Speed differences between male and female fiddler crabs

ISABELLA ALMA, TEO KIM, JABBARI BAKKO, AND MELANIE SCHMIDT

Department of Biology, Amherst College, 426 McGuire Life Sciences Building, Amherst, Massachusetts 01002 USA

INTRODUCTION

Sexual selection is a form of natural selection in which individuals of one sex preferentially mate with individuals of the opposite sex based on the presence of particular traits (Kirkpatrick 1987). These traits can be used to attract members of the opposite sex, as well as to compete with members of the same sex for mates (Kirkpatrick 1987). Through competition for mates, this selected characteristic becomes exaggerated over generations, as individuals with the favored trait reproduce more successfully and/or more frequently than those lacking it (Andersson 1994). This perpetuation of the preferred trait eventually results in distinguishable morphological differences between sexes (Andersson 1994). While sexual dimorphism has reproductive benefits, it may impose a life-history cost on the dimorphic sex (Höglund & Sheldon 1998). Costs of dimorphism manifest differently in different species, examples include a greater susceptibility to predation in male barn swallows (Møller & Nielsen 1997), limited aerobic metabolism during threat displays in side-blotched lizards (Brandt 2003), and decreased stability during locomotion in male stag beetles (Goyens et al. 2015).

Fiddler crabs (*Uca pugilator)* are sexually dimorphic (Crane 1975). Females have two small feeding claws, while males have one feeding claw and a large major claw that can comprise nearly half of a male's mass (Crane 1975). Males use this major claw in competition with other males for burrows and in waving displays to attract female fiddler crabs (Hyatt & Salmon 1978). A large major claw is favored both by intra- and inter-sexual selection. Males with larger claws tend to win more intra-sexual competitions for territory, allowing them to build and protect burrows at more optimal locations (Jennions and Backwell 1996). In addition to providing shelter, these burrows are the sites for mating between male and female *Uca pugilator*: after mating, the female crab stays deep in the males' burrow for several days to incubate her eggs (Christy 1987). Therefore, optimal burrows for males to protect are those which will not flood or collapse, damaging the un-hatched eggs (Christy 1987).

To attract female mates, males stand outside of their burrow and wave their major claw (Hyatt & Salmon 1978). Females prefer males with larger major claws than smaller ones (McLain and Pratt 2007; Oliveira & Custödio 1998). Though sexual selection in fiddler crabs is multifactorial, female preference for large male major claw size may be related to the relationship between claw size and burrow safety, representing females' attempt to exert control over the security of their eggs (Christy 1987).

Because sexual dimorphism can have detrimental effects, threatening a sex's survival, (Møller & Nielsen 1997; Brandt 2003; Goyens et al. 2015), we are interested in the costs of having a large major claw for male fiddler crabs. Some costs of sexual dimorphism in fiddler crabs have already been reported. Male fiddler crabs must compensate for the cost of only having one feeding claw by foraging more frequently (Caravello 1987; Weissburg 1992). Additionally, males with large major claws have higher mass-specific metabolic rates and have lower treadmill endurance capacity than those without (Allen & Levinton 2007).

We asked whether having such a large claw relative to body mass would negatively impact the males' ability to avoid predation. Specifically, we investigated differences in male and female speed in the presence of a perceived threat using an artificial runway. Because dimorphism may impose locomotive costs, the males' large major claw hindering their balance and stability while moving (Goyens et al. 2015), we hypothesize that speed is relative to claw size. We hypothesize that on average males with large claws will be slower than females.

METHODS

We obtained fifty-seven *Uca pugliator* (fiddler crabs) for this study. The length of the major (longest) claw was determined by measuring from the tip of the claw to the first joint, and the crabs' carapace widths were measured at its widest point. We placed crabs in a one-meter long runway, which was 10 cm wide and 15 cm tall. To trigger an escape response, we "chased" the crabs with a paintbrush and timed how long it took each crab to move from one end of the runway to the other. Each crab completed the run three times and every individual's average speed was calculated. This process was completed for each of the twenty-nine females and twenty-eight males.

With alpha set at 0.05 for all tests, we ran two-sample t-tests to determine if there were differences by sex in major claw length and carapace width. We also ran a linear regression to see if claw size increased with increasing carapace width for males or females. In fiddler crab experiments, size is often matched by sex (Caravello 1987; Bildstein 1989; Lim 2008). This was not possible in our experiment, so instead we divided speed by carapace width to account for possible differences in size by sex. We then ran an additional t-test to determine if there was a difference in relative speed by sex.

