Honesty Is Costly in a Deceptive System: Locomotor Costs of Producing Large and Strong Weapons for the Crayfish *Cherax destructor*

Lana A. Waller[1]
Simon P. Lailvaux[2]
Robbie S. Wilson[1,*]
[1]School of the Environment, University of Queensland, St. Lucia, Queensland 4072, Australia; [2]Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148

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ABSTRACT

Theory predicts that signals of strength should reliably reflect an individual's fighting ability, with the costs of producing and/or displaying high-quality signals maintaining their reliability. Crustaceans offer a unique system to explore these costs because signal (chela) size and reliability (strength relative to size) can be decoupled—chela muscles are concealed beneath an exoskeleton, allowing some individuals to display large but weak chelae. In this study, we quantified the locomotor costs associated with weapon size and reliability in males and females of the crayfish *Cherax destructor* using both correlative analyses and experimental manipulations. We measured chela size, strength, and swimming performance of crayfish when intact, after an initial chela removal treatment (control, one, or two), and again after removal of the remaining chela/chelae. We predicted that larger chelae would reduce swimming performance because of added mass and drag and that relatively stronger individuals (greater reliability) would swim slower because of energetic investment in muscle. We found that males and females with larger chelae swam more slowly and that speed increased following the removal of one (11.6%) and two (14.6%) chelae. Individuals with relatively larger chelae showed a greater increase in speed after both chelae were removed. Crayfish with relatively stronger chelae swam more slowly, but this pattern did not hold after chela removal. Our study is the first to demonstrate the independent costs of both signal size and their reliability. While individuals must bear the costs of signaling large weapons, the costs of their reliability may also incentivize the use of unreliable weapons.

Keywords: costs, signals of strength, swimming speed, unreliable signals, weapon size.

Introduction

Animals often engage in disputes with conspecifics over access to resources, such as food, mates, or territories (Parker 1974; Maynard Smith and Harper 2003; Wilson et al. 2007). However, engaging in disputes is energetically costly and can lead to injury or death, even for the winner (Wilkinson and Shank 1976). Many animals use signals of strength, and thus their potential to inflict damage on their opponents, to resolve disputes before they escalate to physical contests. This minimizes the costs associated with aggressive interactions for both contestants. Signals, however, should accurately and reliably reflect an individual's actual fighting capacity; otherwise, they would provide no benefit to a receiver and are likely to be ignored (Searcy and Nowicki 2005). The reliability of signals of strength is thought to be maintained via either mechanistic limitations to signals (known as index signals) or the costs associated with their production and display (Searcy and Nowicki 2005). Index signals are those in which the magnitude of the signal is mechanistically linked to its actual quality (Maynard Smith and Harper 1995, 2003). For example, male collared lizards (*Crotaphytus collaris*) signal their strength to opponents by displaying their jaw muscles. Because the size of the jaw muscles directly correlates with greater bite force, the magnitude of the signal is mechanistically linked to the quality of that being advertised and cannot be faked (Lappin et al. 2006). In contrast, signal reliability can be maintained when only high-quality individuals can endure the costs of producing and/or bearing the signals, known as receiver-independent costs, or the costs imposed by receivers of the signals, referred to as receiver-dependent costs (Zahavi 1975, 1977; Maynard Smith and Harper 2003; Hurd and Enquist 2005). Receiver-independent costs include reduced growth or lowered physical fitness (Emlen 2001), poorer locomotor function (Evans and Hatchwell 1992; Evans and Thomas 1992), increased predation (Rosenthal et al. 2001), compromised immune response (Clotfelter et al. 2007), and decreased fecundity when metabolic energy is preferentially allocated to the production of signals (Ghalambor et al. 2004). Receiver-dependent costs arise when there is a greater likelihood that competitors with "similar" signal magnitudes escalate contests (Molles and Vehrencamp

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*Corresponding author; email: r.wilson@uq.edu.au.

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2001) or when unreliable signalers are exposed as frauds and punished by conspecifics (Tibbetts and Dale 2004).

Unreliable signals are those in which the magnitude of the signal does not accurately represent the intrinsic quality being advertised by the signaler (Maynard Smith and Harper 2003). Although theory predicts that unreliable signals of strength should not be widespread in nature, they are more common than previously considered (Wilson et al. 2007; Lailvaux et al. 2009; Walter et al. 2011). Most examples of unreliable signaling come from studies of intraspecific aggression of crustaceans. Crustaceans use their enlarged front claws (chelae) as weapons to inflict injuries during physical contests (Sneddon et al. 1997; Bywater et al. 2008; Lailvaux et al. 2009) but also in displays to signal their potential to cause costly injuries (Arnott and Elwood 2010). While most disputes are settled during the signaling stage, the individual with the stronger chela force generally wins when contests escalate to physical combat (Wilson et al. 2007; Bywater et al. 2008; Walter et al. 2011). The chela muscles that underpin this force, however, are concealed within an exoskeleton, which enables the potential decoupling of chela size and underlying strength. Crustaceans also grow by shedding their exoskeleton, and while the new exoskeleton hardens quickly, the underlying muscle takes longer to regenerate, contributing to variation in chela strength for any given size (Graham and Angilletta 2022). As a result, individuals can display large chelae without necessarily having the strength to match their signals (Lailvaux et al. 2009). While this mismatch has often been interpreted as dishonest signaling, recent work suggests that unreliable signals are not always used deceptively (Graham and Angilletta 2022). For example, some crayfish species escalate to fights based on body size rather than chela size (Graham et al. 2020; Graham and Angilletta 2020, 2022), even though others still rely on unreliable cues to resolve disputes despite being weak (Wilson et al. 2007; Walter et al. 2011; Angilletta et al. 2019). Nonetheless, the unreliability of chela size for many species still makes it difficult for competitors to accurately assess the strength of an opponent's weapon without engaging in physical contact.

Unreliable signaling among many crustaceans offers a unique opportunity to explore the costs of both the magnitude of the signal (weapon) and its reliability (strength for weapon size). Theory predicts that both the magnitude of the signal and its reliability should be independently costly, with the greatest costs experienced by those individuals with the largest and strongest weapons (Maynard Smith and Harper 2003). Larger weapons may both inhibit locomotor function and require more energy to be diverted away from other functions in order to grow, while the larger muscles in stronger weapons may require more energy for growth and maintenance. Although these predictions are indirectly supported by some previous studies, others are more equivocal. For example, male slender crayfish (*Cherax dispar*) with larger chelae for their size swim more slowly, but weapon strength (i.e., reliability) does not affect swimming performance when chelae were intact (Wilson et al. 2007, 2009); in the same species, female swimming is not affected by chela size or strength (Wilson et al. 2009). Although stronger chelae are more energetically costly than weaker chelae for male two-toned fiddler crabs (*Gelasimus vomeris*; Bywater et al. 2014), it is unclear whether the magnitude of this cost is sufficient to affect growth or whole-animal function.

