

Costs of bearing a sexually selected ornamental weapon in a fiddler crab

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Summary

1. Sexually selected structures with dual function of combat and display are likely to be honest signals of male quality to opponents and mates, but should be costly to produce and maintain.
2. Male fiddler crabs use a single greatly enlarged claw as both a weapon in agonistic contests with other males and an ornament to attract females for mating. Given the extreme size of this structure (up to half the total body mass), there is surprisingly little evidence for costs as predicted by theory.
3. We experimentally investigated several potential costs of the large claw to male sand fiddler crabs *Uca pugilator*. Mass-specific metabolic rates were significantly higher and treadmill endurance capacity significantly lower for males bearing an intact major claw compared with those without.
4. In contrast, presence of the claw did not affect maximal sprint speeds, suggesting that the massive structure does not compromise the ability of male crabs to evade predators. These counterintuitive results conform to recent theoretical models of energy costs of locomotion.
5. Our study provides empirical support for a key assumption of sexual selection theory – energetic and endurance-related locomotor costs incurred while bearing this ornamental weapon act in opposition to sexual selection favouring larger claws.

Key-words: armament, ornament, energetic constraint, locomotor performance, *Uca pugilator*

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Introduction

Darwin's (1871) theory of sexual selection posits that the expression of extravagant morphological characters or behavioural displays leads to differential reproductive success among individuals, mediated through competition for mates (Andersson 1994). A central premise of most models of sexual selection is that reproductive benefits of further trait exaggeration are eventually balanced by costs to fitness such as increased susceptibility to predators and parasites or reduced growth rate and energy storage (Kirkpatrick 1987; Andersson 1994; Zuk & Kolluru 1998). As a consequence, sexually selected ornaments, weapons and displays are expected to function as reliable signals of male quality to potential opponents and choosy females (Grafen 1990; Johnstone 1995; Berglund, Bisazza & Pilastro 1996). Unlike facultative traits expressed only sporadically, more permanent morphological structures may be metabolically

or biomechanically costly in a variety of contexts, both reproductive and routine. For example, large antlers of moose are effective weapons in male–male competition but are energetically expensive to bear and limit foraging effectiveness (Solberg & Saether 1993; Moen, Pastor & Cohen 1999). Similarly, elongated caudal fins of male swordtail fishes are attractive to females but impose hydrodynamic costs that significantly increase metabolic rates during courtship and general swimming (Basolo & Alcaraz 2003).

Fiddler crabs of the genus *Uca* are model organisms for testing theories of sexual selection; they provide one of the most extreme examples of sexual dimorphism in the animal kingdom and their mating system involves both competition among males and female choice. Whereas female crabs have two small claws used for feeding, males have one small feeding claw and one greatly enlarged major claw that can comprise nearly half the total body mass in some species (Crane 1975). Males use the major claw as a weapon in agonistic contests with other males for control of breeding burrows in preferred locations and wave it in species-specific displays to attract receptive females for mating

(Crane 1975; Christy 1982, 1983; Pope 2000). This structure is sufficiently massive that to provide extra support lateral-waving species have enlarged legs and carapace on whichever side of the body the major claw is located (Takeda & Murai 1993). Fitness benefits accruing to large males with relatively large claws are well documented; such males win more contests, display with greater vigour and are attractive to females (Hyatt & Salmon 1978; Christy 1983; Jennions & Backwell 1998; Pratt & McLain 2002; Pratt, McLain & Lathrop 2003). In contrast, there is far less evidence for predicted costs of the claw. This is particularly surprising given its extreme size and positive allometric growth throughout much of life.