RESULTS

For all crabs, major claw length ranged from 0.47 to 56 mm with a mean of 18.94 mm. Mean carapace width was 15.43 mm and ranged from 8 to 23 mm. The average speeds ranged from 0.019 to 0.2 m/s with a mean of 0.082 m/s.

The range of claw length was from 0.47 to 29 mm for females and from 19 to 56 mm for males (Fig. 1). Mean major claw length was significantly larger for males than for females ($t=2.13$, $df=55$, $p=0.02$, Table 1). Males also had larger carapace width than females ($t=4.77$, $df=55$, $p<0.001$). Female claw length increased as carapace size increased ($F=16.80$, $p<0.001$, $R^2=0.38$, Fig. 5), but male claw length did not ($F=0.02$, $p=0.88$, $R^2=0.0009$, Fig. 2). Relative speed (speed/carapace width) was greater for females than males ($t=2.55$, $p=0.007$, $df=55$, Fig. 3).

TABLE 1. Average claw length of an individual's longest claw and carapace width, both by sex, plus or minus the standard error.

Sex	Longest Claw (mm)	Carapace Width (mm)
Female	8.67±1.03	13.83±0.48
Male	29.57±1.05	17.10±0.49

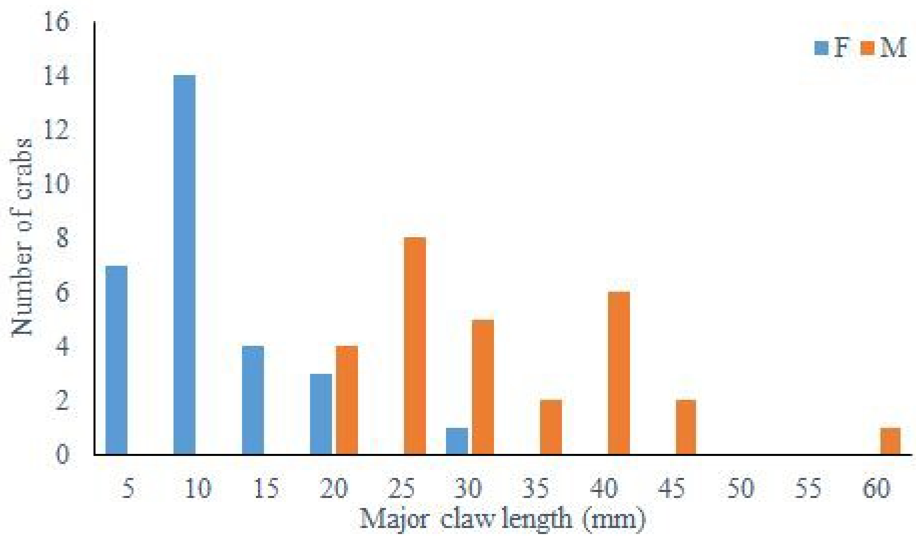

FIG. 1. Major claw length distribution of female and male fiddler crabs (*Uca pugliator*). N=29 females and 28 males.

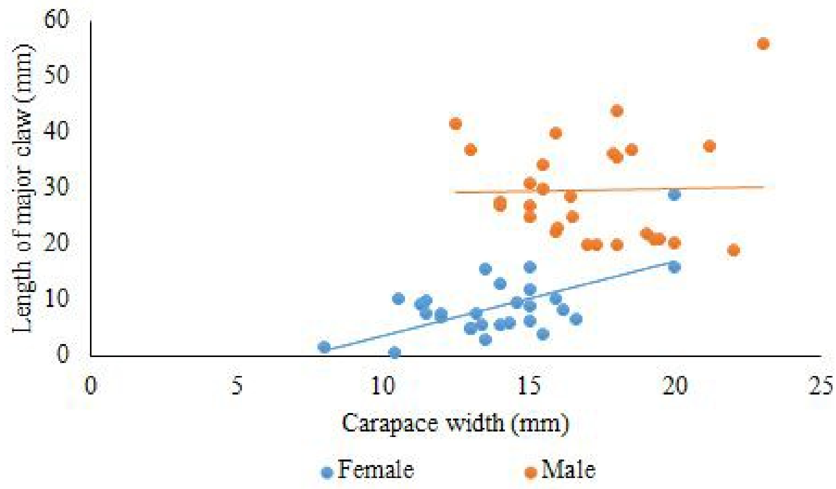

FIG. 2. Length of major claw as a function of carapace size for female and male fiddler crabs (*Uca pugliator*). Female equation of line: y = 1.3339x - 9.7683. Male equation of line y = 0.1081x + 27.72.