Quantifying the costs of exaggerated signals is often complicated by a reliance on correlative analyses alone rather than by including manipulative experiments. Higher-quality individuals may invest not only in higher-quality costly signals but also in other traits that compensate for these costs, which can effectively mask their detection when using correlative analyses (Møller 1996; Oufiero and Garland 2007; Husak et al. 2011). For example, male scarlet-tufted malachite sunbirds (*Nectarinia johnstoni*) with longer tails should have lower flight performances because of the increased drag associated with these signals; however, males with long tails often possess relatively larger wingspans that compensate for these effects (Evans and Thomas 1992). The costs of long tails were revealed only by using experiments that manipulated the length of the tail feathers (Evans and Hatchwell 1992). In a similar way, manipulative experiments can also reveal the absence of presumed costs for exaggerated traits on functions like locomotor performance. For example, experimental elongation of the tail ornaments of male red-billed streamertails (*Trochilus polytmus*) did not decrease flight maneuverability at low speeds (Clark 2011). Thus, exploring the costs of both the magnitude of the signal (weapon) and its reliability (strength for weapon size) in crayfish would be strengthened by the inclusion of both correlative and manipulative experiments.

In this study, our aim was to quantify the magnitude of the locomotor costs associated with weapon size and reliability for males and females of the crayfish *Cherax destructor* using both interindividual correlative analyses and experimental manipulations. Male and female *C. destructor* crayfish use their enlarged chelae as signals of strength during aggressive interactions, and like most other crustaceans, larger chelae are often stronger; however, there is substantial among-individual variation in strength for any given chela size (Walter et al. 2011). While females routinely rely on the signaling of relative chela size to settle dominance, males more frequently escalate disputes to the fighting stage, which imposes social costs on unreliable signalers whose chelae are weaker than they appear (Walter et al. 2011). We predicted that chela size would be positively correlated with chela strength for both males and females but that individuals would vary substantially in strength for any given chela size, indicating variation in signal (un)reliability, as found in previous studies of crayfish (Wilson et al. 2007, 2009; Walter et al. 2011). We then evaluated the locomotor costs of chelae for male and female crayfish. We predicted that males and females with relatively larger chelae would be slower swimmers because of the greater mass and hydrodynamic drag of larger chelae when moving through the water and the energetic investment into chelae at the expense of investment in tail muscle (which is used for swimming). We complemented this correlative analysis with a manipulative experiment in which we remeasured swimming performance after the removal of one, two, or no chelae from each crayfish (time 2) and then again after the removal of all chelae (time 3). In these experiments, we predicted that the swimming speed for males and females would increase proportionally to the number and size (and mass) of chelae removed because of the greater mass and hydrodynamic drag of larger chelae when moving through the water. Finally, we explored the potential costs of signal reliability by quantifying the relationship between chela force and swimming speed. We expected that if crayfish produce strong chelae, this energetic investment into greater and higher-quality muscle would be associated with less energy available for investment in tail muscle and their swimming speed would be slower. Thus, we provide a novel approach by independently testing the costs of weapon size and strength.

Material and Methods

Study Animals

We obtained 71 male and 74 female *Cherax destructor* (Clark 1936) from a commercial aquaculture facility (Yabby Dabba Doo, Karuah, Australia) that raised and maintained animals in large, open-air natural ponds where they were able to aggressively interact with competitors throughout their life. Crayfish were transported to a laboratory at the University of Queensland (St. Lucia, Australia) where they were housed individually in 5-L plastic containers filled with dechlorinated water. Animals were fed every 2 d using commercial sinking pellets (vege wafers, Aqua One, Kong's, Ingleburn, Australia). All individuals were maintained in the laboratory for at least 48 h before use in experiments, and only those crayfish that were intermoult and retained intact left and right chelae were used in the study. Crayfish with obvious asymmetry in chela size were excluded, but as chela regeneration could not be reliably identified, any undetected cases were considered to reflect natural variation.

Morphology

We recorded the initial body mass, body length, and chela sizes of each crayfish. Body mass was measured using an electronic balance (±0.001 g; FX-500i, A&D, Adelaide, Australia). Body length and chela sizes were determined from images captured using a digital camera (Casio Exilim EX-100F, Casio Computer, Tokyo) and analyzed using ImageJ (Schneider et al. 2012). An object of known length was placed in the field of view to enable accurate calibration of images. We defined body length as the distance from the tip of the rostrum to the end of the tail. Seven measurements were taken from each chela, including propodus width at the carpus and dactyl joints, pollex and dactylus widths, length of the propodus to the dactyl joint, and lengths of the pollex and dactylus (fig. 1). We ran a principal component analysis (PCA) using all seven measurements recorded for all individuals combined to collapse correlated measures of chela dimensions into new uncorrelated orthogonal variables. The first principal component (PC1) was used as a measure of chela size, as all vectors loaded in the same direction and explained 94% of the variation in the data. As both chelae are approximately symmetrical in this

