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Sexual dimorphism in performance and muscle allocation in the western painted crayfish *Faxonius palmeri longimanus* (Faxon, 1898) (Decapoda: Astacidea: Cambaridae)

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ABSTRACT

Multiple performance traits in animals can be affected by the same morphological feature. Armaments, or morphological weapons, and ornaments, morphological features used to attract mates, can have important influences on individual fitness. For example, ornaments of aquatic animals that improve fighting abilities or reproductive success can increase drag, resulting in decreased swimming performance. We investigated the effects of chela size on pinching force and escape performance in the western painted crayfish, *Faxonius palmeri longimanus* (Faxon, 1898). We predicted that individuals with larger chelae would swim more slowly than individuals with smaller chelae, and that males would be disproportionately affected because of male-biased sexual size dimorphism in chela size. We found support for our hypothesis that individuals with larger chelae would swim more slowly, but males and females were equally affected by large chela size, such that the differences in the scaling of chela growth did not correspond with differences in swimming performance for a given size. We also found that increased chela size in females corresponded strongly with increased strength. This was not necessarily the case for males, which exhibit three times as much variance in chela strength for a given chela size than females, potentially suggesting the use of dishonest signaling in this species. Muscle allocation differences between the sexes could also suggest that males can dishonestly signal their competitive abilities, such that weak males can have large chela. Our data support the idea of tradeoffs and lead us to further hypothesize about the roles of different life history strategies within the western painted crayfish.

Key Words: allometry, behavior, tradeoffs, weapons

INTRODUCTION

The size of morphological features can influence agonistic interactions (e.g., Sneddon *et al.*, 2000; Lailvaux *et al.*, 2005; Lappin *et al.*, 2006; Emlen, 2008) or escape ability (e.g., Losos & Sinervo, 1989; Fitzpatrick *et al.*, 2003; Domenici *et al.*, 2008), two important behaviors that affect fitness. Increasing the size of morphological features can often result in a more robust performance, whether that be fighting, fleeing, or other traits. Other performance traits, however, could be negatively affected as a result. These tradeoff scenarios have long fascinated animal ecologists because of the selective pressures that arise as conspecifics develop novel mechanisms by which to cope with these reduced capabilities.

Hydrodynamic drag on armaments or ornaments can affect motor function in aquatic habitats; therefore, relatively large features that increase fighting ability and/or reproductive success can result in decreased swimming performance (Basolo & Alcaraz, 2003; Langerhans *et al.*, 2005; Wilson *et al.*, 2009; but see Allen & Levinton, 2007; Trappett *et al.*, 2013, and Johnson *et al.*, 2014 for challenges to this). Swimming performance generally increases with body size, suggesting that the growth rate of structures underlying swimming performance (e.g., tail shape, fin size, muscle mass) is sufficient to prevent growing morphological features to result in increased drag.

Crayfishes do not necessarily follow this pattern. Chela size scales positively with body size in many crustaceans (Hartnoll,

1982), and this allometric pattern often differs between the sexes (reviewed in Mariappan *et al.*, 2000), resulting in male biased sexual size dimorphism. Wilson *et al.* (2009) suggested a functional tradeoff in male, but not female, slender crayfish (*Cherax dispar* Riek, 1951), where relative chela size was negatively correlated with swimming speed. By extension, swimming speed should be negatively correlated to body size. Such negative relationship is seemingly a result of the positive allometric relationship between chela and body size, the disproportionately fast-growing chelae create more drag that the slower-growing body cannot overcome.

Despite this apparent tradeoff, large chelae are important for many ecological functions, including mating (Stein, 1976; Snedden, 1990), anti-predator defense (Stein, 1976), and male-male competition (Stein, 1976; Snedden, 1990; Schroeder & Huber, 2001). Chela size also predicts dominance in many decapod taxa (Lee & Seed, 1991; Correa *et al.*, 2003; Wilson *et al.*, 2007). Chela size, however, is not necessarily a good predictor of chela strength (Wilson *et al.*, 2007; Lailvaux *et al.*, 2008), and consequently chela strength is not necessarily a good indicator of dominance (Wilson *et al.*, 2007) leading some to conclude that crayfishes might use dishonest signaling (Wilson *et al.*, 2007; 2009). Furthermore, some decapods, such as the lobster *Homarus americanus* H. Milne Edwards, 1837, exhibit behavioral shifts as they grow. Large individuals become less likely to retreat from threats, opting instead to mount a defensive response with their large chelae (Lang *et al.*, 1977).