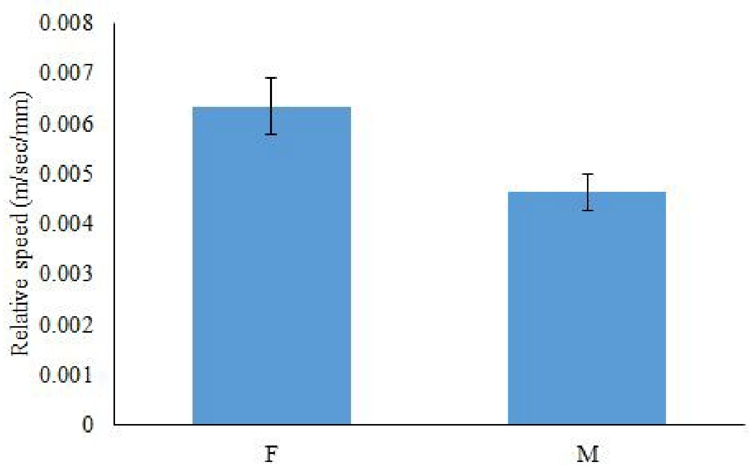

FIG. 3. Mean relative speed (average speed/carapace width) of female and male fiddler crabs (*Uca pugliator*). Standard error shown.

DISCUSSION

Male crabs had a slower escape speed than female crabs, relative to carapace size. This indicates that the large major claws of males, although beneficial in attracting mates and defending burrows (Jennions and Backwell 1996; McLain and Pratt 2007; Oliveira & Custödio 1998), may be costly with respect to speed. Although the males' enlarged major claw does not attract more predators than females' smaller claws (Bildstein 1989), our experiment suggests that it can slow males' getaway speeds, making it more difficult for them to escape the predators that do attack them. By hindering the males' escapes, the large major claw may be costly with respect to survival in the presence of predators.

To improve this study, males and females should be matched by carapace width to better account for the influence of size on speed. Additionally, a larger sample size and more trials should be used for results more accurately representing the broader *Uca pugliator* population. Further inquiry is needed to verify that the large major claw of males was actually the cause of the males' slower speed. A study on this might compare the "escape" times of males with a large major claw to those of males with their major claw removed. Alternatively, females could undergo timed trials before and after an artificial major claw was added to one of their feeding claws to determine if the added weight impacts their speed. One might also run similar timed trials with other species to determine if other sexually dimorphic features such as antlers, enlarged mandibles, and other ornamental weapons also impede locomotion.

The large major claw has been shown to be detrimental to male fiddler crabs, forcing them to spend greater time foraging than females (Caravello 1987; Weissburg 1992), lowering their endurance, and increasing mass-specific metabolic rates (Allen & Levinton 2007). The results of this experiment support the prediction that males with major claws are slower than female crabs and may indicate that in fiddler crabs, as in stag beetles (Goyens, et al. 2015), sexual dimorphism hinders locomotion. This suggests that sexual dimorphism may place a burden on more aspects of an organism's life history than previously suspected. Sexually selected plumage brightness in male birds has reproductive benefits based on female choice but has detrimental impacts on viability (Promislow 1992). Our results suggest that ornamental weapons may follow a similar pattern; while their appearance may positively influence chances of mating and reproducing (McLain and Pratt 2007; Oliveira & Custödio 1998), these sexually dimorphic characters may also impose a cost on the organism, lessening its chances of survival.

AUTHOR CONTRIBUTIONS

T.K. and J.B. performed the statistical analyses and created corresponding figures. M.S. was the primary writer of the Methods and Results sections of the report. M.S. and I.A. were the primary writers of the Introduction and Discussion sections of the report. All contributors have reviewed and are satisfied with the final version of the report.

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