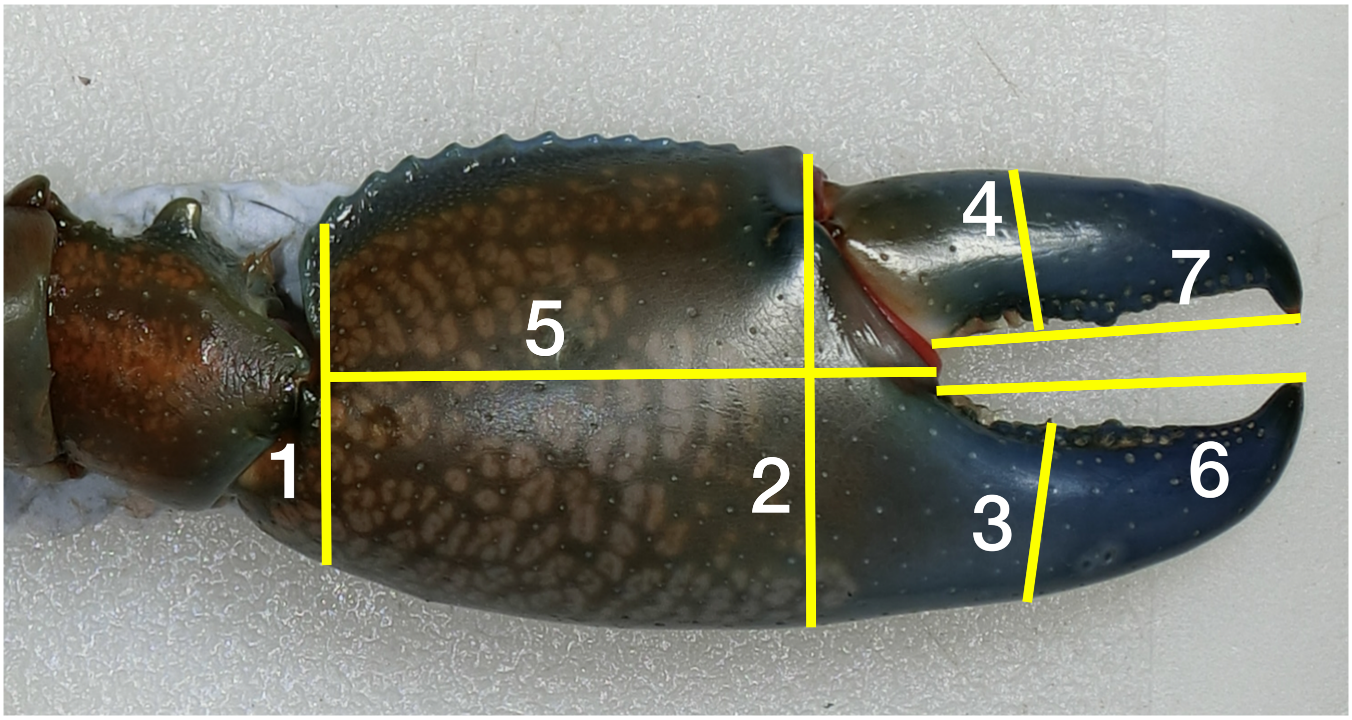

Figure 1. Seven measurements taken to describe the size of each chela of *Cherax destructor*. These measurements included (1) propodus width at the carpus joint, (2) propodus width at the dactyl joint, (3) width of the pollex, (4) width of the dactylus, (5) length of the propodus to the dactyl joint, (6) length of the pollex, and (7) length of the dactylus. Photo by Lana Waller.

species, we used the mean PC1 score for the left and right chelae combined as each individual's measure of chela size in subsequent analyses.

Chela Strength

We quantified the maximum strength of the left and right chelae of each crayfish using a custom-built force transducer that consisted of two metal plates separated by a third metal plate, as described in detail in Wilson et al. (2007). Strain gauges were attached to the outer side of the two metal plates and were connected to a Wheatstone bridge linked to a bridge amplifier (AD Instruments, Sydney; Wilson et al. 2007). Force applied to the metal plates as the crayfish clamped their chela onto them was measured using PowerLab (AD Instruments). Strain gauges were calibrated using known weights, and the millivoltage output was converted to Newtons. Crayfish readily closed their chela on the transducer plates. All force measures were conducted at 23°C. To maximize repeatability, we standardized the position of chela closure on the metal plates, ensuring that measures were taken near the base of the dactylus. The strength of each crayfish was measured over two consecutive days, collecting force data from a minimum of three grabs for each chela on each day of testing. For subsequent analyses, we selected the greatest force produced by each chela across the 2 d and used the mean of these forces as the measure of an individual's maximum performance (Wilson et al. 2007; Walter et al. 2011).

Swimming Speed

We quantified the swimming speeds of each crayfish by filming at least three startle responses on each day of testing. To elicit a maximal swimming bout, we placed crayfish into the center of a swimming arena (glass aquarium: 600 mm × 600 mm × 150 mm) and touched the front of their chelae with large wooden forceps (Wilson et al. 2009). All trials were conducted at 23°C. We recorded each swimming sequence at 240 fps by positioning an iPhone 14 Pro camera (Apple, Cupertino, CA) directly beneath the glass-bottomed aquarium to record the movement without surface distortion. An object of known length was placed within the field of view to enable calibration of the distances. Videos were analyzed using Kinovea (ver. 0.9.5; https://www.kinovea.org/). The point midway between each crayfish's eyes was digitized to enable consistent tracking of a clear point across each frame within a swim sequence. We calculated the total distance moved by each crayfish over the first 120 ms of each swim sequence and converted this distance to speed (cm s^{-1}). We used the first 120 ms of the startle response because it approximates the time for one complete tail-beat sequence (Wilson et al. 2009). The startle response was generally linear and biplanar. Consequently, we analyzed responses that began only from a stationary position and led to a powerful backward stroke that did not breach the water surface. The beginning of the startle response was taken as the frame before movement was first detected. At each stage of the experiment, we retested the swimming performance of each individual over two consecutive days so that we had a minimum of six swimming sequences for each animal. We used all swimming sequences in subsequent analyses comparing the effects of chela removal treatments on swimming performance. When examining relationships between swimming speed and chela strength, only the maximum speed per individual was used.

Experimental Manipulation of Chelae

After we measured the initial morphology, strength, and swimming performance of all individuals (time 1), we then randomly allocated each crayfish to treatments in which (1) no chelae were removed, (2) one chela was removed (randomizing the left or right chela), or (3) both chelae were removed to form treatments for time 2 measures. To remove the chelae, we applied pressure with metal tongs at the carpus joint near the base of the chela, and the crayfish readily detached their chela (Stoeckel et al. 2011). Regardless of treatment, all crayfish were handled for the same length of time. After chela manipulation, crayfish were rested for 24 h, and swimming performance was then retested again on two consecutive days (time 2) using identical methods, as described above. Remaining chelae were then removed for all crayfish across all treatment groups. Crayfish were rested for another 24 h after chela removal, and the swimming performance was retested on two consecutive days (time 3).

Statistical Analyses

We examined the relationship between chela size and body length in males and females using a multiple regression model fitted with the lm function in the stats R package (R Core Team 2024). We also compared chela size with chela force using the gls function from the nlme package, applying an exponential variance structure to account for increasing variation in chela force with increasing chela size (Zuur et al. 2009; Pinheiro et al. 2024). To examine the relationship between chela size and sex with an individual's maximum swim speed, we performed an ANCOVA using the lm and anova functions and included body length as an additional covariate to account for size. The resulting partial regression coefficients therefore represent the association between chela size and speed with the effects of body length statistically removed (Kachigan 1991).