Because of the importance of both chela size and escape ability, crayfishes with large chelae should have two options that either maximize fighting ability or escape performance. They could invest more in chela musculature and perform better when intrasexual conflicts escalate to fights, or they could invest more muscle in their tails to increase swimming power, overcoming the increased drag from their large chelae.

Here we examined the influence of chela size on swimming speed in the western painted crayfish, *Faxonius palmeri longimanus* (Faxon, 1898) (= *Orconectes palmeri*, see Crandall & De Grave, 2017). We also quantified muscle mass to explore the relationship between chela size and swimming speed. Is the allometric relationship of chela growth similar to that of tail growth? How does muscle allocation influence this relationship? We subsequently tested for sex-specific effects related to this tradeoff, specifically if male *F. p. longimanus* used different growth or muscle allocation strategies than females. We tested three hypotheses in the context of these questions. First, we predicted that larger crayfish will have slower swimming (retreat) speeds than smaller ones due to the scaling relationship between chela and body size. Second, we predicted that sexual dimorphism in chela size will underlie sexually dimorphic performance differences; that is, males will pinch with a greater force than females but will also swim more slowly for a given body size. Finally, we predicted that crayfish that allocate relatively more muscle to their chelae will allocate relatively less muscle to their tails, and vice versa.

MATERIALS AND METHODS

We collected 35 male (identified by the presence of modified pleiopods at the coxae of the fifth pereopods) and 28 female (identified by the presence of a large gonopore at the coxae of the third pereopods) *F. p. longimanus* from a creek in Little Rock, AR, USA during fall 2016. Crayfish were transported to the University of Central Arkansas and housed individually in 45 × 12.5 × 9 cm (l × w × h) containers with approximately 5 cm of water and two objects in which to hide (a small PVC tube and a tile placed at an angle at the back of the container) until they were dissected. We fed them twice weekly with commercially available shrimp pellets and changed enclosure water the day after feeding.

Retreat speed

To quantify retreat speed, we drew a small white dot on the carapace of individual crayfish and placed them in a 50 × 37.5 cm (l × w) container with approximately 5 cm of water placed under a heat lamp. Water temperature was maintained at ~22 °C. We gently tapped on the head of the crayfish to induce retreat. Retreat was recorded at 30 FPS using a Casio Exilim EF-X1 camera (Casio; Cover, NJ, USA) and repeated three consecutive times per individual, or until they would no longer retreat (two individuals retreated only twice).

We digitized videos to obtain position data for each trial using the simple acceleration and velocity recording application (SAVRA) (Donihue & Kazez, 2014). The scaled position data were smoothed using the mean square error (MSE) quantile spline in the assist package (Ke & Wang, 2002) in R (version 3.4.0; R Core Team, 2017). The maximal instantaneous velocity attained during each trial (from the three runs) was calculated from the fitted splines.

Chela strength

Using a custom-built force transducer, we quantified chela strength by having crayfish pinch two metal plates connected to a load cell feeding into an amplifier unit. This unit was connected to a multimeter and displays DC voltage in direct proportion to force (in newtons, N). We alternated between right and left chela and took three measurements per side. Maximum force was recorded for each chela. Six crayfish (two males, four females) would not perform and were excluded from force analyses.

Morphology

We measured wet mass of each crayfish using an analytical balance (± 0.1 mg) and measured carapace length from the tip of the rostrum to the middle of the posterior edge of the carapace, tail length from the second abdominal somite to the end of the telson (we chose the second somite because the first somite is covered partially by the carapace), tail width at the second abdominal somite, left and right chela length from the carpal joint to the end of the pollex, left and right chela width, left and right chela depth, and left and right dactyl length from the dactyl joint to the dactyl tip (Fig. 1) using digital calipers (± 0.01 mm), following Weagle & Ozburn (1970). An additional 17 males and 27 females *F. p. longimanus* from the collection at the University of Central Arkansas were included for these measurements, excluding mass. Nine out of the 107 total crayfish we measured (8.4%) were missing one claw. Although this asymmetry could influence some interpretations, the relatively small number of incomplete individuals should only have a marginal effect, and therefore we did not remove these individuals from our dataset.