Among other taxa, some of the clearest examples of natural selection opposing sexual selection are male displays that attract predators in addition to prospective mates. Larger and more brightly coloured male guppies are preferred by females but survive poorly in the presence of piscivorous fish (Reznick & Endler 1982; Endler & Houde 1995). Reproductively active male frogs vocalize in conspicuous choruses to attract females but multiple predators respond as well, imposing counter-selection on call frequency and volume (Ryan 1985). Putative costs relating to the predation risk of bearing a conspicuous major claw have been reasonably well studied for Fiddler Crabs. From a human perspective, males are easier to detect visually and might therefore be at higher risk from other visual predators (Jordão & Oliveira 2001a). Contrary to this expectation, large male fiddler crabs commonly exhibit enhanced survival relative to juveniles or females (Bildstein, McDowell & Brisbin 1989; Backwell, O'Hara & Christy 1998; Iribarne & Martinez 1999; Johnson 2003; but see Koga *et al.* 2001). Presence of the major claw may deter many potential predators due to increased handling time (Bildstein *et al.* 1989; Iribarne & Martinez 1999).

There is better evidence for a foraging cost borne by male *Uca*. Fiddler crabs scoop sediment into their mouths with the single small claw if male, and both claws if female, where specialized mouthparts scour algae, bacteria and detritus from the mud or sand (Miller 1961). Male *Uca pugnax* compensate partially for the lack of a second feeding claw by increasing their feeding rate and overall foraging time, but they can never gain energy as quickly as females (Weissburg 1992, 1993). To compound the problem, metabolic rates of male crabs in air are almost 17% higher than for females of similar mass, presumably because the presence of the major claw increases the proportion of striated muscle tissue in males relative to females (Weissburg 1993; Levinton & Judge 1993). Fiddler crabs that have lost their major claw can grow a new one, but regeneration may take place at the expense of general body growth (Hopkins 1982) and Backwell *et al.* (2000) found regenerated major claws of male *Uca annulipes* to be of lesser mass than equivalent-length original claws. These observations suggest that producing the major claw represents a significant developmental cost to male fiddler crabs.

Here we experimentally investigate several other potential costs of the major claw to male sand fiddler crabs *Uca pugilator* (Bosc). Fiddler crabs are ideal for investigating the effects of such a trait on individual performance because they can be induced to autotomize (cast off) their major claw without apparent harm, allowing us to compare individuals that differ only in the presence or absence of this sexually selected feature. We ask whether presence of the claw affects metabolic rate or two components of locomotor performance – endurance capacity and maximum sprint speed. Metabolism and endurance represent indirect physiological costs related to increased energy expenditure while sprint speed represents a possible direct cost of increased predation risk.

Methods

We collected surface-active male *U. pugilator* from Flax Pond, a *Spartina alterniflora* salt marsh located on the northern shore of Long Island, New York, USA (40°58'N, 73°08'W), in the summers of 2001–03. Prior to experimentation, crabs were held in the laboratory at 20 °C in large aquaria with re-circulating seawater and fed TetraMarine invertebrate food *ad libitum*. We used adult crabs similar in size to those displaying in the breeding areas of the marsh (mean carapace width \pm SD = 18.95 \pm 1.37 mm; n = 232). For each crab, we measured mass to the nearest 0.01 g with a Sartorius 2205 balance, carapace width to the nearest 0.01 mm with digital calipers, and volume to the nearest 0.1 mL by water displacement.

METABOLIC COSTS: AERIAL AND AQUATIC RESPIRATION

We induced crabs to autotomize their claw immediately after capture and held them without food for 48 h prior to experimentation. We estimated metabolic rates of male *U. pugilator* with and without a major claw in air and seawater as O₂ depletion in closed systems. Aerial respiration was measured with an Ametek S-3A oxygen analyser. Crabs (n = 40 with claw, n = 38 without claw) were placed in separate Lucite chambers (4.7 cm diameter, 4 cm height, 55 mL internal volume) containing 5 mL of filtered seawater and kept in a constant temperature water bath of 20 °C. We allowed individuals to acclimate for 1 h while air was pumped continuously through the system before sampling the ambient air and closing the valves. Air inside each chamber was resampled after exactly 1 h. Oxygen depletion was determined by multiplying the per cent change in O₂ during the experimental period by the chamber volume (adjusted by subtracting the volume of the added seawater and crab).