To analyze the effect of chela removal on swimming speed, we fitted a linear mixed effect model using the lme function from the nlme R package (Pinheiro and Bates 2024). We fitted this model with swimming speed as the explanatory variable, body length and chela size as covariates to account for size, and an interaction between sex, chela removal treatment, and time (i.e., times 1, 2, or 3). We included all measures of an individual's swimming speed in the model and therefore used a nested random effect structure to control for individual variation in speeds between days and within each day. For the random effects, each measure of swimming speed was nested within day (i.e., to account for variation between the 2 d we measured speed), which was nested within crayfish identity to account for repeated measures. Swimming speed data were transformed using a Box-Cox transformation (boxcox function) in the MASS R package to improve model fit and meet model assumptions (noted as an exponent of 0.6 in table S1 [tables S1, S2 are available online]; Venables and Ripley 2002). Model fit cannot be assessed using the DHARMa R package with models from the nlme R package, so we refitted the model using the lmer function from the lme4 R package to assess the diagnostics (Bates et al. 2015; Hartig 2022). We assessed the significance of predictors based on deletion tests using log-likelihood ratios in the MASS R package (stepAIC function). This automated stepwise approach iteratively compares models based on Akaike information criterion values and enabled us to determine the minimum adequate model (i.e., simplest model that explained the largest amount of variation; Venables and Ripley 2002). We then refitted the minimum adequate model using restricted estimate maximum likelihood to account for the loss of degrees of freedom when estimating fixed effects, thus providing less biased estimates of variance components (Patterson and Thompson 1971; Silk et al. 2020). To test for differences among levels of the predictors of the linear mixed model, we used the emmeans function from the emmeans package to extract contrasts comparing the speeds between sexes across the different testing sessions (times 1, 2, and 3) for all treatment groups, and the P values were adjusted using the Tukey method (Lenth 2024).

We tested whether an individual's increase in swimming speed following chela removal was associated with the relative size of their chela before removal. To do this, we used an ANCOVA to examine the relationship between the proportional change in swimming speed (speed at time 3 vs. time 1) with their chela mass as a proportion of their total mass for males and females.

To describe the relationship between swim speed and chela force, we performed an ANCOVA by fitting a general linear model with chela force and sex as the predictor variables and included body length and chela size as additional covariates to correct for size. We fitted two separate models, one using the initial swim speeds with the fully intact crayfish (time 1) and a second using the swim speeds of crayfish after all chelae had been removed (time 3).

To visualize the multiple regression and general linear models, we used the visreg (visreg function) and ggplot2 (ggplot function) packages to plot the partial residuals, which illustrate the relationship between the response variable and the variable of interest, while accounting for the effects of the other variables in the model (Wickham 2016; Breheny and Burchett 2017). Similarly, we visualized the linear mixed effect model using the ggplot2 package to plot the estimated marginal means (extracted from the emmeans function), which are the means of model predictions after controlling for other factors in the model (Wickham 2016; Lenth 2024). We conducted all statistical analyses in R (ver. 4.4.1; R Core Team 2024). Significance was taken at the level of $P < 0.05$, and results are presented as means ± SEM.

Results

Chela Size, Strength, and Maximum Swimming Performance

Male and female *Cherax destructor* did not differ in body length (males, 78.6 ± 2.6 mm; females, 80.3 ± 2.3 mm; $F_{1,143} = 0.24$, $P = 0.63$) or mean chela size (PC1: for males, −0.08 ± 0.33; for females, 0.02 ± 0.26; $F_{1,141} = 1.81$, $P = 0.18$). However, the chela size of males increased at a greater rate with body length than that of females ($F_{1,141} = 2.39$, $P = 0.02$). Chela force increased with chela size for both males and females (fig. 2), but the chela force of males increased at a greater rate with chela size than that of females ($F_{1,141} = 10.45$, $P = 0.002$). Before any chela manipulations occurred, male and female crayfish with relatively larger chelae were also more likely to be slower swimmers for any given body length ($F_{1,141} = 5.56$, $P = 0.02$).

Comparison of Swimming Speeds between Treatments and Testing Sessions

The minimum adequate model that best described the variation in swim speed retained the three-way interaction between sex, treatment, and testing session (table S1). At time 1 before any chela manipulations, swimming speeds did not differ among treatment groups or sexes (all contrasts, $P > 0.05$; fig. 3; for details on all post hoc contrasts, see table S2).

At time 2, males with one chela (group B) or two chelae (group C) removed swam significantly faster (group B, 67.3 ± 0.1 cm s^{-1}, $P = 0.01$; group C, 69.1 ± 0.1 cm s^{-1}, $P < 0.001$) than males in the control group (group A; 60.3 ± 0.1 cm s^{-1}; fig. 3). Swimming speeds of males with one or two chelae removed did not significantly differ ($P = 0.51$). Females with one chela removed (group B) swam at 66.4 ± 0.1 cm s^{-1} (table S2); the only difference among females was between those with two chelae removed (group C) and those in the control group (group A), as group C females swam significantly faster (69.1 ± 0.1 cm s^{-1}, $P = 0.002$) than controls (61.2 ± 0.1 cm s^{-1}). Males and females did not differ in speed within each treatment group (all contrasts, $P > 0.05$).

We also compared the swimming speeds of crayfish between times 1 (when all chelae were intact) and 2 (when chela manipulations were made). We found that males with one or two chelae removed (groups B and C) swam 10.8% ($P < 0.001$) and 9.5% ($P < 0.001$) faster, respectively, at time 2 than at time 1 (fig. 3). Males in the control group (group A) also swam significantly faster at time 2 (3.2%; $P = 0.005$; table S2). Similarly, females with one or two chelae removed (groups B and C) swam 6.6% ($P < 0.001$) and 7.4% ($P < 0.001$) faster, respectively, at time 2 than at time 1. Swimming speeds of females in the control group (group A) did not significantly vary between times 1 and 2 ($P = 0.05$).

At time 3 when all chelae were removed from all crayfish, swimming speeds did not differ between males and females or from their previous time 2 groupings (all contrasts, $P > 0.05$; fig. 3; table S2).

Proportional Change in Swimming Speed after Chela Removal

An individual's proportional increase in swimming speed from time 1 (both chelae present) to time 3 (both chelae removed) was positively associated with their relative chela mass ($F_{1,139} = 16.58$, $P < 0.001$; fig. 4). In other words, individuals whose chelae composed a larger proportion of their body mass showed a greater increase in swimming speed after both chelae were removed.