To test for underlying phenotypes determining retreat speed and chela strength, we euthanized crayfish and removed and weighed (± 0.1 mg, wet mass) the abdominal flexor muscle from the tail and the left and right cheliped closer muscles from the palm of the chelae.

Statistical analyses

All statistical analyses were performed using R (R Core Team, 2017). Statistical significance was determined at $P < 0.05$. We used the entire data set ($N = 107$) for analyses of external morphological features. If performance, body mass, or muscle mass was included, the data set was reduced and excluded preserved specimens ($N = 63$; $N = 57$ for force data). All individual chela and tail measurements were highly correlated within individuals, so chela and tail variables were reduced to one variable each using principal components analysis (PCA). Because not

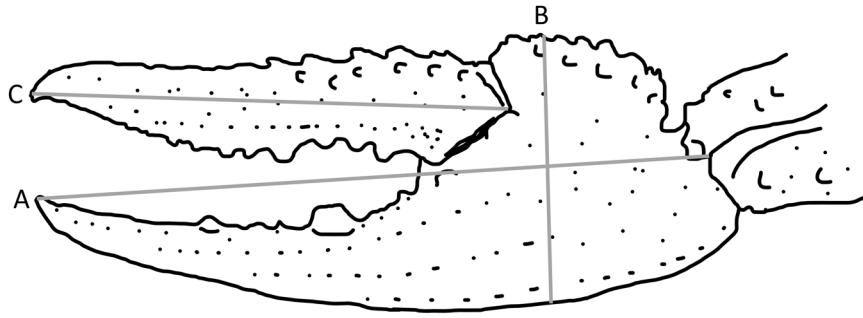


Figure 1. Line drawing of a claw of *Faxonius palmeri longimanus*, illustrating measurements for claw length (A), claw depth (B), and dactyl length (C).

Table 1. Mean body and performance characteristics with 1 SD in parentheses. AF, abdominal flexor; CC, cheliped closer.

	Carapace length (mm)	Mass (g)	Tail length (mm)	Tail width (mm)	Chela length (mm)	Chela width (mm)	Chela depth (mm)	Dactyl length (mm)	Retreat speed (m/s)	AF muscle mass (g)	Chela force (N)	CC muscle mass (g)
Overall	22.8 (0.27)	4.5 (0.13)	22.5 (0.27)	10.1 (0.14)	17.7 (0.40)	7.4 (0.18)	4.4 (0.10)	10.6 (0.24)	0.71 (0.01)	0.41 (0.01)	5.7 (0.29)	0.08 (0.01)
Male	22.9 (0.39)	4.6 (0.18)	22.2 (0.33)	9.6 (0.16)	19.3 (0.60)	8.0 (0.27)	4.8 (0.15)	11.6 (0.37)	0.69 (0.01)	0.39 (0.01)	5.7 (0.39)	0.10 (0.01)
Female	22.8 (0.38)	4.3 (0.20)	22.7 (0.42)	10.5 (0.23)	16.2 (0.45)	6.7 (0.22)	4.0 (0.12)	9.6 (0.27)	0.74 (0.01)	0.42 (0.01)	5.7 (0.43)	0.06 (0.01)

every crayfish had both chelae (nine individuals were missing one claw) and chela measurements did not differ between left and right sides (t-test, all $P > 0.24$), for each individual we used average chela length, width, and depth, and average dactyl length in the PCA. The first PC axis (PC1) accounted for more than 97% of variation in chela variables and more than 94% in tail variables among individuals. The first PC-axis for each structure will hereafter be referred to as “chela size” and “tail size,” respectively.

We tested for differences between sexes in both absolute (ANOVA) and size-corrected (ANCOVA) morphological and performance variables. We also performed multiple regression to assess the morphological features that influence maximum retreat speed. Our fully saturated model included chela size, tail size, abdominal flexor muscle mass, and carapace length. We compared all possible models containing these predictors using AIC (Burnham & Anderson, 2003) to identify the model accounting for the most variation in retreat speed.

