integrity.

Existing evidence supporting cost-minimization comes primarily from the muscle-filled weapons of arthropods (Somjee et al., 2021). However, cost-minimization could also apply to vertebrates. Many vertebrates bear sexually selected traits that are not muscle-filled and comprise metabolically inactive tissues. Cervid antlers, for example, are energetically expensive to grow but comprise mostly dead tissue once fully grown (Landete-Castillejos et al., 2019; Somjee, 2021). Nonetheless, these traits still require metabolically active tissues, such as specialized vertebrae and muscles, to support them (Vander Linden & Dumont, 2019). Allometric comparisons between relatively inexpensive sexually selected traits and their metabolically active supporting structures could elucidate how taxonomically widespread cost-minimization is. Indeed, across organs, vertebrates show positive allometry in metabolically inexpensive tissues like skeleton (Prange et al., 1979) and negative allometry in metabolically active tissues like brains (Martin, 1981). It is reasonable, then, to predict a similar trend within sexually selected traits.

Furthermore, cost-minimization likely applies to non-sexually selected structures as well. For example, walking legs, mandibles, and raptorial appendages comprise exoskeleton and soft tissue. If energetic maintenance costs are high and energy is limited, then these structures could be under similar cost-minimizing pressures.

Interestingly, in my study, *A. heterochaelis* female weapons scaled with negative allometry (Fig. 17d). This is likely because female snapping shrimp reduce relative claw sizes during the breeding season as they invest more in egg production and brood care (e.g. *Alpheus angulosus*, (Heuring & Hughes, 2019)). In my dataset, I found ovigerous *Alpheus heterochaelis* females, but I did not find ovigerous *A. estuariensis* females, which could explain why *A. heterochaelis* female weapons scaled with negative allometry but *A. estuariensis* female weapons did not. Nonetheless, the trends found in *A. heterochaelis* females matched my predictions: exoskeleton scaled more positively allometrically than soft tissue, soft-tissue proportions decreased with weapon size, and more exaggerated weapons comprised proportionally more exoskeleton.

Although I did not measure resting metabolic rate per se, resting metabolic rate is correlated to muscle mass in arthropods, especially those with muscle-filled weapons (O'Brien et al., 2019). For example, across several species of insects, particularly those with high weapon muscle mass, individuals with greater muscle mass have higher resting metabolic rates (O'Brien et al., 2019). Similar trends are seen in crustaceans: in another species of fiddler crab (*Uca vomeris*), regenerated claws contain less muscle than non-regenerated claws, and individuals bearing regenerated claws consume 43% less oxygen than individuals with non-regenerated claws (Bywater et al., 2014, 2015). It is reasonable to assume, then, that the substantial variation in metabolically active tissue proportions reported here impose corresponding differences in resting metabolic rate.

Interestingly, negative allometry in metabolic rate even occurs within tissue types, and future work could examine how within sexually selected traits, tissue-specific energetics scale with size.

My findings demonstrate that positive allometry and exaggeration of sexually selected traits are facilitated by reduced investment in metabolically expensive tissues as size increases. Reduced investment in muscles is surprisingly salient even in species where muscles play a major role in competitive interactions. These results, therefore, suggest that cost-minimization could be a behaviorally and taxonomically widespread strategy to grow large and exaggerated sexually selected structures.

5. Conclusions

In this dissertation, I outlined a landscape of tradeoffs and benefits that underlie predictable variation in weapon size across sex, season, and body size. These findings provide elusive evidence for the handicap principle and the cost-minimization hypothesis (Grafen, 1990a, 1990b; Johnstone, 1997; Nur & Hasson, 1984; Penn & Számadó, 2020; Somjee, 2021; Zahavi, 1975, 1977). They also extend these hypotheses in novel directions to explain sex differences, seasonal variation, and exaggeration in weaponry. The findings are a launchpad for future research that links trait expression with fitness costs and benefits in natural field settings. The integration of behavioral experiments, functional studies, and field observations provide a rigorous framework that can be used for future research.

In Chapter 2, I discovered that big-clawed snapping shrimp (*Alpheus heterochaelis*) use weapons as cost-imposing armament. I also determined that contestants in this species benefit from large weapons through increased offensive capacity. That suggests that large weaponry in this species facilitates cumulative assessment through scaling of opponent-imposed costs. This framework of integrating biomechanics and behavioral ecology provides a pathway to identify precise mechanisms of contest assessment and animal behavior. More broadly, quantifying contest-relevant RHP correlates like offensive capacity and endurance could advance the game theory of contests. For example, the experimental predictions used to determine

contest assessment strategies derive from assumptions that offensive capacity, endurance, and defensive capacity scale linearly with RHP (Arnott & Elwood, 2009; Palaoro & Briffa, 2017; Payne, 1998). By contrast, I found that offensive capacity scales supralinearly. This is likely common across species because weapons often scale with positive allometry (Emlen, 2008; Kodric-Brown et al., 2006; O'Brien et al., 2019; Somjee, 2021). Nonlinear scaling trends in contest-relevant metrics could alter, nullify, or even upend the empirical predictions derived from theory (Palaoro & Briffa, 2017). Therefore, quantifying these metrics and parameterizing theoretical models with them could yield more sound and precise predictions to be used by experimentalists.

In Chapter 3, I found support for the handicap principle and extended it to explain sex and seasonal differences in weapon investment. I found that males and females from three snapping shrimp species (*Alpheus heterochaelis*, *Alpheus angulosus*, and *Alpheus estuariensis*) exhibit resource allocation tradeoffs between weapons and abdomens. For male *A. heterochaelis*, the group for which I had the greatest sample size and statistical power, the smallest individuals showed the steepest tradeoff. Furthermore, I discovered that weapons are particularly burdensome for females and particularly beneficial for males. Female *A. heterochaelis* exhibited tradeoffs between weapon size and egg production, whereas males benefited from large weaponry through increased pairing success. These sex-specific, reproduction-related tradeoffs and benefits can explain why males have larger proportional weapon sizes than females and

why that sex difference amplifies during the breeding season. This provides elusive evidence and breathes new life into the handicap hypothesis, a canonical theory in evolutionary biology (Johnstone, 1997; Penn & Számadó, 2020; Searcy & Nowicki, 2005; Zahavi, 1975, 1977). Future research into other species with sexually dimorphic sexual traits could reveal how generalizable the findings are across the animal kingdom.

Finally, in Chapter 4, I found support for a recent hypothesis called the cost-minimization hypothesis. This hypothesis proposes that an animal species can achieve positive allometry of costly traits by suppressing energetic maintenance costs (Somjee, 2021; Somjee et al., 2021). I found support for this in two species of snapping shrimp and a species of fiddler crabs: As weapon size increased, the proportion of the weapon made of energetically inexpensive exoskeleton increased, and the proportion made of energetically expensive soft tissue decreased. Furthermore, I extended this hypothesis to explain weapon exaggeration, defined as how much larger a weapon is than predictions made by scaling relationships. As residuals from the weapon scaling relationship increased, the proportion of the weapon made of energetically inexpensive exoskeleton increased, and the proportion made of energetically expensive soft tissue decreased. Currently, support for the cost-minimization hypothesis comes entirely from arthropods (Somjee et al., 2021; Somjee, Woods, et al., 2018). It would be interesting to test these ideas with vertebrates. For example, future work could test the hypothesis in cervids by quantifying the scaling of the energetically inert antlers versus the energetically

expensive muscles used to support those antlers (Landete-Castillejos et al., 2019; Somjee, 2021). Furthermore, snapping shrimp weapon expression is plastic: Individuals can alter investment into weaponry each month during molts (Cooney et al., 2017; Pereira et al., 2014; Read & Govind, 1991, 1997). This could allow for future experimental manipulations within an individual to test how changes to nutrients, competition, and environmental conditions can impact trait expression and cost suppression.