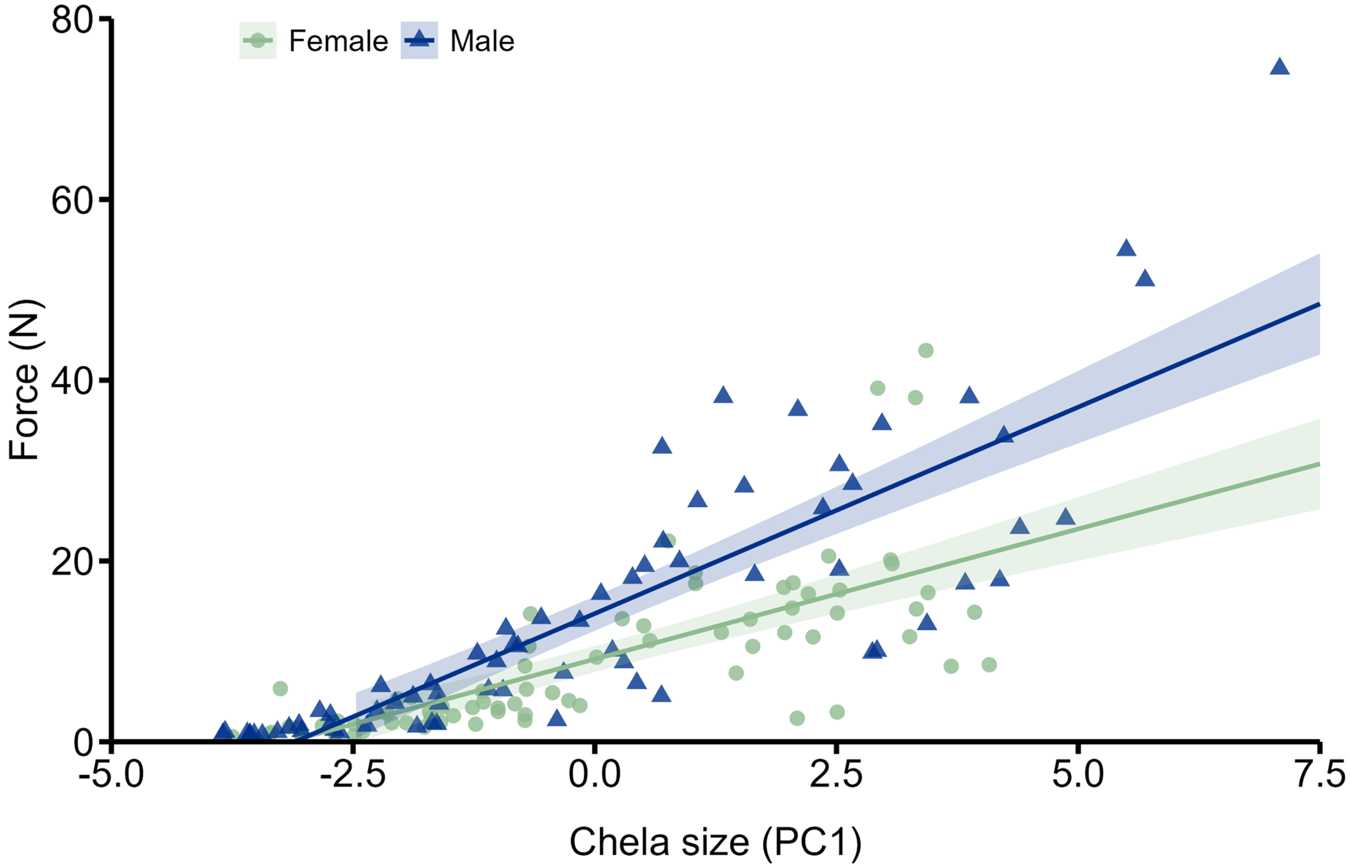

Figure 2. Relationship between chela size (first principal component [PC1]) and chela force (N) for male ($n = 71$) and female ($n = 74$) *Cherax destructor* crayfish. For each sex, data points represent the maximum force generated by each individual, the fitted line accounts for increasing variation in chela force with increasing chela size, and the shaded area shows the 95% confidence intervals around the predicted means.

Males and females did not differ in swimming speed for any given proportional change in chela mass ($F_{1,139} = 1.79$, $P = 0.18$).

Relationship between Chela Strength and Maximum Swimming Performance

Relatively stronger crayfish had slower speeds during time 1, when both chelae were intact ($F_{1,140} = 5.16$, $P = 0.03$; fig. 5*A*), but this relationship did not differ between males and females ($F_{1,140} = 2.4$, $P = 0.12$). Using the statistical model, we determined that a 50% increase in chela strength was associated with a 2.8% and 2.7% decline in swimming speed for males and females, respectively. After chelae were removed at time 3, relatively stronger females still swam significantly more slowly, but there was no longer an association between relative chela force and swimming speed for males ($F_{1,137} = 4.72$, $P = 0.03$; fig. 5*B*).

Discussion

We used a correlative and manipulative approach to quantify the locomotor costs associated with large and strong chelae in male and female *Cherax destructor*. As predicted, male and female *C. destructor* crayfish with larger chelae were generally stronger, but there was substantial variation among individuals in force for any given chela size. Using our correlative approach, we found that males and females with relatively larger chelae were more likely to be slower swimmers. Furthermore, when we removed chelae using experimental manipulations, swimming speed increased as the number of chelae were removed. Individuals whose chelae represented a larger overall proportion of their body mass also swam faster after their chelae were removed. Finally, we found that male and female crayfish with relatively stronger chelae were more likely to be slower swimmers when both chelae were intact.

The negative correlation we observed between chela size and swimming speed before any chela manipulations suggests that larger chelae are indeed a burden for the swimming performance of crayfish. Direct causal evidence for the cost of larger chelae on swimming was also provided from our experimental removal of one or two chelae that resulted in an increase in swimming speed of approximately 11.6% and 14.6%, respectively. The mechanistic basis of the trade-off between weapon size and swimming performance may be driven by (i) the energetic costs of building larger chelae and thus diverting energy away from the growth of other traits that support locomotor propulsion and/or (ii) the greater mass and surface area of larger chelae that may increase