To test for allometric differences between the sexes that could explain any observed relationships, we \log_{10} -transformed the morphological variables and used the lmodel2 function in the lmodel2 package (Legendre, 2014) to calculate ordinary least squares (OLS) regression (Kilmer & Rodríguez, 2017). Although OLS slopes can simply be calculated as the slope from a linear regression including \log_{10} -transformed variables, the lmodel2 package reports 95% CIs which are useful when assessing relationships that may be close to isometric. Because PC scores include negative values, they cannot be \log_{10} -transformed. We therefore used \log_{10} -transformed mean chela length and tail length for allometric analyses. We feel confident that these measurements are representative of chela and tail size, respectively, because of their strong correlations with the other associated morphological variables.

We used ANCOVA to test for differences between the sexes in the pattern of muscle allocation to chelae and tails. In this analysis, we used the residuals of the regression of tail flexor muscle mass on carapace length as the dependent variable, residuals of the regression of cheliped closer-muscle mass on carapace length as the covariate, and sex as the independent variable. A significant interaction term would indicate a difference between the sexes in the pattern of muscle allocation. Results were virtually identical when the dependent variable and covariate were switched.

RESULTS

Morphology

Although male and female *F. p. longimanus* did not differ in body size ($F_{1,105} = 0.077$, $P = 0.78$; carapace length range for males and females, respectively: 16.56–29.71 mm; 17.46–29.22 mm), both sexes exhibited some sex-specific patterns of morphological variation. Absolute chela size was significantly larger in males than in females ($F_{1,105} = 17.96$, $P < 0.001$; Table 1). This pattern was maintained when accounting for variation in carapace length ($F_{1,103} = 75.667$, $P < 0.001$); however, the scaling of chela size with carapace length also differed between the sexes (interaction term; $F_{1,103} = 7.696$, $P = 0.007$; Fig. 2A). The difference in chela size between the sexes increased as carapace length increased. Chela size was a strong predictor of cheliped closer-muscle mass across all samples ($r^2 = 0.86$, $P < 0.001$) and within each sex independently (males, $r^2 = 0.84$; females, $r^2 = 0.86$). Absolute cheliped closer-muscle mass differed significantly between the sexes ($F_{1,61} = 10.53$, $P = 0.002$). The significant sex effect was eliminated after accounting for variation in chela size ($F_{1,59} = 0.499$, $P = 0.483$), but male and female cheliped closer-muscle mass increased with chela size at different rates ($F_{1,59} = 4.992$, $P = 0.029$; Fig. 2B).

Although females did not have absolutely larger tails than males ($F_{1,105} = 2.24$, $P = 0.14$), they did have larger tails after accounting for carapace length ($F_{1,103} = 13.21$, $P < 0.001$). There was, however, a significant sex*carapace length interaction term ($F_{1,103} = 9.130$, $P = 0.003$). Female tail size increased with carapace length at a faster rate than in males. Absolute abdominal flexor muscle mass in the tail did not differ significantly between the sexes ($F_{1,61} = 1.29$, $P = 0.26$) nor after accounting for tail size ($F_{1,59} = 0.362$, $P = 0.550$). Tail size was a significant predictor of abdominal flexor muscle mass ($F_{1,59} = 56.376$, $P < 0.001$), but there was no significant sex*tail size interaction ($F_{1,59} = 0.296$, $P = 0.589$) unlike in the chelae.

Performance

Males did not differ from females in chela closing force on an absolute scale ($F_{1,55} = 0.00$, $P = 0.98$), nor when accounting for chela size (ANCOVA; $F_{1,53} = 1.929$, $P = 0.171$). Maximum chela force significantly increased with chela size ($F_{1,53} = 19.049$, $P < 0.001$), with no significant sex*chela size interaction ($F_{1,53} = 2.763$, $P = 0.102$). Maximum chela force also increased with cheliped