The gold standard of support for the handicap principle is to link trait expression to fitness implications (Kotiaho, 2001; Kotiaho et al., 1998; Møller & de Lope, 1994; Mappes et al., 1996). The benefits we identified in securing and maintaining mates are reasonable proxies for fitness benefits, and the tradeoffs in egg production are reasonable proxies of fitness costs. However, because snapping shrimp have massive population sizes, are cryptic, and molt each month, it's difficult to quantify fitness in the field. Furthermore, snapping shrimp regenerate their weapons (Govind et al., 1986; Pereira et al., 2014). This makes experimental manipulations of weapon expression challenging.

Future research into the costs and benefits of weaponry should target systems where lifetime fitness is measurable and costly traits are manipulable. For example, previous work on barn swallow tail feather ornaments has tied trait expression to survival in the field and identified mechanisms of fitness costs by experimentally lengthening or shortening those feathers (Møller & de Lope, 1994). Meanwhile,

permanent manipulation of weaponry in terminally molting insects has revealed tradeoffs related to reproductive success (Miller et al., 2019; Somjee, Miller, et al., 2018). Long-term observational studies paired with controlled experiments in tractable, manipulable taxa would establish with certainty that costs and benefits underlie variation in weapon investment.

Taken together, these studies resolve a series of paradoxes regarding animal weaponry. First, I showed that animal weapons scale honestly because they are costly. The interaction between costs and benefits of weaponry explain size variation across body sizes, sexes, and breeding seasons. Then, I showed that individuals can suppress some of these costs to achieve positive allometry and weapon exaggeration. These findings support the now-classic handicap principle and the more recent cost-minimization hypothesis. Furthermore, I co-opted the logic of these existing theories to explain seasonal differences and exaggeration in weaponry. At present, the novel extensions that I propose exist only as verbal models. Still, they are logical and compelling given the empirical evidence provided in this dissertation. The most vital avenue of future research is to collaborate with theorists to formalize these ideas and to establish experimental guidelines for testing them.

Appendix A — Supplemental Materials for Chapter 2

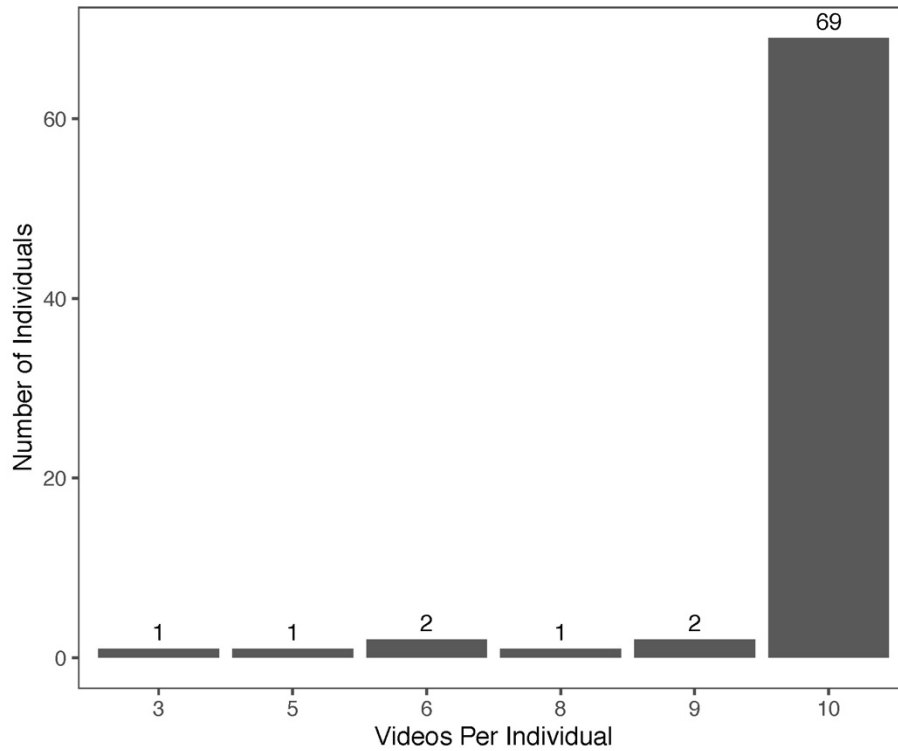


Figure 20: Most individuals were recorded for a full complement of 10 videos. Very few were recorded for 3 – 9 videos before individuals ceased to snap.

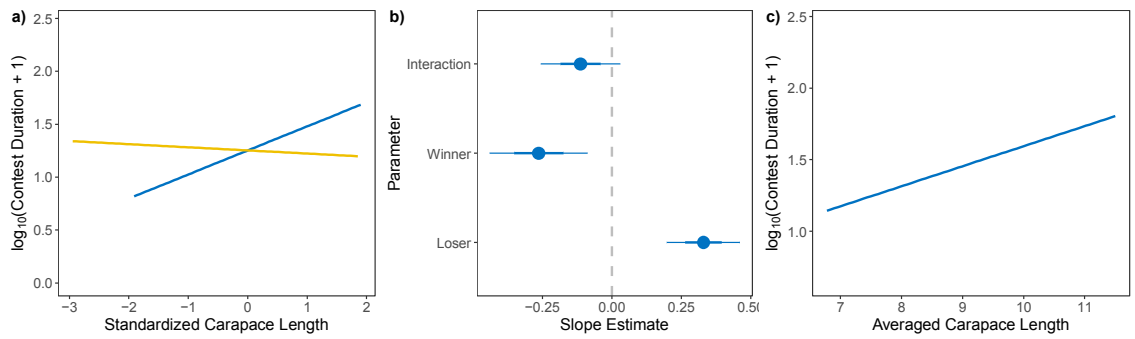


Figure 21: a, b) Total contest duration was negatively correlated with winner carapace length and negatively correlated with loser carapace length. In size-matched contests, the averaged carapace length was positively correlated with contest duration. This suggests cumulative assessment or a switching assessment strategy.

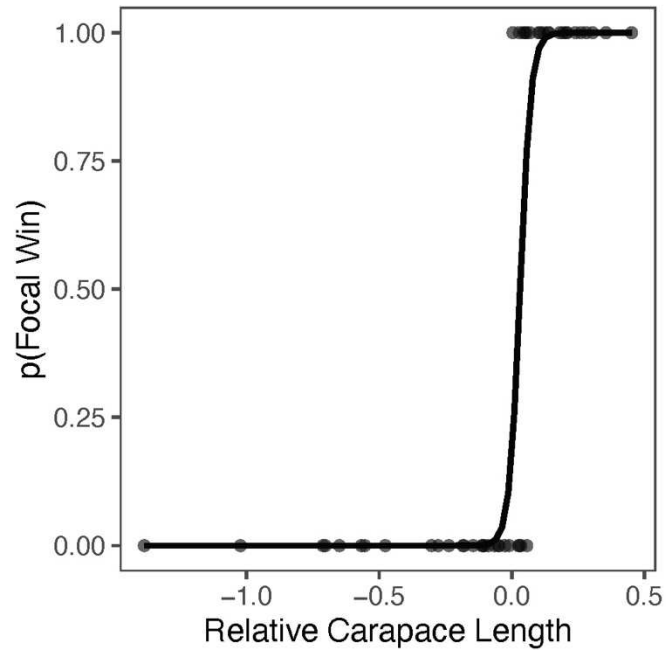


Figure 22: Binomial generalized linear regression demonstrating that carapace length is a good proxy for RHP. One individual was randomly chosen to be the focal individual and the other was designated the opponent. Focal win is 1 if that individual won or 0 if that individual lost. Relative carapace length was calculated as $1 - \text{opponent carapace length} / \text{focal carapace length}$, where 0 indicates identically sized focal individuals and opponents, more negative numbers indicate that the focal individual is smaller than the opponent, and more positive numbers indicate that the focal individual is larger than the opponent. Each point represents one contest.