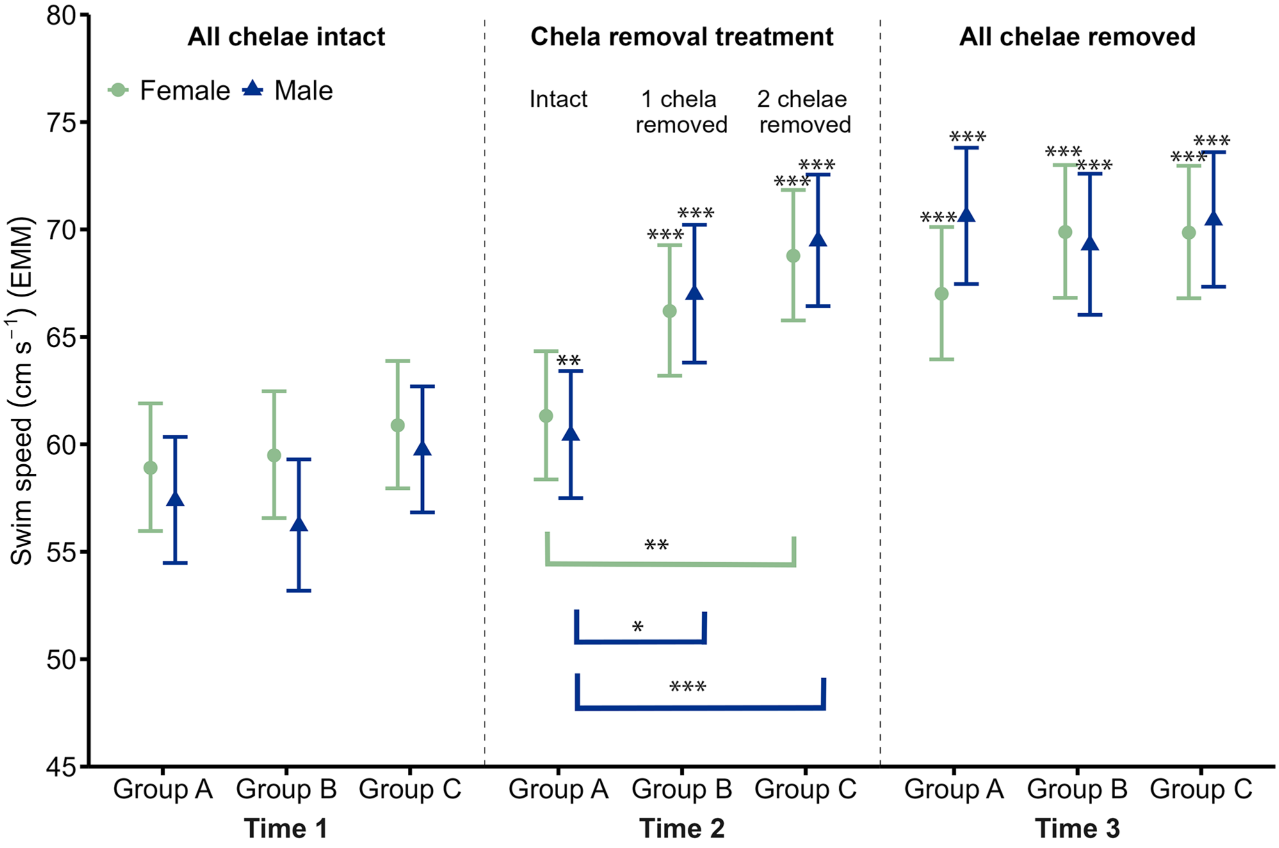

Figure 3. Mean swimming speeds (cm s^{-1}) of male ($n = 71$) and female ($n = 74$) *Cherax destructor* crayfish across the three testing sessions (before chela manipulation treatments were applied [time 1], after the initial chela manipulation treatments [time 2], after all individuals had both chelae removed [time 3]) and treatment groups (control [group A], one chela removed at time 2 [group B], both chelae removed at time 2 [group C]). Data points represent the estimated marginal means (EMMs) ± 95% confidence intervals derived from the linear mixed model examining the swimming speeds for each sex and treatment group across the three testing sessions after statistically accounting for body length and chela size (table S1). See table S2 for details of all post hoc contrasts between sexes, sessions, and treatment groups. To facilitate plotting, EMMs and confidence intervals are back transformed to show original scale. Significant differences between groups are marked by brackets and asterisks, while asterisks above an EMM demonstrate a significant difference from the time 1 speed. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

hydrodynamic drag when swimming. Like other species of crayfish, *C. destructor* propels itself backward using a powerful tail flip. Because its chelae trail behind its body when swimming (Wilson et al. 2009; Hunyadi et al. 2020), it is unsurprising that larger chelae could reduce the streamlined shape of a crayfish and increase drag. Larger chelae were also associated with reduced escape velocities and acceleration for males and females of the crayfish *Faxonius rusticus* (Hunyadi et al. 2020). Although male *F. rusticus* possessed larger chelae than females, both sexes suffered the locomotor burden from enlarged weapons (Hunyadi et al. 2020). Male slender crayfish (*Cherax dispar*) also exhibited a trade-off between chela size and swimming speed, but there was no association for females (Wilson et al. 2009). Unlike the male and female *C. destructor* in this study, *C. dispar* males possess substantially larger chelae for any given body length than females, which could have driven the sex-specific trade-off in this species (Wilson et al. 2009).

Trade-offs between weapons and locomotor ability are seen in other taxa. For example, the endurance and running speeds of male sand fiddler crabs (*Leptuca pugilator*) have been found to increase following the removal of their enlarged chela (Martin 2019), although other studies have reported no effect on speed in this species (Allen and Levinton 2007). A similar cost is observed in male *Tidarren sisyphoides* spiders, where removal of one pedipalp (a key reproductive organ) increased speed by 44% (Ramos et al. 2004). Although pedipalps are not signals of strength, their large size likely impairs locomotor performance in a similar manner to chelae. For *C. destructor*, the reduced speeds of males and females with larger chelae likely have important ecological consequences. Faster speeds of both terrestrial and aquatic animals are often associated with an increased ability to escape from predators (Miles 2004; Walker et al. 2005). For example, faster ornate tree lizards (*Urosaurus ornatus*) were more likely to survive until the following sampling period than slower lizards (regardless of size; Miles 2004), and guppies (*Poecilia reticulata*) with faster speeds were more likely to escape predator strikes (Walker et al. 2005). Similarly, male *F. rusticus* crayfish with larger chelae suffered higher predation rates by birds (Berrill and Arsenault 1984), suggesting that weapon size can indeed impact survival. Although the approximate 14.6% increase in speed following removal of both