We measured respiration of crabs in seawater with a Strathkelvin 949 dissolved oxygen measuring system (comprising a 1302 microcathode oxygen electrode, associated 781 oxygen meter and analysis software). Crabs (n = 26 with claw, n = 23 without claw) were placed

individually in a RC400 acrylic respiration chamber (11.5 cm diameter, 10.5 cm height, 730 mL internal volume) in a constant temperature water bath of 20 °C. The water inside the chamber was stirred with a magnetic spinbar to homogenize the distribution of dissolved O₂; the chamber floor was perforated to permit water flow while providing the crabs a stable platform upon which to stand. Crabs were allowed to acclimate for 30 min in filtered and sterile air-saturated seawater before the chamber was sealed. Dissolved O₂ concentration in the chamber was recorded continuously for the following 15 min. We determined O₂ depletion by calculating the change in O₂ during the experimental period from the recorded trace, multiplied by the adjusted chamber volume (preliminary measurements showed that increasing the length of experimental periods did not alter estimates of O₂ consumption). In both experiments, changes in O₂ concentration in chambers with no crab served as a control.

LOCOMOTOR PERFORMANCE: ENDURANCE CAPACITY

We exercised individual crabs on a motorized treadmill (Pro-Form 285T modified with a Dayton 4Z861 10 : 1 speed reducer) at a velocity of 4 m min⁻¹ (0.24 km h⁻¹) in two separate experiments. This velocity represents the mid-range of *U. pugilator* running speeds studied by Full & Herreid (1984) (0.06–0.40 km h⁻¹), and is just above a performance threshold for male crabs. Individuals running at this speed or higher lose stamina much faster than crabs running at slower velocities. After a 10-min acclimation period on the treadmill at 25 °C crabs were run to fatigue. Following the protocol of Full & Herreid (1984), we defined fatigue as the time when a crab did not maintain pace with the treadmill, dragged its abdomen and did not respond to prodding. A few crabs ran for longer than 90 min; these trials ended before a failure event was recorded and the ultimate fate of the crab beyond the assay interval was therefore unknown (i.e. right-censored data; Allison 1995).

Treatments in the first endurance experiment consisted of similarly sized males: (1) with their major claw intact (control; $n = 20$); (2) with no major claw but mass equivalent to the missing structure added to the mid-dorsal carapace ($n = 15$); and (3) with no major claw or added weight ($n = 15$). We added appropriate mass to each crab by attaching a small metal washer to their carapace with cyanoacrylate glue. In the second endurance experiment all crabs ($n = 15$) had their major claw intact. Treatments consisted of: (1) weight added to the crabs' carapace; (2) weight added to their claw; and (3) no weight added (control). Over a 3-day period, each crab was exercised under all treatment conditions (one trial per day). Treatments were randomly assigned to crabs; each individual was represented only once per treatment and treatments

were equally represented on each day. In this experiment metal washers were attached to each crab's carapace or claw using Velcro patches such that the combined mass of the washer and patches was equal to 30% of the individual's body mass. This arrangement allowed for weights to be easily added or removed depending on the daily assigned treatment. Thirty per cent was arbitrarily chosen to represent the additional load carried by a crab having two major claws – rare for *Uca*, but possible (authors' personal observations). The large claw comprised $30.2 \pm 1.9\%$ (mean \pm SD) of the total body mass of fiddler crabs in this study.

LOCOMOTOR PERFORMANCE: MAXIMUM SPRINT SPEED

We determined the sprint speed of male *U. pugilator* with and without a major claw, and with and without added weight by running marked individuals in a straight raceway at 25 °C. The wooden raceway measured 1.80 m long \times 0.20 m wide \times 0.24 m high and had a running surface of packed sand. Autotomization of the major claw was induced immediately following capture and all crabs were allowed to recover for 48 h prior to experimentation. Treatments consisted of crabs ($n = 10$ per treatment) with: (1) an intact major claw; (2) no major claw; (3) an intact major claw and weight equivalent to 30% of their body mass added to their carapace (using washers and cyanoacrylate glue as described above); and (4) no major claw but added weight. We released individual crabs at one end of the track and chased them to the other end. Each crab was subjected to four trials, with approximately 1 h between each run. Crabs from different treatment groups were distributed randomly during each set of trials. Trials were recorded from above with a digital video camera (Canon GL1, recording at 30 frames s⁻¹) and crab running velocities calculated as the time required to cover a marked distance. We used the single fastest trial to estimate maximum running speed for each individual in our analysis.