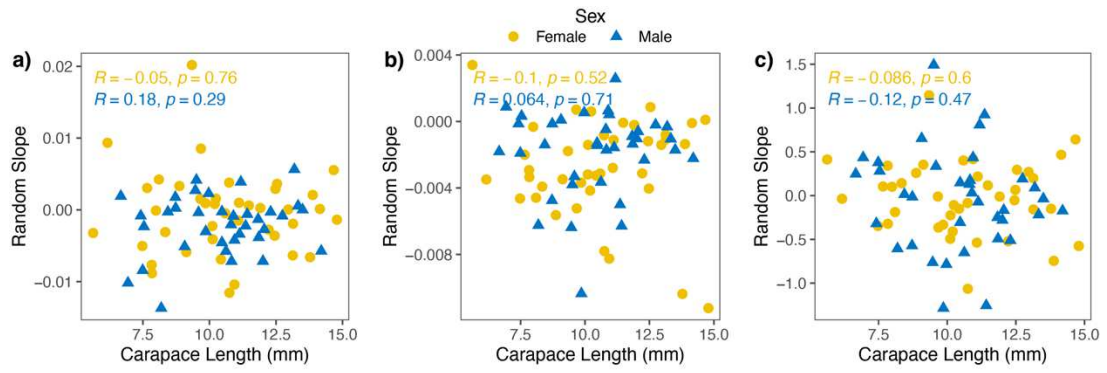


Figure 23: Random slopes of performance ~ snap number were uncorrelated with carapace length.

Table 4: Ethogram of snapping shrimp (*Alpheus heterochaelis*) contest behaviors.

Behavior	Description
Approach	Initial movement of shrimp towards each other
Fanning	Beating of pleopods towards posterior
Antennulation	Touch opponent's antennae
Chelae Overlap	Both chelae touch opponent's chelae
Open Chela Display	Fully opens major chelae but does not strike afterwards
Lunge	Brief, rapid advance towards opponent
Probing	Shrimp advances and makes brief contact with the opponent's chelae
Pinch	Close minor chelae on opponent's appendage
Cocked Claw	Fully open major chelae
Snap	Rapid closure of major chela associated with cavitation sound
Tailflip	Rapid backward movement associated with flick of tail
Pincer Snap	Rapid closure of minor chela
Click	Rapid closure of major chela but with reduced sound, often performed in quick succession
Retreat	Directed movement away from opponent
Chase	Pursuit of retreating opponent
End	End of contest bout

Table 5: Model summary for initiation phase duration. $R^2 = 0.1531$, $F = 2.351$, $df = 3$ and 44 , $p = 0.06$.

Coefficient	Estimate	Std. Error	t-value	p-value	AIC Importance
Intercept	0.60490	0.04805	12.589	3.5e-16	N/A
Loser Carapace Length	0.12322	0.04916	2.507	0.0160	0.75
Winner Carapace Length	-0.15440	0.06612	-2.335	0.0242	0.69
Winner Carapace Length:Loser Carapace Length	-0.06738	0.05362	-1.257	0.2156	0.24

Table 6: Model summary for presnapping phase duration. R2 = 0.05488, F = 0.8516, df = 3 and 44, p = 0.4733.

Coefficient	Estimate	Std. Error	t-value	p-value	AIC Importance
Intercept	0.500447	0.084655	5.912	4.55e-07	N/A
Loser Carapace Length	0.062011	0.086604	0.716	0.478	0.34
Winner Carapace Length	-0.001596	0.116483	-0.014	0.989	0.34
Winner Carapace Length:Loser Carapace Length	0.098254	0.094470	1.040	0.304	0.05

Table 7: Model summary for snapping phase duration. $R^2 = 0.2517$, $F = 4.709$, $df = 3$ and 42 , $p = 0.00637$.

Coefficient	Estimate	Std. Error	t-value	p-value	AIC Importance
Intercept	0.94808	0.09254	10.245	3.15e-13	N/A
Loser Carapace Length	0.40178	0.09467	4.244	0.000112	1.0
Winner Carapace Length	-0.30484	0.12734	-2.394	0.020998	0.74
Winner Carapace Length:Loser Carapace Length	-0.17288	0.10327	-1.674	0.101226	0.41

Table 8: Model summary for entire contest duration. R2 = 0.3332, F = 7.328, df = 3 and 44, p = 0.0004351.

Coefficient	Estimate	Std. Error	t-value	p-value	AIC Importance
Intercept	1.31487	0.06946	18.929	< 2e-16	N/A
Loser Carapace Length	0.33190	0.07106	4.670	2.84e-05	1
Winner Carapace Length	-0.25570	0.09558	-2.675	0.0104	0.89
Winner Carapace Length:Loser Carapace Length	-0.11088	0.07752	-1.430	0.1597	0.41

Table 9: Model summary for scaling relationship of maximum sound pressure level as function of \log_{10} (claw mass). Claw mass was measured in grams and sound pressure level as dB re 1 μ Pa.

Predictor	Coefficient Estimate	Standard Error	t-value	p-value
Intercept	214.056	3.108	68.868	$<2*10^{-16}$
\log_{10} (claw mass)	25.022	3.149	7.946	$-1.94*10^{-11}$
male	1.484	3.714	0.400	0.691
\log_{10} (claw mass)*male	3.214	4.045	0.795	0.429
Model Statistics: r-squared = 0.7380, r = 0.8590, $F_{3, 72} = 67.61$, $p < 2*10^{-16}$				

Table 10: Model summary for scaling relationship of \log_{10} (max bubble duration) maximum sound pressure level as function of \log_{10} (claw mass). Claw mass was measured in grams and bubble duration was measured in seconds.

Predictor	Coefficient Estimate	Standard Error	t-value	p-value
Intercept	8.176×10^{-4}	3.090×10^{-5}	26.458	$< 2 \times 10^{-16}$
\log_{10} (claw mass)	3.608×10^{-4}	3.131×10^{-5}	11.524	$< 2 \times 10^{-16}$
male	1.692×10^{-4}	3.693×10^{-5}	4.583	1.88×10^{-5}
\log_{10} (claw mass)*male	1.509×10^{-4}	4.021×10^{-5}	3.753	0.000351
Model Statistics: r-squared = 0.9043, r = 0.9509, $F_{3, 72} = 226.8$, $p < 2 \times 10^{-16}$				

Table 11: Model summary for scaling relationship of \log_{10} (max average angular velocity) maximum sound pressure level as function of \log_{10} (claw mass). Claw mass was measured in grams and average angular velocity as rad/sec.

Predictor	Coefficient Estimate	Standard Error	t-value	p-value
Intercept	-41.43	201.65	-0.205	0.838
\log_{10} (claw mass)	-2452.12	204.31	-12.002	$<2*10^{-16}$
male	1033.60	240.95	4.290	$5.48*10^{-5}$
\log_{10} (claw mass)*male	1197.59	262.39	4.564	$2.02*10^{-5}$
Model Statistics: r-squared = 0.7583, r = -0.8708, $F_{3, 72} = 75.28$, $p < 2*10^{-16}$				

Table 12: Model summary for average angular velocity endurance model.

Random Effects			
	Variance	Standard Deviation	
Intercept	1.801e-2	0.13421	
Snap Number	3.907e-5	0.00625	
Fixed Effects			
	Estimate	Standard Error	t
Intercept	3.2591798	0.0156795	207.863
Snap Number	-0.0012446	0.008781	-1.417
sample size: 603 snaps, 76 individuals			

Table 13: Model summary for bubble duration endurance model.

Random Effects			
	Variance	Standard Deviation	
Intercept	2.065e-2	1.43694	
Snap Number	1.188e-5	0.003447	
Fixed Effects			
	Estimate	Standard Error	t
Intercept	-3.300975	0.016567	-199.246
Snap Number	-0.002344	0.000486	-4.824
sample size: 735 snaps, 76 individuals			

Table 14: Model summary for sound pressure level endurance model.

Random Effects			
	Variance	Standard Deviation	
Intercept	138.997	11.7897	
Snap Number	0.363	0.6025	
Fixed Effects			
	Estimate	Standard Error	t
Intercept	188.07531	1.38303	135.987
Snap Number	-0.03856	0.08469	-0.455
sample size: 735 snaps, 76 individuals			

Table 15: Likelihood ratio tests testing the effect of snap number on average angular velocity as a function of \log_{10} (claw mass). Claw mass was measured in grams, and average angular velocity as rad/sec. Δ AIC is the change in AIC after removing snap number from the model.