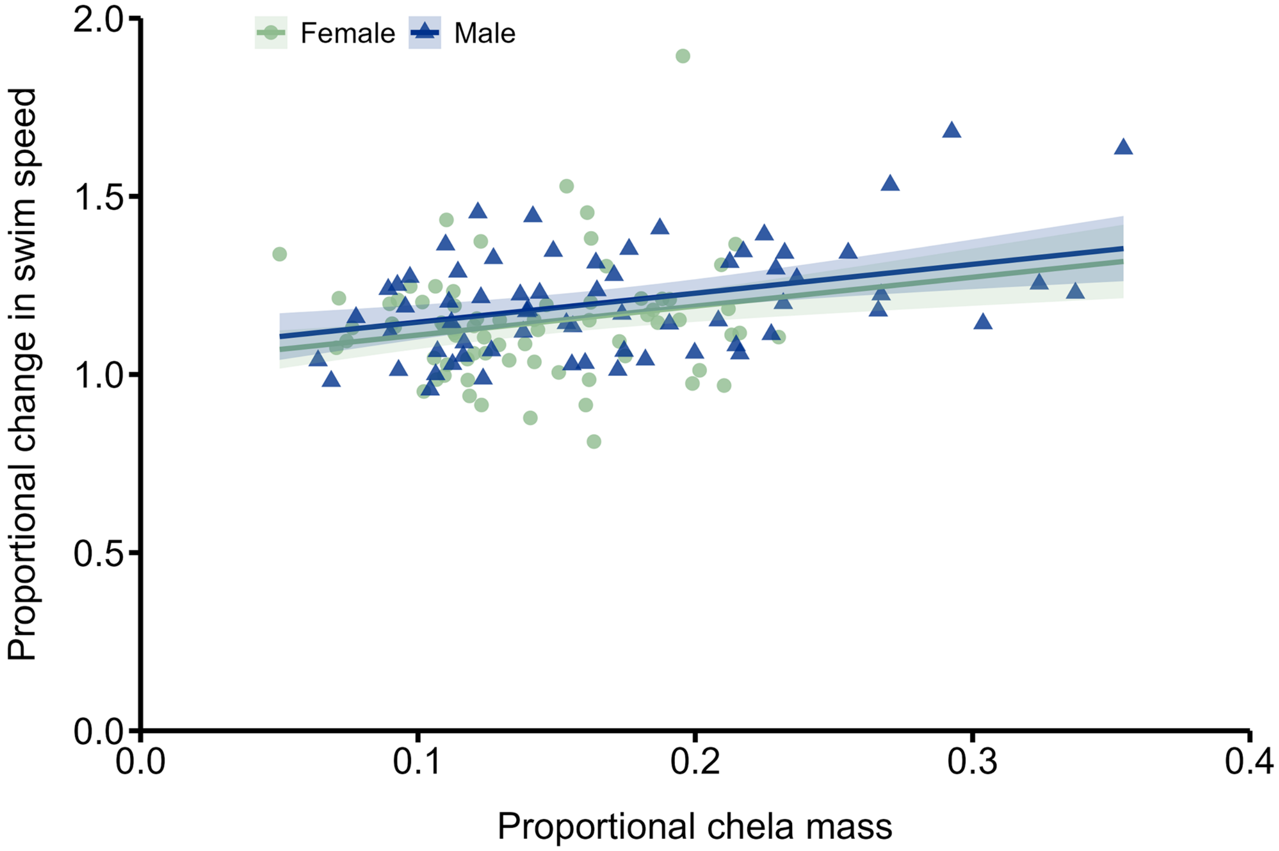

Figure 4. Relationship between an individual's chela mass as a proportion of total mass (total chela mass/total mass) and their proportional change in swimming speed after removal of both chelae (speed with no chelae/speed with intact chelae) for male ($n = 69$) and female ($n = 74$) *Cherax destructor* crayfish. The shaded area shows the 95% confidence intervals around the predicted means.

chelae in *C. destructor* may not exceed the speed of predator strikes, even modest gains in escape performance could affect survival. While crayfish will benefit from producing larger chelae because they can intimidate opponents during disputes with conspecifics, large chelae can have costly consequences (Walter et al. 2011). Therefore, the display of these weapons provides information to a receiver on both the probability of their strength—albeit with variance—and their ability to survive with the additional locomotor burden of their larger weapons.

We predicted that stronger weapons for any given chela size would also be associated with a locomotor cost. In support of this prediction, we found that relatively stronger males and females were significantly slower swimmers. However, only the females that were relatively stronger were also slower swimmers after chela removal. Taken together, this suggests that stronger weapons also have costs that manifest in poorer swimming speeds. The underlying mechanism for this cost is likely to result from the greater investment to grow more muscle and the energetic costs of maintaining it. Energy diverted to the growth and maintenance of chela muscle may result in fewer resources available to allocate to tail muscle or structure. This trade-off may be even more pronounced in females, as only stronger females exhibited slower speeds once both chelae were removed. Alternatively, some of the variation may reflect differences related to the stage of moulting, even though all individuals were intermoult (Graham et al. 2022). While these correlative data do not provide a causal link, to the best of our knowledge this is the first study to demonstrate the cost for reliable signals of strength in a crayfish species with unreliable signaling. Although males of the western painted crayfish (*Faxonius palmeri longimanus*) that possessed relatively greater chela muscle mass had lower mass of tail muscle, females of this species with more chela muscle mass also had greater tail muscle mass (Robinson and Gifford 2019). In addition, Wilson et al. (2009) found that chela strength was not associated with an individual's speed in males and females of *C. dispar*. The differences between *C. destructor* and other species remain unclear, and future research is needed to explore ecological and life history factors driving this trade-off.

Stronger weapons, like the chelae of crayfish, are important for an individual's fighting success; however, the production of high-quality weapons can come at an energetic cost to locomotion. For example, male Asian house geckos (*Hemidactylus frenatus*) with a greater bite force, and thus larger heads, exhibited a reduced sprint performance (Cameron et al. 2013). Fighting ability and locomotion likely pose conflicting demands, and because resources are finite, the average individual must prioritize where to allocate their resources. In *C. destructor*, most disputes are resolved by assessing chela size, and conflicts usually escalate to fights only