STATISTICAL ANALYSES

We compared aerial and aquatic respiration of crabs with and without a major claw with analyses of covariance (ANCOVA) using body mass as the covariate. Data were transformed using a $\ln(x)$ function to control for unequal variances and non-normality and we tested the assumption of homogeneity of slopes. Differences in times to fatigue among crabs in the treadmill endurance experiments were evaluated with failure-time statistics that can incorporate censored data (PROC LIFETEST; SAS 2004). Endurance functions were compared using Wilcoxon's signed ranks test followed by pairwise multiple comparisons to determine specific differences between treatment groups (Allison 1995). Significance levels were corrected with the sequential Bonferroni technique using an experiment-

wise error rate of $\alpha = 0.05$ (Dunn–Sidak method; Sokal & Rohlf 1995). Mean time to fatigue in the second endurance experiment was also analysed with repeated measures analysis of variance (RM-ANOVA) on $\ln(x)$ -transformed data, followed by planned orthogonal contrasts. Failure time statistics are not explicitly designed for repeated measures analyses and the lack of censored data in this experiment means that assumptions of ANOVA are more likely met than in the first endurance experiment. We compared differences in maximum sprint speed with two-way ANOVA with presence of the claw and added weight as fixed factors. All analyses were done with SAS 9.0.

Results

METABOLIC COSTS: AERIAL AND AQUATIC RESPIRATION

In both air and water, total O_2 consumption increased significantly with mass for crabs with and without a major claw (air: $F_{1,75} = 351.03$, $P < 0.001$; water: $F_{1,46} = 91.55$, $P < 0.001$; Fig. 1a,b). Regression coefficients

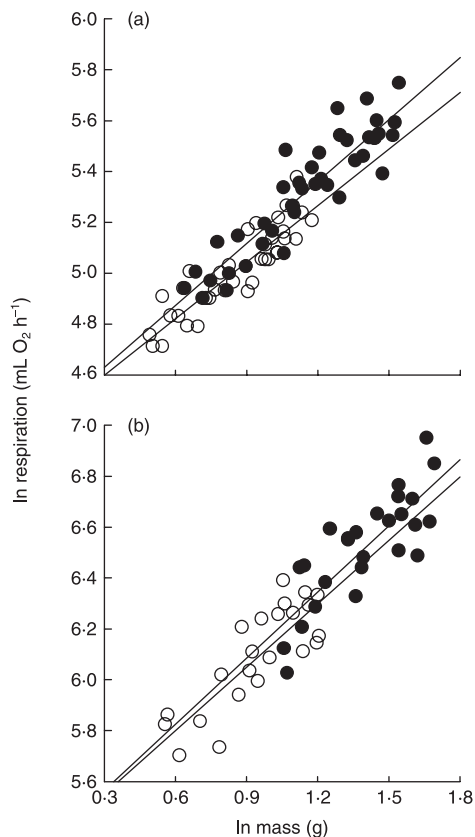


Fig. 1. Allometry of O_2 consumption rates of male fiddler crabs in (a) air and (b) seawater for individuals with [filled circles; (a) $y = 0.81 \cdot x + 4.39$, $r^2 = 0.84$, $n = 40$; (b) $y = 0.87 \cdot x + 5.30$, $r^2 = 0.66$, $n = 26$] and without [open circles; (a) $y = 0.74 \cdot x + 4.38$, $r^2 = 0.80$, $n = 38$; (b) $y = 0.83 \cdot x + 5.20$, $r^2 = 0.68$, $n = 23$] a major claw. P -values are from ANCOVA with body mass as the covariate: (a) < 0.001 ; (b) 0.374 .