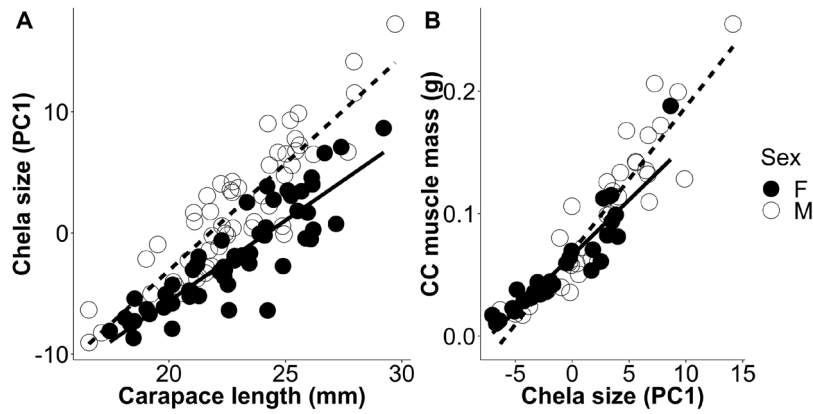


Figure 2. Relationship between carapace length and chela size (A). Males (dashed line) grow larger chelae faster than females (solid line). Relationship between chela size and muscle mass (B). Males (dashed line) increase muscle size for a given chela size faster than females (solid line). CC, cheliped closer.

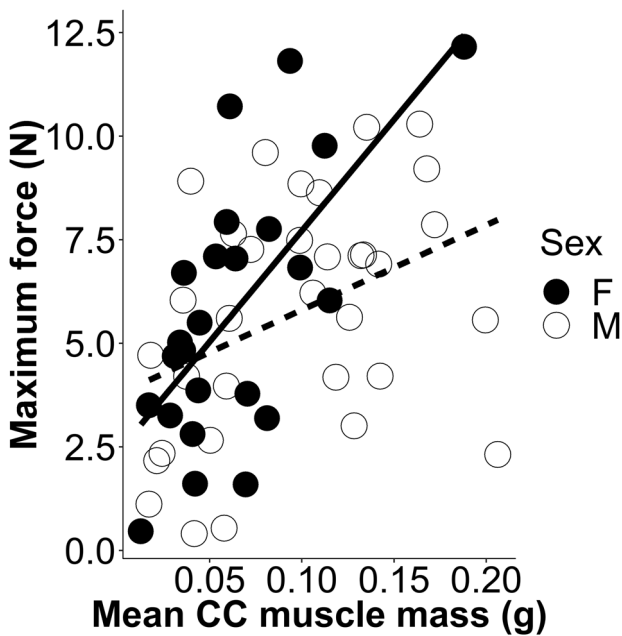


Figure 3. Relationship between cheliped closer-muscle mass and chela force. Female (solid line) muscle mass is a stronger predictor ($R^2 = 0.43$) than male muscle mass (dashed line; $R^2 = 0.15$).

closer-muscle mass ($F_{1,53} = 15.016$, $P < 0.001$) with a significant sex*closer-muscle mass interaction ($F_{1,53} = 4.216$, $P = 0.045$; Fig. 3). Chela closing force increased with cheliped closer-muscle mass in females at a faster rate than in males. Furthermore, female muscle mass predicted chela force almost three times as well as male muscle mass (female: $r^2 = 0.43$; male: $r^2 = 0.15$).

Females tended to swim faster than males on an absolute scale ($F_{1,61} = 3.55$, $P = 0.064$). Retreat speed significantly decreased with body size ($F_{1,59} = 8.826$, $P = 0.004$) and females swam significantly faster than males when accounting for carapace length ($F_{1,59} = 4.578$, $P = 0.037$). There was no significant sex*carapace length interaction ($F_{1,59} = 0.059$, $P = 0.809$). There was a negative relationship between chela size and retreat speed ($r^2 = 0.32$, $P < 0.001$). When accounting for carapace length in a multiple regression, chela size was the only significant predictor of retreat speed (carapace length, $t = 1.168$, $P = 0.247$, partial regression coefficient ($\hat{\gamma}$) = 0.15; chela size, $t = -4.352$, $P < 0.001$, $r = -0.49$). Males and females did not differ significantly in retreat speed when accounting for variation in chela size ($F_{1,59} = 0.040$,

Table 2. Comparison of models predicting retreat speed from morphological traits; CL, carapace length; CS, chela size; TS, tail size; AF, abdominal flexor muscle mass. The model with the lowest AIC and the most parsimonious model are bolded.