Model	AIC	BIC	logLik	deviance	χ^2	f	p-value
reduced	-1968.6	-1955.4	987.31	-1974.6	N/A	-	N/A
full	-2007.3	-1980.8	1009.63	-2019.3	44.643	3	$1.102 \cdot 10^{-09}$
Δ AIC = 38.7							

Table 16: Likelihood ratio tests testing the effect of snap number on bubble duration as a function of $\log_{10}(\text{claw mass})$. Claw mass was measured in grams, and bubble duration in seconds. ΔAIC is the change in AIC after removing snap number from the model.

Model	AIC	BIC	logLik	deviance	X²	f	p-value
reduced	-2935.5	-2921.7	1470.7	-2941.5	N/A	-	N/A
full	-3031.8	-3004.2	1521.9	-3043.8	102.28	3	$<2.2 \cdot 10^{-16}$
$\Delta\text{AIC} = 96.3$							

Table 17: Likelihood ratio tests testing the effect of snap number on sound pressure level as a function of \log_{10} (claw mass). Claw mass was measured in grams, and sound pressure level in dB re 1 μ Pa. Δ AIC is the change in AIC after removing snap number from the model.

Model	AIC	BIC	logLik	deviance	X²	f	p-value
reduced	4478.9	4492.7	-2236.5	4472.9	N/A	-	N/A
full	4434.2	4461.8	-2211.1	4422.2	50.696	3	3.452*10 ⁻⁹
Δ AIC = 44.7							

Table 18: AIC comparison of beta regression models in *Uca pugilator* males. Outputs were created using the dredge() function in the R package MuMIn. Each possible model is shown in a separate row, and log-likelihoods, AICc, Δ AICc, and AICc weight are also shown for each model.

Intercept	$\log_{10}(\text{claw mass})$	Snapping claw residual	df	logLik	AICc	Δ AICc	weight
-1.863	-0.7022	N/A	3	95.369	-184.2	0.00	0.654
-1.844	-0.6806	-0.8188	4	95.913	-183.0	1.27	0.346

Appendix B — Supplementary Materials for Chapter 3

Table 19: Scaling slopes for $\log_{10}(\text{snapping claw length})$ and $\log_{10}(\text{abdomen length})$ as a function of $\log_{10}(\text{rostrum-to-telson length})$. All measurements were taken in millimeters. 95% confidence intervals for slopes are shown in brackets after the slope estimate.

	<i>A. heterochaelis</i> males	<i>A. heterochaelis</i> females	<i>A. angulosus</i> males	<i>A. angulosus</i> females	<i>A. estuariensis</i> males	<i>A. estuariensis</i> females
Snapping claw scaling slope	1.193 [1.149] 1.238]	1.000 [0.967 1.033]	1.489 [0.934 2.044]	1.013 [0.709 1.308]	1.207 [1.096 1.318]	1.173 [1.029 1.316]
Abdomen scaling slope	1.027 [1.013 1.042]	1.015 [1.004 1.026]	0.934 [0.837 1.031]	1.064 [0.978 1.149]	0.934 [0.876 0.992]	1.064 [1.007 1.121]

Table 20: Model summary for abdomen-snapping claw tradeoffs in *Alpheus angulosus*. * p<0.05; ** p<0.01; * p<0.005**

<i>Dependent variable:</i>	
Abdomen Residual	
Snapping Claw Residual	-0.113*** (0.026)
Constant	-0.000 (0.002)
Observations	53
R ²	0.273
Adjusted R ²	0.259
Residual Std. Error	0.012 (df = 51)
F Statistic	19.142*** (df = 1; 51)

Table 21: Model summary for abdomen-snapping claw tradeoffs in *Alpheus estuariensis*. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Abdomen Residual	
Snapping Claw Residual	-0.142* (0.064)
Constant	0.000 (0.001)
Observations	45
R ²	0.103
Adjusted R ²	0.082
Residual Std. Error	0.007 (df = 43)
F Statistic	4.924* (df = 1; 43)

Table 22: Model summary for abdomen-snapping claw tradeoffs in *Alpheus heterochaelis*. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Abdomen Residual	
Snapping Claw Residual	-0.123*** (0.012)
Constant	-0.000 (0.0004)
Observations	677
R ²	0.139
Adjusted R ²	0.138
Residual Std. Error	0.010 (df = 675)
F Statistic	109.257*** (df = 1; 675)

Table 23: Model summary for size-dependent tradeoff between abdomen residuals and snapping claw residuals for *Alpheus heterochaelis* males. Positive interaction term indicates that as carapace length increases, the tradeoff between snapping claw residuals and abdomen residuals decreases. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Abdomen Residual	
Snapping Claw Residual	-0.387*** (0.085)
Carapace Length	-0.001*** (0.0003)
Interaction	0.025*** (0.008)
Constant	0.011*** (0.003)
Observations	329
R ²	0.234
Adjusted R ²	0.227
Residual Std. Error	0.009 (df = 325)
F Statistic	33.166*** (df = 3; 325)

Table 24: Model summary showing no size-dependent tradeoff between abdomen residuals and snapping claw residuals for *Alpheus heterochaelis* females.

*p<0.05; **p<0.01; ***p<0.005

<i>Dependent variable:</i>	
Abdomen Residual	
Snapping Claw Residual	-0.119* (0.060)
Carapace Length	-0.001*** (0.0003)
Interaction	0.001 (0.006)
Constant	0.009*** (0.003)
Observations	348
R ²	0.154
Adjusted R ²	0.147
Residual Std. Error	0.010 (df = 344)
F Statistic	20.920*** (df = 3; 344)

Table 25: Model summary showing that snapping claw residuals did not predict female maximal sound pressure level. *p<0.05; **p<0.01; *p<0.005**

Dependent variable:

	Max Sound Pressure Level (dB re 1 uPa)
log ₁₀ (Claw Mass)	24.495*** (3.717)
Snapping Claw Residual	52.646 (134.394)
Interaction	79.314 (132.893)
Constant	213.726*** (3.647)
Observations	40
R ²	0.572
Adjusted R ²	0.537
Residual Std. Error	6.239 (df = 36)
F Statistic	16.049*** (df = 3; 36)

Table 26: Model summary showing that snapping claw residuals did not predict female maximal bubble duration. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Max Bubble Duration (sec)	
log ₁₀ (Claw Mass)	0.0004*** (0.00003)
Snapping Claw Residual	0.0004 (0.001)
Interaction	0.0004 (0.001)
Constant	0.001*** (0.00003)
Observations	40
R ²	0.850
Adjusted R ²	0.837
Residual Std. Error	0.00004 (df = 36)
F Statistic	67.783*** (df = 3; 36)

Table 27: Model summary showing that snapping claw residuals did not predict female maximal average angular velocity. * p<0.05; ** p<0.01; * p<0.005**

<i>Dependent variable:</i>	
Max Average Angular Velocity (rad/sec)	
log ₁₀ (Claw Mass)	-2,486.871*** (181.963)
Snapping Claw Residual	3,478.511 (6,579.674)
Interaction	5,234.176 (6,506.190)
Constant	-63.338 (178.534)
Observations	40
R ²	0.842
Adjusted R ²	0.828
Residual Std. Error	305.445 (df = 36)
F Statistic	63.757*** (df = 3; 36)

Table 28: Model summary showing that snapping claw residuals did not predict male maximal sound pressure level. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Max Sound Pressure Level (dB re 1 uPa)	
log ₁₀ (Claw Mass)	26.502*** (2.177)
Snapping Claw Residual	56.663 (85.788)
Interaction	-25.760 (84.560)
Constant	213.511*** (1.977)
Observations	36
R ²	0.863
Adjusted R ²	0.851
Residual Std. Error	4.280 (df = 32)
F Statistic	67.432*** (df = 3; 32)

Table 29: Model summary showing that snapping claw residuals did not predict male maximal bubble duration. *p<0.05; **p<0.01; *p<0.005**

Dependent variable:

	Max Bubble Duration (sec)
log ₁₀ (Claw Mass)	0.001*** (0.00003)
Snapping Claw Residual	0.001 (0.001)
Interaction	0.002 (0.001)
Constant	0.001*** (0.00003)
Observations	
	36
R ²	0.909
Adjusted R ²	0.901
Residual Std. Error	0.0001 (df = 32)
F Statistic	107.068*** (df = 3; 32)

Table 30: Model summary showing that snapping claw residuals did not predict male maximal average angular velocity. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
	Max Average Angular Velocity (rad/sec)
log ₁₀ (Claw Mass)	-1,370.772*** (200.123)
Snapping Claw Residual	3,025.541 (7,887.771)
Interaction	-2,657.354 (7,774.900)
Constant	859.746*** (181.787)
Observations	36
R ²	0.604
Adjusted R ²	0.567
Residual Std. Error	393.525 (df = 32)
F Statistic	16.269*** (df = 3; 32)

Table 31: Summary tables for models showing tradeoffs between snapping claw residuals and egg mass volume residuals. * p<0.05; ** p<0.01; * p<0.005**

<i>Dependent variable:</i>	
	Egg Mass Volume Residual
Snapping Claw Residual	-630.261* (250.982)
Constant	2.238 (4.247)
Observations	37
R ²	0.153
Adjusted R ²	0.128
Residual Std. Error	25.258 (df = 35)
F Statistic	6.306* (df = 1; 35)

Table 32: Summary tables for models showing tradeoffs between snapping claw residuals and egg count residuals. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Egg Count Residual	
Snapping Claw Residual	-1,120.278* (546.016)
Constant	3.979 (9.239)
Observations	37
R ²	0.107
Adjusted R ²	0.082
Residual Std. Error	54.949 (df = 35)
F Statistic	4.210* (df = 1; 35)

Table 33: Summary tables for models showing tradeoffs between snapping claw residuals and average egg volume. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Average Egg Volume (mm ³)	

Snapping Claw Residual	-1.368*
	(0.630)
Constant	0.461***
	(0.011)
<hr/>	
Observations	37
R ²	0.119
Adjusted R ²	0.094
Residual Std. Error	0.063 (df = 35)
F Statistic	4.715* (df = 1; 35)
<hr/>	
<i>Note:</i>	*p<0.05; **p<0.01; ***p<0.005

Table 34: Interaction between carapace length and snapping claw residuals show that average egg volume/weapon tradeoffs are strongest for small individuals.

*p<0.05; **p<0.01; ***p<0.005

<i>Dependent variable:</i>	
Average Egg Volume (mm ³)	
Snapping Claw Residual	-15.852* (6.306)
Carapace Length (mm)	-0.0003 (0.010)
Interaction	1.241* (0.538)
Constant	0.456*** (0.116)
Observations	37
R ²	0.241
Adjusted R ²	0.172
Residual Std. Error	0.061 (df = 33)
F Statistic	3.496* (df = 3; 33)

Table 35: ANOVA table testing if snapping claw residuals are predicted by sex, paired status, and their interaction. Both paired status and its interaction with sex were significant predictors. *p<0.05; **p<0.01; *p<0.005**

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
male	1	0.00111	0.0011111	1.460	0.227209
paired	1	0.00615	0.0061506	8.0926	0.004634**
male:paired	1	0.00336	0.003366	4.4155	0.036132*
Residuals	486	0.3711264	0.0007636	NA	NA

Table 36: Model summary showing that male pairing success is a function of snapping claw residual but not carapace length. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
	Paired
Snapping Claw Residual	16.876*** (5.770)
Carapace Length (mm)	0.137 (0.084)
Constant	-1.459 (0.859)
Observations	233
Log Likelihood	-153.156
Akaike Inf. Crit.	312.311

Table 37: Model summary showing that female pairing success is a function of carapace length but not snapping claw residual. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
	Paired
Snapping Claw Residual	3.384 (4.872)
Carapace Length (mm)	0.284*** (0.069)
Constant	-3.188*** (0.732)
Observations	253
Log Likelihood	-163.753
Akaike Inf. Crit.	333.505

Table 38: Snapping claw residuals did not predict the relative rostrum-to-telson length of their partner in females.*p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
Partner's Relative Rostrum-to-Telson Length	
Snapping Claw Residual	0.659 (0.353)
Constant	-0.057*** (0.008)
Observations	111
R ²	0.031
Adjusted R ²	0.022
Residual Std. Error	0.088 (df = 109)
F Statistic	3.477 (df = 1; 109)

Table 39: Snapping claw residuals predicted the relative rostrum-to-telson length of their partner in males. *p<0.05; **p<0.01; *p<0.005**

<i>Dependent variable:</i>	
	Partner's Relative Rostrum-to-Telson Length
Snapping Claw Residual	0.878*** (0.304)
Constant	0.039*** (0.008)
Observations	111
R ²	0.071
Adjusted R ²	0.063
Residual Std. Error	0.079 (df = 109)
F Statistic	8.344*** (df = 1; 109)

Table 40: Seasonal morphological shift t-tests. Each t-test represents a row in the table, and the response variable for that t-test is shown in the left-most column.

***p<0.05; **p<0.01; ***p<0.005**

	Diff. between groups	Non- breeding Snapping Claw Residuals	Breeding Snapping Claw Residuals	t	p-value	df
Female Snapping claw Residual	-0.0031416	-0.0026902	0.0004514	-0.6415478	0.5232794	69.4235
Male Snapping claw Residual	-0.0215942	-0.0183781	0.0032162	-5.520575	4e-07***	81.24774
Female Abdomen Residual	0.0026658	0.0022828	-0.000383	1.886613	0.0628752	79.24422

Male	0.0041563	0.0035373	-0.000619	2.832303	0.0059894	71.99196
Abdomen					**	
Residual						

Table 41: Model summary showing female seasonal shifts in allometry.

		<i>Dependent variable:</i>
		$\log_{10}(\text{Snapping Claw Length (mm)})$
$\log_{10}(\text{Rostrum-to-Telson Length (mm)})$		1.163***
		(0.051)
Breeding		0.262***
		(0.077)
Interaction		-0.183***
		(0.054)
Constant		-0.588***
		(0.072)
Observations		348
R ²		0.914
Adjusted R ²		0.913
Residual Std. Error		0.033 (df = 344)

Table 42: Model summary showing no male seasonal shifts in scaling slope.

<i>Dependent variable:</i>	
log ₁₀ (Snapping Claw Length (mm))	
log ₁₀ (Rostrum-to-Telson Length (mm))	1.234*** (0.056)
Breeding	0.126 (0.086)
Interaction	-0.073 (0.061)
Constant	-0.640*** (0.079)
Observations	329
R ²	0.905
Adjusted R ²	0.904
Residual Std. Error	0.031 (df = 325)
F Statistic	1,029.595*** (df = 3; 325)
<i>Note:</i>	*p<0.05; **p<0.01; ***p<0.005

Table 43: Model summary showing male seasonal upward shift snapping claw size.