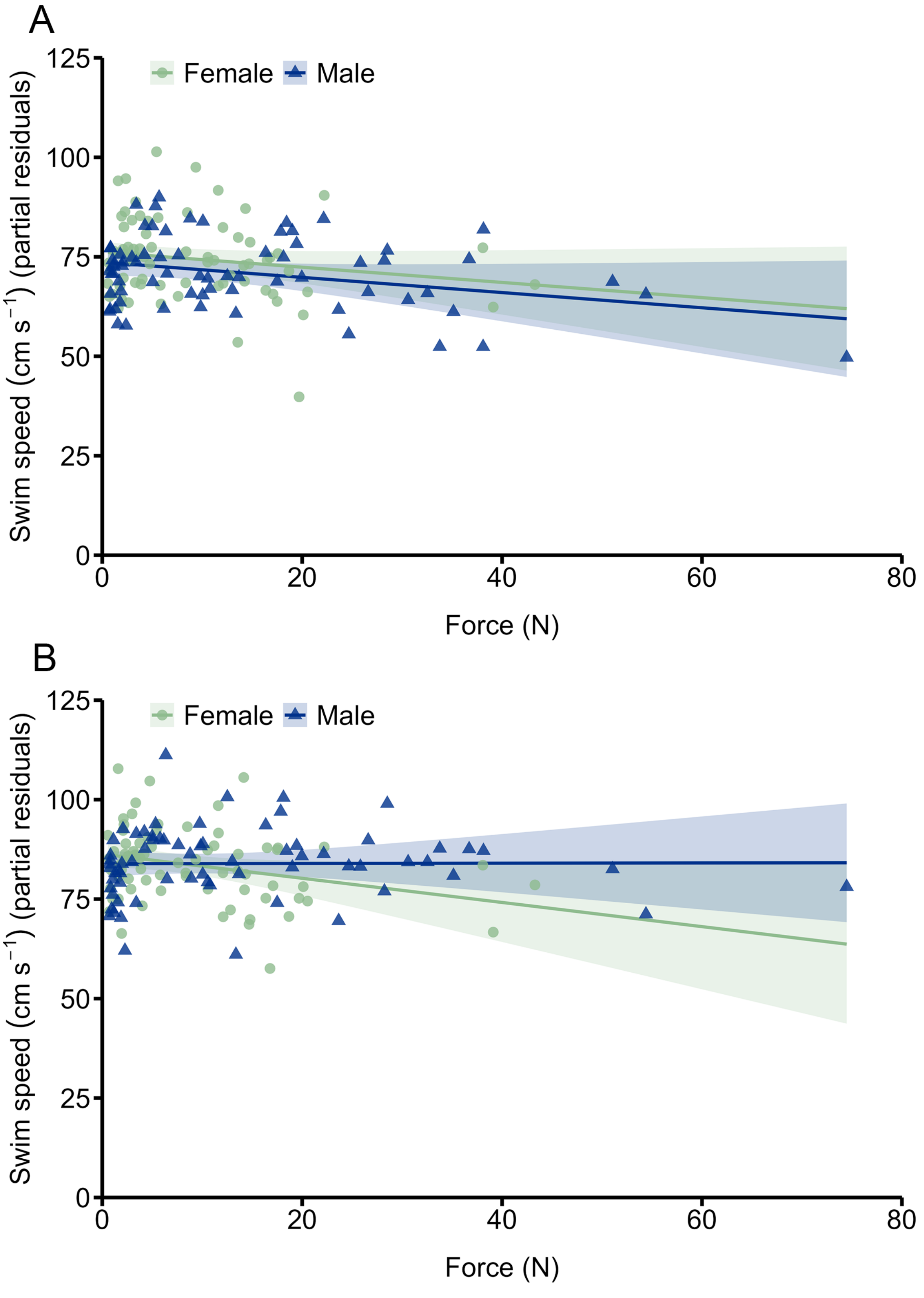

Figure 5. Relationship between chela force (N) and swimming speed (cm s^{-1}) for male and female *Cherax destructor* crayfish with intact chelae (*A*; males: $n = 71$; females: $n = 74$) and both chelae removed (*B*; males: $n = 69$; females: $n = 74$). Data points represent partial residuals, which are the adjusted measures of swimming speed that account for body length and chela size. The shaded area shows the 95% confidence intervals around the predicted means.

between individuals with a similar chela size (Walter et al. 2011). Females primarily rely on signaling to resolve disputes, which allows females who produced weak chelae for their size to acquire higher-than-expected dominance for their underlying chela strength (Walter et al. 2011). Given that female *C. destructor* crayfish can often acquire resources using unreliable chelae, our findings suggest that they could also save resources by not investing in chela muscle and instead allocating them toward their swimming performance. In contrast, males showed a steeper increase in force for any given chela size than females, although we did not assess whether this translated into greater signal reliability. *Cherax destructor* males more frequently escalate conflicts to fights, which should directly limit the benefits accrued to males who signal unreliably (Walter et al. 2011). However, our findings suggest that males who were weaker for their size, and thus possess unreliable signals of strength, were faster when both chelae were intact. Therefore, this benefit could also provide an important incentive for unreliability in *C. destructor* males, despite the higher likelihood of combat. While the threshold at which differences in strength affect the likelihood of escalation remains unknown, some crayfish may be ignorant of their own strength (Angilletta et al. 2019), which could make unreliable signaling risky. Nonetheless, our results suggest that the locomotor advantage associated with unreliability could be preferable for some individuals.

Our study shows that for *C. destructor*, visual assessments of its opponent's weapon size (signal of strength) does indeed provide information about the probable strength of its opponent (with variance) and the magnitude of the costs imposed by the weapon. However, the strength of the weapon and the magnitude of the costs imposed by investing in its strength can still be ascertained only by escalating disputes to physical contact. The escalation of disputes will then entail the inevitable risks and energetic costs of combat. The utility of unreliable signals during disputes over resources, and how the reliability of signals of strength are affected by the ecological or social environment, remains unclear. Studies of fiddler crabs suggest that the social environment may shape the magnitude of signal reliability within a population—that is, the variance in strength for any given chela size (Bywater and Wilson 2012). Males from higher-density populations of two-toned fiddler crabs (*Gelasimus vomeris*) had more reliable signals of strength than lower-density populations, presumably because their strength is more likely to be tested by opponents and they are less likely to benefit from unreliable signaling (Bywater and Wilson 2012). Future studies could experimentally test the conditions under which greater population-level signal (un)reliability will occur and how the likelihood of being tested by opponents or the risks for testing opponents will affect it. For example, crayfish could be raised in varying densities that would influence both the social and proximity costs incurred by unreliable signalers, which should in turn increase the incentives for producing more reliable signals of strength. The energetic costs from investing more in chela muscle at the expense of tail muscle should be more evident in high-density populations and differ from equivalent traits in low-density populations.

In this study, we demonstrated that producing large and reliable chelae are costly for the swimming performance of male and female *C. destructor*. By independently assessing the costs of signal size and reliability, our study provides new insights into the use of unreliable weapons. While large chelae are beneficial for crayfish when signaling their strength, our findings suggest that males and females must pay the cost to grow and display their large weapons. In addition, we demonstrated that there was a greater cost for possessing relatively stronger chelae. However, given that most disputes are resolved before fights occur, there remains an energetic incentive to produce unreliable signals of strength, which may contribute to the degree of signal reliability in a population. Manipulative studies of signal reliability—perhaps using experiments that vary the social environment—could further enhance our understanding of the trade-offs associated with signal reliability and its frequency in natural populations.

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