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Natural History Note

Thermoregulation as an Alternate Function of the Sexually Dimorphic Fiddler Crab Claw

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ABSTRACT: Fiddler crabs are highly sexually dimorphic. Males possess one small (minor) feeding claw and one greatly enlarged (major) claw; females possess two small claws. The major claw is used to attract mates and for burrow defense, but it is costly for the male to possess. We tested the hypothesis that the major claw also functions as a thermoregulatory structure, a function that would allow males to spend a greater amount of time at the surface, foraging and attracting potential mates. Fiddler crabs *Uca panacea* were exposed to a source of radiant heat and body temperatures were monitored. Four groups of crabs were tested: intact males, males with the minor claw removed, males with the major claw removed, and females. The body temperatures of males without the major claw increased more rapidly and reached higher values than did those of males with the major claw intact, but the results from these animals were similar to those of females. These results support the hypothesized thermoregulatory function of the major claw. The major claw may function as a heat sink, transferring heat away from the body and dissipating it into the air. Enhanced thermoregulatory ability provided by the major claw may partially ameliorate the energetic costs of possessing such a large claw.

Keywords: sexual dimorphism, thermoregulation, fiddler crab, *Uca panacea*, heat sink, major claw.

Introduction

Sexual dimorphism is a common feature of many species and may include differences in body size, morphology, coloration, or ornamentation between the sexes. In general, sexual dimorphism is the product of sexual selection (Andersson 1994), and it often takes the form of exaggerated male traits, armaments, or ornaments that confer reproductive advantages through either increased mate attraction or successful intrasexual competition for mates or preferred breeding habitat (Shuster and Wade 2003). Such traits are costly for the male to possess (Kotiaho 2001), as

they can increase predation risk (Koga et al. 2001; Pruden and Uetz 2004), energetic costs (Evans and Thomas 1992; Allen and Levinton 2007), or foraging costs (Evans and Thomas 1992). The cost of possessing an exaggerated morphological trait moderates the degree of exaggeration of the trait. At some point, the reduction in fitness will outweigh the potential reproductive benefit (Kirkpatrick 1987; Andersson 1994; Fitzpatrick et al. 1995; Kotiaho et al. 1998). Thus, natural selection often limits the degree of sexual dimorphism (Endler 1980, 1983). There can also be ecological causation for sexual dimorphism; in some cases, sexual dimorphism can arise or be maintained because of ecological differences between the sexes (Slatkin 1984; Shine 1989; Cooper 2010). Thus, the form and degree of sexual dimorphism are shaped by both sexual selection and natural selection (Endler 1983; Andersson 1994; Kotiaho et al. 1998; Stuart-Fox and Ord 2004).

Fiddler crabs (genus *Uca*) are model organisms for studies of sexual dimorphism and sexual selection. A highly conspicuous trait in this group is the extreme difference in claw size and morphology between the sexes (Crane 1975). Males possess one small (minor) feeding claw and one greatly enlarged (major) claw, whereas females possess two small feeding claws (fig. 1). The major claw is used to attract potential mates and in male-male territoriality conflicts (Christy and Salmon 1984; Pope 2000a). The highly ritualistic mating behaviors and extreme dimorphism in claw size have stimulated a large number of studies that explore the form, function, and costs of sexual dimorphism in fiddler crabs.

The major claw of male fiddler crabs has several functions (table 1). Male fiddler crabs perform elaborate, species-specific claw-waving displays that consist of moving the claw in vertical and/or lateral motions (Crane 1975; How et al. 2009). This waving attracts potential mates (Pope 2000a, 2000b), possibly because the movement captures the attention of females. The waving display varies on the basis of the context and the distance to females. Low-intensity waving advertises the presence of the male