<i>Dependent variable:</i>	
	$\log_{10}(\text{Snapping Claw Length (mm)})$
$\log_{10}(\text{Rostrum-to-Telson Length (mm)})$	1.172*** (0.022)
Breeding	0.023*** (0.005)
Constant	-0.553*** (0.031)
Observations	329
R ²	0.904
Adjusted R ²	0.904
Residual Std. Error	0.031 (df = 326)
F Statistic	1,541.657*** (df = 2; 326)
<i>Note:</i>	*p<0.05; **p<0.01; ***p<0.005

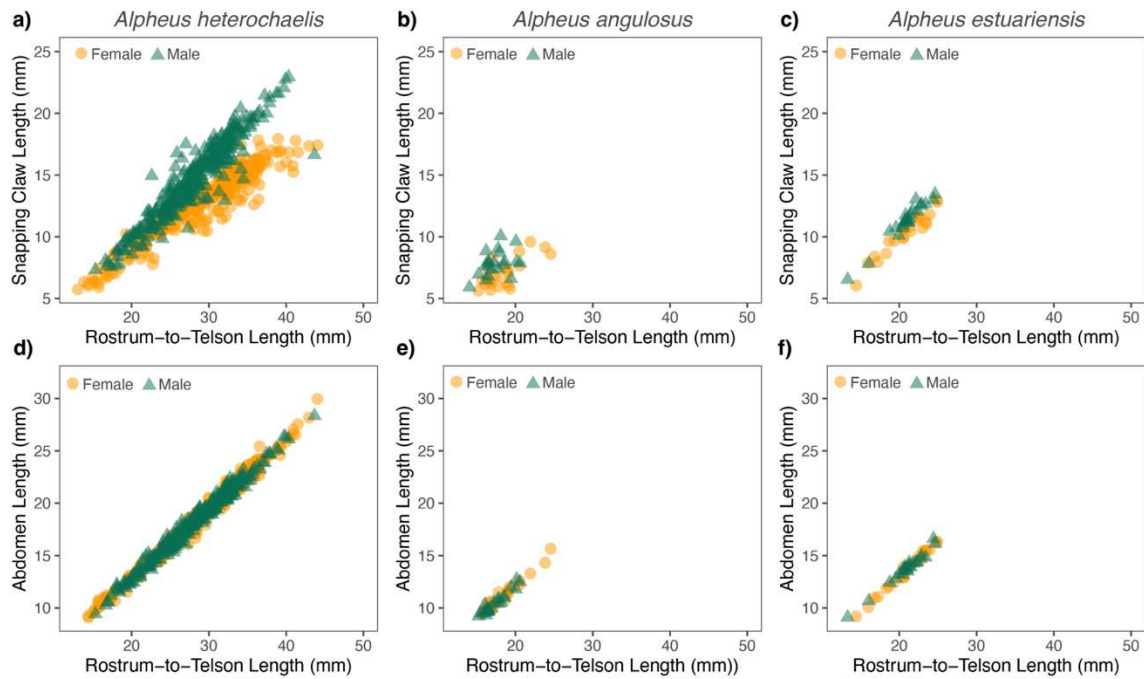


Figure 24: Scaling relationships for snapping claw length and abdomen length shown in linear scaling.

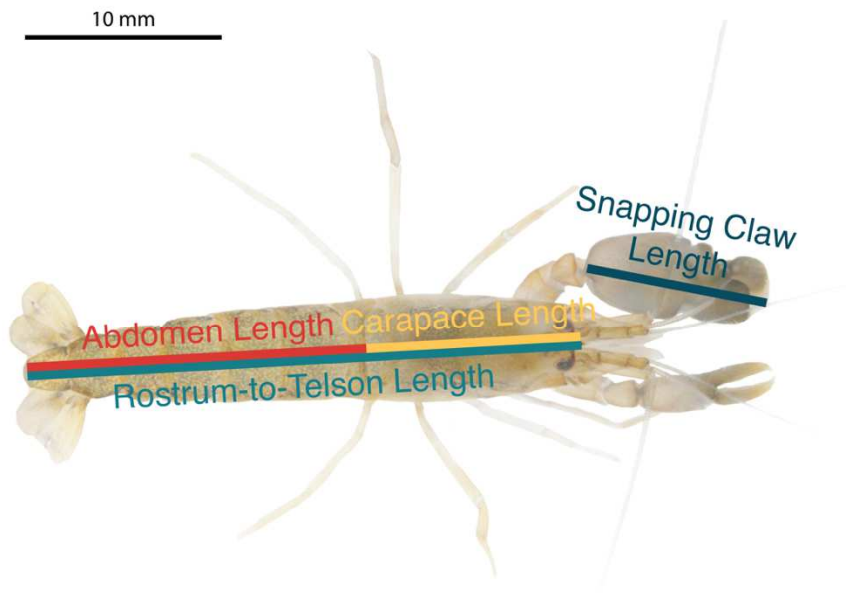


Figure 25: Morphological measurements used in this study. Example shown is an *Alpheus angulosus* female.

Appendix C — Supplemental Materials for Chapter 4

C.1 Mathematical Explanation for Interpreting Interaction Terms

Interaction terms test for differences in slopes between two groups. For this manuscript, I wanted to test if there were differences in scaling slopes of tissue mass depending on tissue type. The models used to test this are defined as follows:

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass}) + \beta_2 * \text{tissue type} + \beta_{int} * \log_{10}(\text{total mass}) * \text{tissue type}$$

where tissue type = 0 for exoskeleton and tissue type = 1 for soft tissue. For exoskeleton, (tissue type = 0), this model simplifies to

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass}) + \beta_2 * \text{tissue type} + \beta_{int} * \log_{10}(\text{total mass}) * \text{tissue type}$$

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass}) + \beta_2 * 0 + \beta_{int} * \log_{10}(\text{total mass}) * 0$$

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass})$$

where α is the intercept and β_1 is the slope. For soft tissue (tissue type = 1), the model simplifies to

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass}) + \beta_2 * \text{tissue type} + \beta_{int} * \log_{10}(\text{total mass}) * \text{tissue type}$$

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_1 * \log_{10}(\text{total mass}) + \beta_2 * 1 + \beta_{int} * \log_{10}(\text{total mass}) * 1$$

$$\log_{10}(\text{tissue mass}) = \alpha + \beta_2 + \beta_1 * \log_{10}(\text{total mass}) + \beta_{int} * \log_{10}(\text{total mass})$$

$$\log_{10}(\text{tissue mass}) = (\alpha + \beta_2) + (\beta_1 + \beta_{int}) * \log_{10}(\text{total mass})$$

where $(\alpha + \beta_2)$ is the intercept and $(\beta_1 + \beta_{int})$ is the slope. The coefficient for the interaction term (β_{int}) , then, represents for difference in slopes for soft tissue $(\beta_1 + \beta_{int})$ and exoskeleton (β_1) . Mathematically, it is the difference in slope between soft tissue and exoskeleton: $(\beta_1 + \beta_{int}) - (\beta_1) = \beta_{int}$.

The coefficients of the model, then, can be interpreted as follow:

α = the intercept when tissue type = 0 (i.e. for exoskeleton)

β_1 = the scaling slope of tissue mass when tissue type = 0 (i.e. for exoskeleton)

β_2 = the shift in intercept when tissue type = 1 (i.e. for muscle)

β_{int} = the shift in scaling slope when tissue type = 1 (i.e. for muscle). Importantly,

when this value is negative, that indicates a negative shift in slope (i.e. muscle has a shallower scaling relationship than exoskeleton).