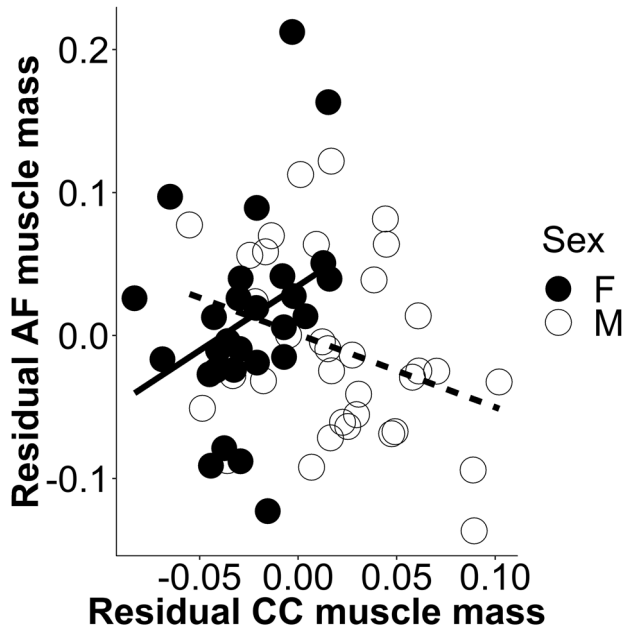
Model predictors	AIC	Δ AIC
CS + AF	-127.080	0.000
CS	-127.035	0.045
CL + CS	-126.451	0.628
CS + TS	-125.317	1.763
CS + TS + AF	-125.254	1.825
CL + CS + AF	-125.181	1.898
CL + CS + TS	-124.531	2.549
CL + CS + TS + AF	-123.524	3.556
CL + AF	-112.176	14.903
CL + TS + AF	-111.203	15.876
CL	-111.166	15.914
CL + TS	-109.362	17.718
TS	-109.319	17.761
TS + AF	-108.784	18.296
AF	-103.782	23.298

$P = 0.843$), nor was there a significant sex*chela size interaction effect ($F_{1,59} = 0.348$, $P = 0.557$) on retreat speed. Absolute tail size was weakly (and positively) correlated with retreat speed ($r^2 = 0.096$, $P = 0.014$). This relationship, however, was eliminated when accounting for variation in carapace length in a multiple regression ($t = 0.432$, $P = 0.667$). Females had faster retreat speeds than males when accounting for variation in tail size ($F_{1,59} = 5.432$, $P = 0.023$). This did not correspond with a significant effect of abdominal flexor muscle mass on retreat speed (absolute: $r^2 = 0.013$, $P = 0.381$; accounting for carapace length: $t = 1.714$, $P = 0.092$). Again, there was no significant sex*muscle mass interaction ($P > 0.31$ for both). The regression model accounting for the most variation in retreat speed included chela size and abdominal flexor muscle mass (lowest AIC); however, this model differed in AIC score from one containing only chela size by 0.045. Four other models had Δ AIC values less than 2, but all included chela size (Table 2). The most parsimonious model (i.e., fewest estimated parameters) includes only chela size.

Both chela size ($b_{OLS} = 1.55$) and mass of the cheliped closer muscle ($b_{OLS} = 4.94$) scaled positively with carapace length regardless of sex. On average, male chela size ($b_{OLS} = 1.63$) increased faster with carapace length than female chela size ($b_{OLS} = 1.43$), although there was overlap in the 95% CIs (Table 3). Relationships

Table 3. Slope values between \log_{10} -transformed characteristics when regressed against \log_{10} -transformed body size (carapace length). 95% CI indicated in brackets. Symbol in parentheses adjacent to the upper CI indicates allometric relationship (i – isometric, + – positive allometry, – – negative allometry).