of the relationship between respiration rate and body mass were not significantly different between treatments in either analysis (air: $F_{1,74} = 0.64$, $P = 0.425$; water: $F_{1,45} = 0.14$, $P = 0.707$), but there were highly significant differences in intercept between treatments in air ($F_{1,75} = 11.85$, $P < 0.001$). When individuals of the same mass were compared, respiration rates of crabs with a major claw were *c.* 8% higher than those without one. The pattern for crabs in seawater was qualitatively similar – males with a claw had respiration rates *c.* 5% higher than those without one; however, the observed difference was not statistically significant ($F_{1,46} = 0.81$, $P = 0.374$). Owing to water movement in the aquatic chamber (required for accurate determination of dissolved O_2), crabs were not always quiescent during the experimental period. As a consequence our measurements of respiration in air and seawater are not directly comparable. Nevertheless, relative differences in metabolic rates for crabs with and without a major claw should still reflect the cost of the structure in each experiment.

LOCOMOTOR PERFORMANCE: ENDURANCE CAPACITY

Males without a major claw ran for significantly longer than those bearing an intact claw or mass comparable with the missing structure (Table 1; Fig. 2a). Endurance of clawless crabs carrying additional weight was not reduced quite to the level of individuals with an intact claw; inert mass added to the carapace may be carried with greater mechanical efficiency than the major claw (e.g. Kram 1996) and there are no metabolic costs of respiring tissue. For crabs with an intact claw, the addition of extra weight significantly reduced the length of time they could run, regardless of where the weight was placed (Table 1; Fig. 2b). Repeated measures analyses gave similar results ($F_{2,28} = 52.67$, $P < 0.001$), although in this analysis the response was slightly stronger when the mass was added to an individual's claw vs. their carapace ($F_{1,28} = 4.42$, $P = 0.045$). Qualitative observations of running crabs suggested that this was due in part to increased problems with balance and difficulty in holding the heavy claw aloft.

LOCOMOTOR PERFORMANCE: MAXIMUM SPRINT SPEED

Removal of the major claw did not result in faster sprint speeds for male *U. pugilator* ($F_{1,36} = 1.53$, $P = 0.224$); more surprisingly, neither did the addition of a relatively large amount of weight slow the crabs to any appreciable degree ($F_{1,36} = 0.53$, $P = 0.472$; Fig. 3). The interaction between presence of the major claw and addition of weight was not significant ($F_{1,36} = 0.32$, $P = 0.573$).

Discussion

In conjunction with work on fiddler crab foraging by Weissburg (1992, 1993), our study provides empirical

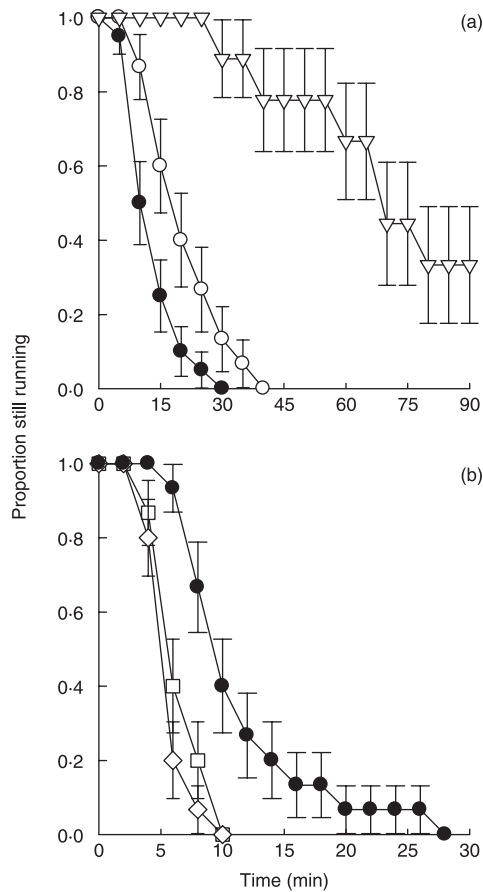


Fig. 2. Proportion (\pm SE) of male fiddler crabs continuing to run at 4 m min^{-1} in the (a) first [intact major claw (filled circle); no major claw (open triangle down); and no major claw, weight added to carapace (open circle)], and (b) second [weight added to carapace (open square); weight added to claw (open diamond); and no weight added (filled circle)] treadmill endurance experiments. In the first experiment, $n = 20$ (intact claw) and 15 (no claw and no claw, weight added to carapace). In the second experiment, $n = 15$. P -values are from Wilcoxon's signed ranks tests: (a) < 0.001 ; (b) < 0.001 .