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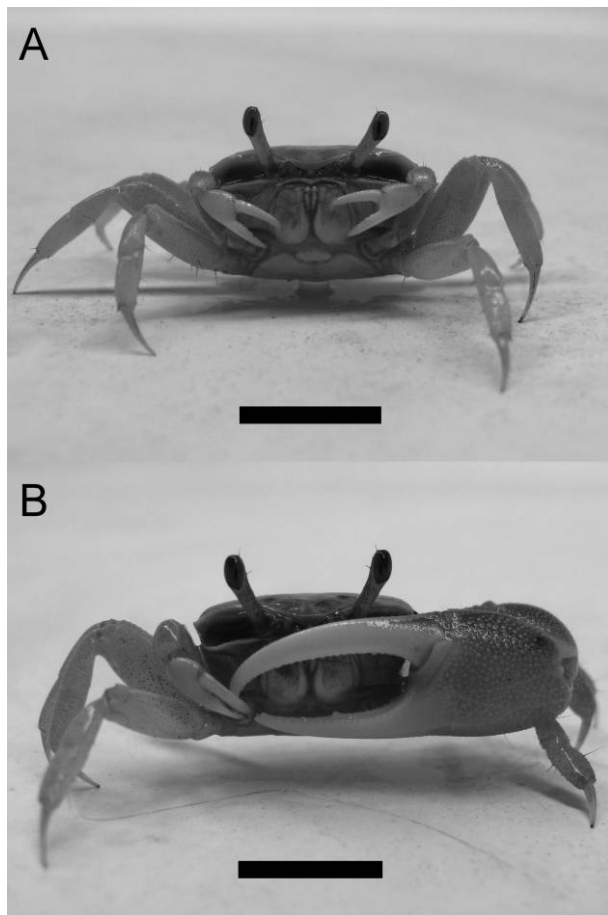


Figure 1: Female (A) and male (B) *Uca panacea*. Scale bars indicate 1 cm.

and the breeding burrow over long distances, while high-intensity waving occurs when females are in close proximity and is directed toward a specific female (Pope 2005). Males with a larger major claw relative to their body size are more successful in attracting potential mates than are males with a relatively smaller major claw, suggesting that claw size also plays a role in female choice (Oliveira and Custodio 1998; Pratt and McLain 2002; McLain and Pratt 2007). Even the height of the wave can be an important target of female choice (Murai et al. 2009). Claw size is also important in intrasexual combat, as males with larger major claws are more successful in territory disputes (Hyatt and Salmon 1978). In many species, the major claw is brightly colored, with colors varying between species. The color of the claw, including reflectance at ultraviolet wavelengths, is used as a species-recognition signal during female mate choice (Detto et al. 2006; Detto 2007; Detto and Backwell 2009).

The costs to a male fiddler crab of possessing such a

greatly enlarged claw are substantial. Waving of the major claw is energetically costly, as is evidenced by increased blood-lactate levels in waving male fiddler crabs (Matsumasa and Murai 2005). The presence of the major claw also results in increased mass-specific metabolic rates and decreased endurance capacity (Allen and Levinton 2007). The foraging ability of male fiddler crabs is altered by the large claw. While foraging, male crabs are limited by their single minor claw; the major claw is not functional for feeding, and males thus have a lower food intake rate than females (Valiela et al. 1974; Weissburg 1992, 1993). Additionally, while at the surface performing the waving display, males are both heat and food stressed (Allen 2007). The conspicuousness of the major claw may further increase predation risk (Koga et al. 2001). Finally, as claw mass increases, the height of the wave decreases, resulting in decreased success in attracting females (Murai et al. 2009). Clearly, the presence of the large male claw has been well explored, showing the mating advantages and potential costs associated with such an ornament.

The major claw of male fiddler crabs is greatly enlarged, despite the costs. Major claw size varies among species, but it can account for nearly one-half of total body mass in some species (Crane 1975; Christy and Salmon 1984). Because of the large size of the major claw, other legs on the same side of the body are often enlarged, presumably for additional support during lateral waving (Huxley and Callow 1933; Takeda and Murai 1993). We hypothesize that the major claw confers additional benefits beyond those related to sexual selection that may partially ameliorate the costs of the major claw and contribute to the high degree of exaggeration in claw size.