	Overall	Male	Female
Body mass	2.70 [2.37 – 3.03] (i)	2.54 [2.18 – 2.90] (–)	2.99 [2.44 – 3.53] (i)
Chela size	1.55 [1.35 – 1.75] (+)	1.63 [1.41 – 1.86] (+)	1.43 [1.21 – 1.65] (+)
Cheliped closer muscle mass	4.94 [3.67 – 6.22] (+)	4.98 [3.48 – 6.47] (+)	5.23 [3.63 – 6.84] (+)
Tail size	0.83 [0.72 – 0.94] (–)	0.70 [0.56 – 0.85] (–)	0.96 [0.80 – 1.11] (i)
Abdominal flexor muscle mass	1.59 [1.21 – 1.97] (–)	1.44 [0.91 – 1.96] (–)	1.77 [1.20 – 2.34] (–)

**Figure 4.** Relationship between residual cheliped closer and residual abdominal flexor muscle mass. Solid regression line represents females, dashed regression line represents males.

between tail size and carapace length differed between sexes; tail size scaled negatively with body size in the overall data set ($b_{OLS} = 0.83$) and for males ($b_{OLS} = 0.70$) but was isometric for females ($b_{OLS} = 0.96$). Abdominal flexor muscle mass ($b_{OLS} = 1.59$) overall scaled negatively with carapace length. This relationship did not differ between the sexes.

Muscle allocation tradeoff

We used ANCOVA to test for a tradeoff in allocation between chela and tail muscle. There was a significant interaction term between sex and cheliped closer-muscle mass ($F_{1,59} = 6.040$, $P = 0.017$). The relationship between relative muscle masses was generally negative for males ($r = -0.31$, $P = 0.065$) and was in a positive direction for females ($r = 0.32$, $P = 0.101$; Fig. 4).

DISCUSSION

We found support for our first hypothesis that larger crayfish would swim more slowly than smaller crayfish. Both sexes exhibit a positive allometric relationship between chela and body size with males having, on average, a steeper slope (though the 95% CI overlap; Table 3), which explains the male-biased sexual dimorphism in chela size. Variation in chela size accounted for the most variance in retreat speed and was the only consistent predictor of retreat speed in regression models. Both sexes were surprisingly similarly affected by increased chela size despite males having

relatively larger chelae; we did not detect a sex-specific functional tradeoff between chela size and retreat speed, as observed in *Chelax dispar* (Wilson *et al.*, 2009). The degree of sexual dimorphism between these two species likely explains this difference. Male *C. dispar* are much larger in both body length and chela size than females (fig. 1 in Wilson *et al.*, 2009) whereas carapace length and chela size are much more similar between adult male and female *F. p. longimanus* (Table 1).

Consistent with our second hypothesis, females had faster retreat speeds than males when controlling for body size. Although females have relatively larger tails than males, it appears that females swam faster than males solely because of their smaller chelae. Tail size was only included in competitive regression models when paired with chela size (Table 2). It is noteworthy that males and females differ in the allometric growth of their tails. Female tail growth is isometric to body size, whereas male tail growth scales negatively. Such condition could represent a behavioral shift in males away from escape to aggressive or defensive behaviors as they grow, which has been observed in many taxa, including insects (Hopkins *et al.*, 2011), lizards (de Barros *et al.*, 2010), and other decapods (Kranse & Wine, 1975; Lang *et al.*, 1977). Escape behavior in the lobster *H. americanus* decreases as individuals age and this corresponds with the emergence of a decreased tail growth rate (the pattern of tail growth begins to exhibit negative allometry; Lang *et al.*, 1977). In another crayfish, *Procambarus clarkia* (Girard, 1852), further, larger individuals took longer to escape, instead opting for a defensive posture (Kranse & Wine, 1975). In other species, however, adults become more likely to flee than juveniles as in the snake *Coluber constrictor* (Creer, 2005) and the gecko *Eublepharis macularius* (Landová *et al.*, 2013).

For female *F. p. longimanus*, however, the maintenance of isometric tail growth throughout ontogeny could be ecologically important as females become large. Large females are generally more fecund than smaller females (Van Deventer, 1937). While having more offspring increases the likelihood that some offspring will survive, there are locomotor costs to bearing offspring (Seigel *et al.* 1987; Lee *et al.*, 1996; Miles *et al.* 2000; Plaut 2002). Because female crayfish carry eggs on their tails, larger females would have an increased weight load that they would have to overcome when retreating. By allocating more resources to tail muscle growth, females can overcome the burden of carrying around developing offspring by retaining the ability to retreat from danger.