support for a key assumption of sexual selection theory – there are significant energetic and locomotor costs associated with the enlarged major claw of male crabs. Mass-specific metabolic rates were higher and endurance capacity lower for individuals bearing an intact claw compared with those without one. Previous studies have demonstrated that waving and fighting associated with courtship by fiddler crabs is physiologically demanding (Matsumasa & Murai 2005), and that

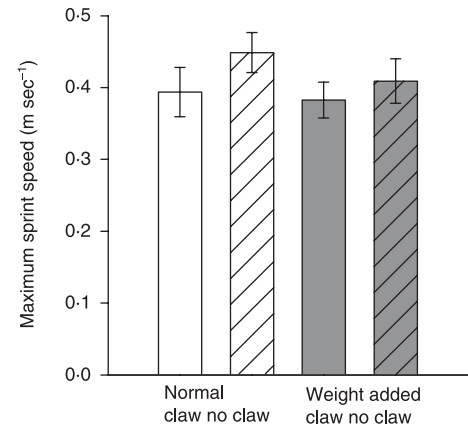


Fig. 3. Mean (\pm SE) maximum sprint speeds of male Fiddler Crabs: no weight added (white bars); weight added to carapace (grey bars); intact major claw (open bars); and no major claw (cross-hatched bars); $n = 10$ per treatment. Neither presence of the major claw, addition of weight or interaction between the two factors was statistically significant with ANOVA (all $P \geq 0.224$).

reproductive activity of several species (including *Uca pugilator*) can be limited by food availability (Backwell *et al.* 1995; Jennions & Backwell 1998; Kim & Choe 2003; authors' unpublished data). Our work provides a mechanistic explanation for these observations and shows that males continue to pay the energetic costs of carrying a large claw even when engaged in nonreproductive activities. A consequence of the positive allometry of the major claw is that associated striated muscle can represent 25–35% of the total body mass of a large male crab (Weissburg 1993; Levinton & Judge 1993); the possession of relatively more respiring muscle tissue may explain the observed higher metabolic rates of intact males compared with those lacking a major claw. Economic analyses for a variety of organisms highlight that even relatively small differences in energetic inputs and expenditures, such as those we documented, can have significant long-term consequences to fitness (Stephens & Krebs 1986).

Additional evidence for the significance of differential metabolic costs to fiddler crabs is provided by biomechanical studies demonstrating that although absolute closing force of the major claw increases with increasing claw size, large crabs are weaker than expected assuming isometric growth (Levinton & Judge 1993; Levinton, Judge & Kurdziel 1995). Crab claws are simple levers;

Table 1. Pairwise multiple comparisons of endurance curves for male *Uca pugilator* in the two treadmill experiments. To keep the experiment-wise error rate $\alpha = 0.05$, comparisons were done using a sequential Bonferroni approach (Dunn–Sidak method; Sokal & Rohlf 1995) following Wilcoxon's signed ranks tests. Individual comparisons marked with an asterisk (*) were statistically significant

Experiment 1		Experiment 2	
Treatment group	Significance	Treatment group	Significance
Control vs. no claw, no weight	*	Control vs. weight added, carapace	*
Control vs. no claw, weight added	*	Control vs. weight added, claw	*
No claw; no weight vs. weight added	*	Weight added; carapace vs. claw	NS

closing force is a function of muscle cross-sectional area (MCA) and the mechanical advantage (MA) of the lever system (Warner & Jones 1976; Schenck & Wainwright 2001). As male fiddler crabs grow, MCA increases more slowly than expected if the claw were growing isometrically, while MA actually decreases. In contrast, the small claws of both male and female fiddler crabs are isometric with respect to both MCA and MA (Levinton *et al.* 1995) and relative closing force remains constant as individuals increase in size. Levinton & Allen (2005) discussed the implications of these results in the context of a trade-off between claw closing force and closing speed; however, an alternative (but not mutually exclusive) explanation is that proportional increases in MCA are constrained by associated metabolic costs of striated muscle.