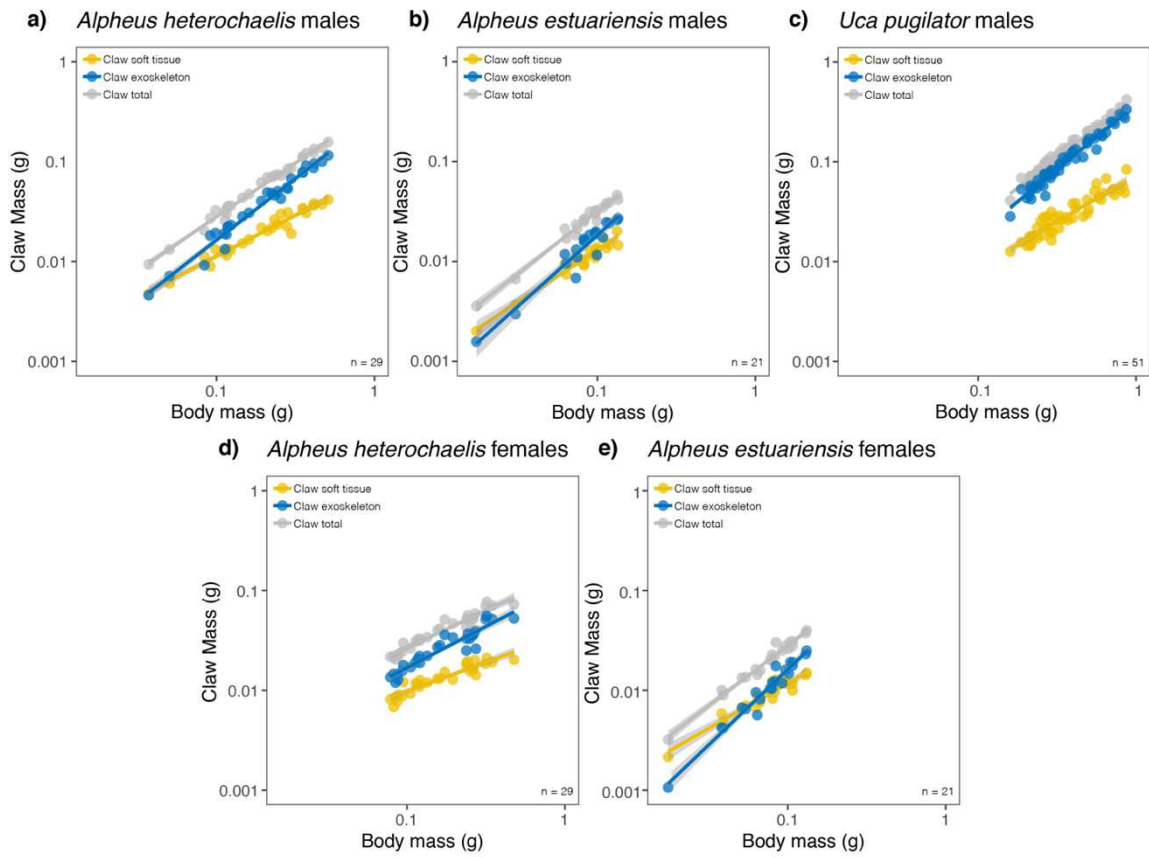


Figure 26: Scaling of tissue types shown in non-logged units. Note that the scales on both axes are still logarithmic to retain linear scaling relationships.

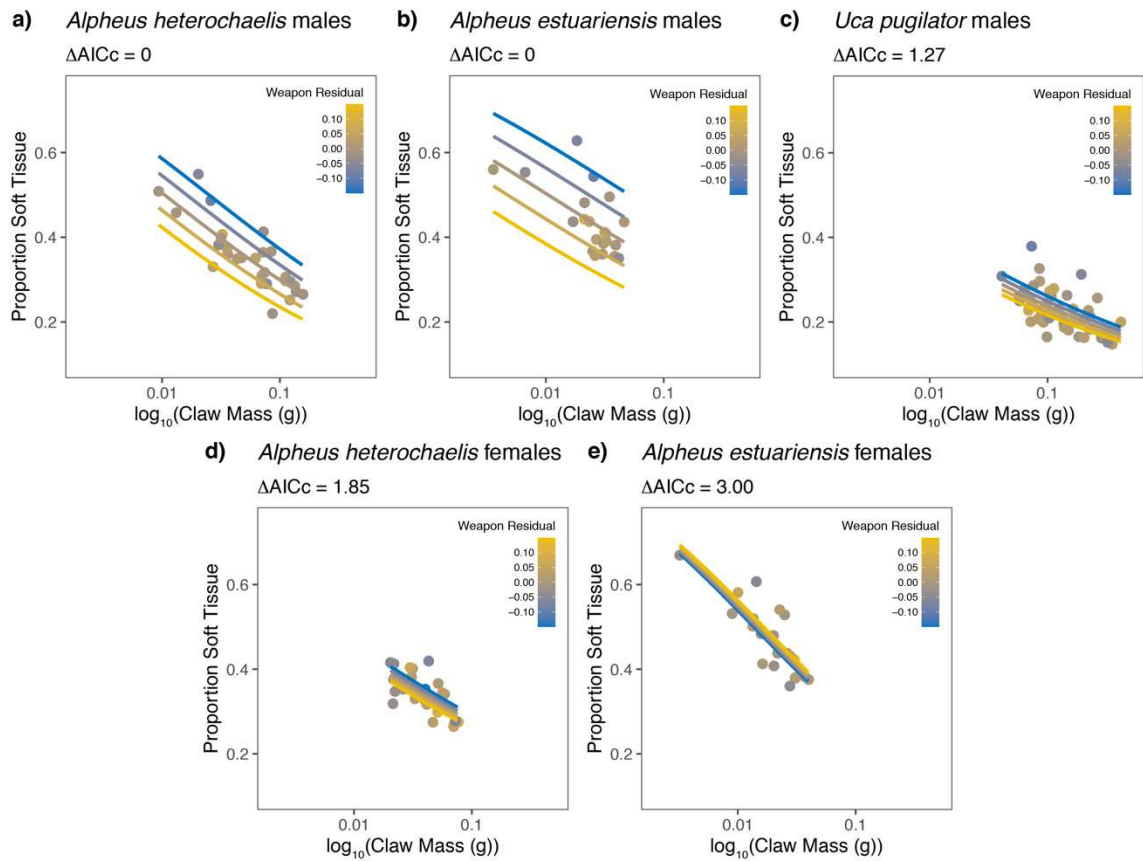


Figure 27: Scaling relationships of proportional soft tissue composition with claw size and claw exaggeration with non-logged axes. Note that the scale on the x-axis is still logarithmic to retain linear scaling relationships.

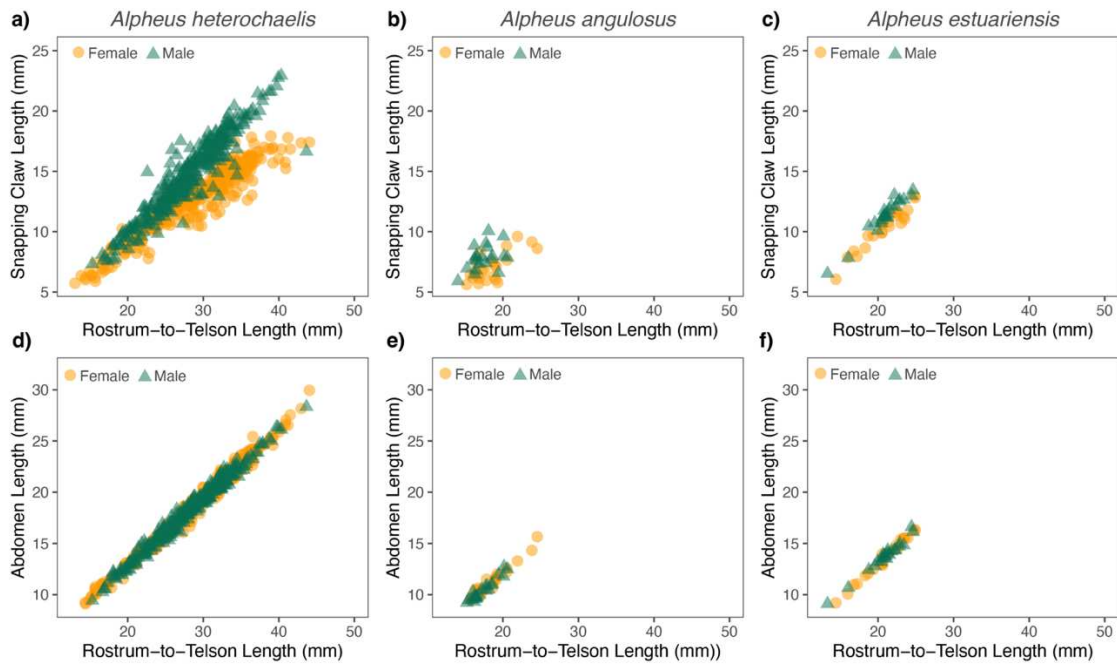


Figure 28: Scaling relationships for snapping claw length and abdomen length shown in linear scaling.