Contrary to our prediction, male chelae were not stronger than female chelae. Chela size was a significant predictor of cheliped closer-muscle mass and chela force, but only chela size and cheliped closer-muscle mass differed between the sexes. There are two likely explanations the absence of a sex effect on chela strength: motivational differences between individuals and sexes or differences in muscle composition or quality.

Motivation can be difficult to assess but can influence results and data interpretations (Losos *et al.*, 2002). But performance measurements, despite this apparent problem, are important in assessing the ecological relevance of morphology (Anderson *et al.*, 2008). It seems unlikely, however, that motivational differences substantially influenced our results. During trials, we used specific criteria of crayfish behavior when pinching the force transducer

(Was the chela securely on the transducer? Did the crayfish lock its arm?) to assess the likelihood of a given pinch being representative of ability. The mean force produced by each sex was also identical; removing a few individuals that may have performed sub-optimally would likely not have shifted the mean enough in either direction to result in a significant sex effect on chela force. We are therefore confident that the measurements of force presented in this study were representative of the performance ability of *F. p. longimanus*.

Differences in muscle composition or quality (Hájek *et al.*, 1973) are more probably answers. There are several muscle characteristics that have been shown to differ between the sexes, which manifest as functional adaptations. For example, the forelimb muscles of male and female bullfrog (*Rana catesbeiana* (Shaw, 1802)) do not differ in relative tetanic force, but male muscles have higher endurance than female muscles, which help them to amplex females for extended periods (Peters & Aulner, 2000). Males of the crayfish *Cherax dispar* exhibit higher variation in their chela force than females (Wilson *et al.*, 2009), which is similar to what we observed in *F. p. longimanus*. Previous work has shown that in *C. dispar* force production of chela muscle differs between the sexes, such that isolated muscle from females produces twice as much force as male muscles (Wilson *et al.*, 2007). Enhanced force production from female muscle could therefore make up for the reduction in muscle mass observed in female chelae in *F. p. longimanus*, though additional experiments are necessary to test this hypothesis.

The functional similarity of chelae in males and females in *F. p. longimanus* likely indicates that selective pressures are similar between the sexes. Sexually antagonistic selection would result in stark dimorphism if different traits were favored. Although we see morphological dimorphism, the lack of performance dimorphism suggests that selection on performance is similar between males and females. Males, which assess conspecific male quality using relative chela size (Snedden, 1990), would be under selection to grow larger chelae, which would help establish dominance and access to females (Stein, 1976; Snedden, 1990), but not necessarily stronger chelae if escalation beyond stereotyped displays is uncommon. This could result in dishonest male signaling; the extreme variation in male chela strength suggests this is the case (Wilson *et al.*, 2007, 2009) while the lack of variation in female strength would indicate their chelae are an honest indicator of ability (Bywater *et al.*, 2008).

Males that allocated relatively less muscle to their chelae allocated relatively more muscle to their tails. Females exhibit the opposite pattern; those that allocate relatively more muscle to their chelae tend to also allocate relatively more muscle to their tails (Fig. 4). These data further support the hypothesis of dishonest signaling in males but honest signaling in females. Males that grow large but weak chelae would need more muscle mass in their tails to overcome the increased drag attributed to their large chelae. But males that grow large and strong chelae could be economical by not investing in tail musculature and retreat speed, opting instead for fighting power over escape ability.

Male and female *F. p. longimanus* both pay a functional cost for growing large chelae. As their chelae grow disproportionately large throughout ontogeny, features underlying swimming performance (tail size and musculature) are outpaced and therefore swimming performance is affected. It remains unknown whether this relationship is caused by drag or another variable. Females, on average, pay a lower cost than males because they possess smaller chelae. These chelae, however, potentially contain high quality muscle such that the size of their chelae is an accurate representation of their strength. This is not necessarily true in males, which may use dishonest signaling. The idea of dishonesty is further supported by intrasexual differences in muscle allocation, such that males that have relatively little chela muscle have more muscle in their tail than expected for their body size. Different life history strategies within the western painted crayfish could explain the

persistence of variation within this species and highlight different mechanisms by which individuals can overcome a functional tradeoff.

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