Energy cost of locomotion is determined by the cost of supporting an animal's weight (a function of force applied by the foot to the ground) and the time course over which it must be supported (a function of stride frequency) (Kram & Taylor 1990). An unweighted individual moving at a given speed will have increased endurance capacity compared with when carrying a load, clearly demonstrated by crabs on the treadmill. Carrying the major claw pushed male *U. pugilator* past a performance threshold where capacity for sustained submaximal locomotion was significantly reduced; the addition of extra weight to already burdened males further degraded performance. In contrast to these results, presence of the major claw and even extra weight had no effect on maximum sprint speeds of crabs over short distances. Our observations match those of two previously published studies of sprint speed in *Uca* (Frix, Hostetler & Bildstein 1991; Jordão & Oliveira 2001b), suggesting that predator escape responses are not generally limited by the large claw. This counter-intuitive result is consistent with predictions of a recent biomechanical model of locomotor performance (Pontzer 2005). Although relative endurance capacity of sprinting crabs with and without a claw should still be determined by total force production as described above (Kram & Taylor 1990), over short time intervals where individuals never reach their maximum sustained power output limb length and stride frequency are the primary drivers of locomotor performance, independent of body mass (Pontzer 2005). As all crabs in the sprint speed experiment were similar in size, the observed absence of variation in maximum sprint speed fits theoretical expectations quite nicely.

Studies of whole organism performance should attempt to identify mechanistic links between phenotype and environment (Arnold 1983). Variation in phenotype (e.g. endurance or sprint speed) presumably relates to variation in whole organism functional capability, affecting how individuals interact with their environment. Although we do not currently know how differences in treadmill performance translate to ecologically relevant variation in the field, there are reasons to believe that they do. Treadmill performance predicts the outcome

of agonistic interactions among lizards (Brandt 2003), and species exhibiting greater endurance capacity on a treadmill also tend to be more active in the field (Garland 1999). Weinstein (1998) used observed variation in treadmill endurance capacity of male *U. pugilator* at different body temperatures in the laboratory to correctly predict effects of temperature on locomotor performance of crabs in the field. The experimental treadmill velocity we used in this study was well within the normal range of locomotor speeds exhibited by unexcited *U. pugilator* in nature (Weinstein 1998; Viscido, Miller & Wethey 2001). Fiddler crabs foraging without nearby shelter spend significant time each day moving in search of food and avoiding predators and many other behaviours (e.g. burrow construction and maintenance, sexual display) also appear to require extended submaximal effort (Crane 1975; Backwell *et al.* 1995; Jennions & Backwell 1998; Matsumasa & Murai 2005), suggesting that the major claw represents a significant encumbrance to sexually mature males. Nevertheless, one goal of future research must be to better link whole-organism performance capacity of fiddler crabs to differential activity in the field, particularly as it relates to carrying the burden of the major claw.

Sexual display is generally found to be extremely metabolically demanding (Ryan 1988; Vehrencamp, Bradbury & Gibson 1989; Hoback & Wagner 1997; Kotiaho *et al.* 1998) and mass loss due to reduced energy intake while involved in endurance competition appears to be common in many taxa (Andersson 1994). Far fewer studies have demonstrated persistent physiological costs associated with bearing a sexually selected morphological structure. The best examples to date are aerodynamic costs of elaborate tail morphology in birds (Møller *et al.* 1998), hydrodynamic costs of swordtails in fish (Basolo & Alcaraz 2003) and energetic costs of antlers in cervids (Moen *et al.* 1999). The significant costs of the enlarged major claw to net energy gain and locomotor performance of male fiddler crabs represent another instance where natural selection is operating in opposition to sexual selection favouring further trait exaggeration.

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