Table 44: Linear models used to produce weapon tissue scaling relationships. All models were statistically significant ($p < 0.05$)

Species and Sex	Total Claw Mass	Soft Tissue Mass	Exoskeleton Mass
<i>Alpheus heterochaelis</i> female	mass = $-0.82857 + 0.74492 \cdot \log_{10}(\text{total mass})$	mass = $-1.42735 + 0.58169 \cdot \log_{10}(\text{total mass})$	mass = $-0.94723 + 0.82601 \cdot \log_{10}(\text{total mass})$
<i>Alpheus heterochaelis</i> male	mass = $-0.47357 + 1.07837 \cdot \log_{10}(\text{total mass})$	mass = $-1.12634 + 0.81980 \cdot \log_{10}(\text{total mass})$	mass = $-0.55377 + 1.23044 \cdot \log_{10}(\text{total mass})$
<i>Alpheus estuariensis</i> female	mass = $-0.34606 + 1.20487 \cdot \log_{10}(\text{total mass})$	mass = $-1.02097 + 0.90604 \cdot \log_{10}(\text{total mass})$	mass = $-0.27857 + 1.51133 \cdot \log_{10}(\text{total mass})$
<i>Alpheus estuariensis</i> male	mass = $-0.26046 + 1.23044 \cdot \log_{10}(\text{total mass})$	mass = $-0.84909 + 1.03541 \cdot \log_{10}(\text{total mass})$	mass = $-0.31928 + 1.41700 \cdot \log_{10}(\text{total mass})$
<i>Uca pugilator</i> male	mass = $-0.34955 + 1.21780 \cdot \log_{10}(\text{total mass})$	mass = $-1.13217 + 0.93167 \cdot \log_{10}(\text{total mass})$	mass = $-0.42618 + 1.29786 \cdot \log_{10}(\text{total mass})$

Table 45: Interaction models used to determine if soft tissue and exoskeleton vary in slope in *Alpheus heterochaelis* females. Negative slopes in the interaction term indicate that soft tissues have more negatively allometric scaling relationships. Each possible model is shown in a separate row, and log-likelihoods, AICc, and Δ AICc are also shown for each model.

Intercept	$\log_{10}(\text{total mass})$	Soft Tissue	Interaction	df	logLik	AICc	Δ AICc
-0.9472	0.8260	-0.4801	-0.2443	5	82.335	-153.5	0.00
-1.0420	0.7039	-0.2897	N/A	4	76.607	-144.5	9.06

Table 46: Interaction models used to determine if soft tissue and exoskeleton vary in slope in *Alpheus heterochaelis* males. Negative slopes in the interaction term indicate that soft tissues have more negatively allometric scaling relationships. Each possible model is shown in a separate row, and log-likelihoods, AICc, and Δ AICc are also shown for each model.

Intercept	$\log_{10}(\text{total mass})$	Soft Tissue	Interaction	df	logLik	AICc	Δ AICc
-0.5538	1.230	-0.5726	-0.4106	5	86.766	-162.4	0.00
-0.7048	1.025	-0.2705	N/A	4	64.348	-119.9	42.44

Table 47: Interaction models used to determine if soft tissue and exoskeleton vary in slope in *Alpheus estuariensis* females. Negative slopes in the interaction term indicate that soft tissues have more negatively allometric scaling relationships. Each possible model is shown in a separate row, and log-likelihoods, AICc, and Δ AICc are also shown for each model.

Intercept	$\log_{10}(\text{total mass})$	Soft Tissue	Interaction	df	logLik	AICc	Δ AICc
-0.2786	1.511	-0.7424	-0.6053	5	59.837	-108	0.00
-0.6231	1.209	-0.05324	N/A	4	44.289	-79.5	28.51

Table 48: Interaction models used to determine if soft tissue and exoskeleton vary in slope in *Alpheus estuariensis* males. Negative slopes in the interaction term indicate that soft tissues have more negatively allometric scaling relationships. Each possible model is shown in a separate row, and log-likelihoods, AICc, and Δ AICc are also shown for each model.

Intercept	$\log_{10}(\text{total mass})$	Soft Tissue	Interaction	df	logLik	AICc	Δ AICc
-0.3193	1.417	-0.5298	-0.3816	5	52.956	-94.2	0.00
-0.5283	1.226	-0.1118	N/A	4	47.147	-85.2	9.03

Table 49: Interaction models used to determine if soft tissue and exoskeleton vary in slope in *Uca pugilator* males. Negative slopes in the interaction term indicate that soft tissues have more negatively allometric scaling relationships. Each possible model is shown in a separate row, and log-likelihoods, AICc, and Δ AICc are also shown for each model.

Intercept	$\log_{10}(\text{total mass})$	Soft Tissue	Interaction	df	logLik	AICc	Δ AICc
-0.4262	1.298	-0.7060	-0.3662	5	136.869	-263.1	0.00
-0.5067	1.115	-0.5449	N/A	4	122.606	-236.8	26.31

Table 50: AIC comparison of beta regression models in *Alpheus heterochaelis* females.
Outputs were created using the dredge() function in the R package MuMIn. Each possible model is shown in a separate row, and log-likelihoods, AICc, Δ AICc, and AICc weight are also shown for each model.

Intercept	$\log_{10}(\text{claw mass})$	Snapping claw residual	df	logLik	AICc	Δ AICc	weight
-1.7680	-0.7840	N/A	3	58.305	-109.6	0.00	0.716
-1.7060	-0.7398	-0.5094	4	58.731	-107.8	1.85	0.283

Table 51: AIC comparison of beta regression models in *Alpheus heterochaelis* males. Outputs were created using the dredge() function in the R package MuMIn. Each possible model is shown in a separate row, and log-likelihoods, AICc, Δ AICc, and AICc weight are also shown for each model.

Intercept	$\log_{10}(\text{claw mass})$	Snapping claw residual	df	logLik	AICc	Δ AICc	weight
1.7190	-0.8688	-2.184	4	53.530	-97.4	0.00	0.73
-1.7510	-0.8945	N/A	3	51.179	-95.4	1.99	0.27

Table 52: AIC comparison of beta regression models in *Alpheus estuariensis* females.
Outputs were created using the dredge() function in the R package MuMIn. Each possible model is shown in a separate row, and log-likelihoods, AICc, Δ AICc, and AICc weight are also shown for each model.

Intercept	$\log_{10}(\text{claw mass})$	Snapping claw residual	df	logLik	AICc	Δ AICc	weight
-2.0820	-1.142	N/A	3	34.763	-62.1	0.00	0.818
-2.0950	-1.149	0.3148	4	34.806	-59.1	3.00	0.182

Table 53: AIC comparison of beta regression models in *Alpheus estuariensis* males. Outputs were created using the dredge() function in the R package MuMIn. Each possible model is shown in a separate row, and log-likelihoods, AICc, Δ AICc, and AICc weight are also shown for each model.

Intercept	$\log_{10}(\text{claw mass})$	Snapping claw residual	df	logLik	AICc	Δ AICc	weight
-1.3910	-0.7021	-3.231	4	32.690	-54.9	0.00	0.805
-1.5030	-0.7730	N/A	3	29.639	-51.9	3.01	0.178

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Biography

Jason Phanliem Dinh was born and raised in Bel Air, Maryland. He graduated summa cum laude with a B.S. in Biology from Duke University in 2018. As an undergraduate, he received departmental distinction for his undergraduate thesis, won the department's James B. Rast Award for Comparative Organismal Biology, entered the Phi Beta Kappa Honor Society, and earned a Summer Student Fellowship at the Woods Hole Oceanographic Institution. He published two first-author papers from his undergraduate research. Jason began his Ph.D. at Duke University in the Biology Department in 2018. He was supported by a National Science Foundation Graduate Research Fellowship. He's published five first-author papers based on his dissertation research focusing on behavioral ecology, evolutionary biology, and sensory neurophysiology. His work is supported by funding from the Company of Biologists, the Crustacean Society, Bass Connections, the Animal Behavior Society, and the Society for Integrative and Comparative Biology. A dedicated educator, Jason completed the Certificate in College Teaching and the Preparing Future Faculty Fellowship. He also is an accomplished science writer, earning a AAAS Mass Media Fellowship and a National Association of Science Writers Summer Diversity Fellowship based at Discover Magazine and an NSF INTERN fellowship based at Science Friday. He has published clips as a freelance journalist in The New York Times, The Atlantic, Science, Popular Science, Hakai Magazine, New Scientist, and elsewhere.