We hypothesize that one such additional benefit of the major claw is increased thermoregulatory ability. If the major claw of male fiddler crabs confers a thermal or thermoregulatory benefit, it may partially ameliorate the energetic costs of possessing it. The major claw may confer a thermal benefit through passive processes, such as evaporative cooling and convective heat transfer, or through active physiological (regulatory) mechanisms. Behavioral mechanisms such as claw waving and changing claw orientation may increase the thermoregulatory benefit of the major claw beyond the passive benefit provided by the structure of the claw itself. Male *Uca rapax* and *Uca pugilator* often emerge from burrows in the morning, facing the sun and extending the major claw (Smith and Miller 1973), possibly as a means of regulating body temperature by rapid heat gain. Additionally, Windsor et al. (2005) demonstrated that heat is rapidly transferred between the body and the major claw of male *U. pugilator*. These observations support the hypothesized thermoregulatory function of the claw. We tested our hypothesis in the fiddler crab *Uca panacea* Novak and Salmon, a sister species

Table 1: Traits and functions associated with the major claw in fiddler crabs, and example studies that explore such traits

Trait, function	Reference
Claw waving:	
To increase conspicuousness to females	Cummings et al. 2008
As a courtship signal to females	Pope 2000a, 2000b
Low-intensity waving:	
To advertise presence over long distances	Pope 2005
High-intensity waving:	
To attract nearby wandering females	Pope 2005
Height of wave:	
To increase attractiveness to females	Murai and Backwell 2006; Murai et al. 2009
Structure of wave:	
As conspecific identification	Salmon et al. 1978; Zucker and Denny 1979
Claw color:	
As conspecific identification	Detto et al. 2006; Detto 2007; Detto and Backwell 2009
Claw size:	
To increase attractiveness to females	Oliveira and Custodio 1998; Pratt and McLain 2002; McLain and Pratt 2007
In male-male territory disputes	Hyatt and Salmon 1978
In thermoregulation	This study

to *U. pugilator* (Novak and Salmon 1974; Rosenberg 2001) that inhabits sandy substrates along the coast of the Gulf of Mexico.

Methods

Adult *Uca panacea* (fig. 1) were collected from a salt marsh at the Mustang Beach Airport, Port Aransas, Texas (27°48.68'N, 97°05.36'W), in July and August, 2010. Crabs were transported to the University of Texas Marine Science Institute where they were placed into holding tanks, which contained running seawater and sand from the collection site, that had been inclined such that approximately one-half of the bottom of the tank was under water. Crabs were fed daily (Wardley Tropical Fish Flake Food and HBH Crab and Lobster Bites) and used in experiments within 1 week of collection.

Relationships between claw size and body size were assessed for male *U. panacea*. Each crab was weighed and induced to autotomize either the major or the minor claw by squeezing the merus of the claw with forceps. This procedure resulted in immediate autotomy of the claw. Autotomy is a common predator defense mechanism among decapod crustaceans (Paul 1915; Robinson et al. 1970; Smith and Hines 1991; Wasson et al. 2002). Crabs are able to autotomize, or self-amputate, an appendage along a defined breaking plane (Paul 1915). Following

autotomy, a diaphragm membrane rapidly seals off the wound to prevent blood loss (Paul 1915), and regeneration of autotomized limbs occurs within several molts. Induced autotomy is a commonly used practice in studies on crustaceans and is generally assumed to result in minimal stress to the organism (Allen and Levinton 2007; Barria and Gonzalez 2008; Patterson et al. 2009). The autotomized claw was weighed immediately after separation. Body mass was determined by subtracting claw mass from total crab mass. Claws were measured on a total of 96 crabs: 48 for determining major claw size and 48 for determining minor claw size. To determine scaling of the major claw with body size, claw mass was regressed against body mass.

To test for differences in thermoregulatory ability between the sexes, both male and female crabs were exposed to a source of radiant heat and body temperatures were monitored. To test the effects of the major claw on thermoregulatory ability, crabs (not the same crabs used for claw measurements) were assigned to one of the following four treatments: (1) intact females, (2) intact males, (3) males with the major claw removed, and (4) males with the minor claw removed. Autotomy was induced, using the method described above. Following claw removal, crabs were held for 1 h at room temperature in inclined tanks (as above) before being used in experiments. None of the crabs died in the hour between claw removal and the start of the experiment.

To normalize water content among crabs, each crab was submerged in a cup of room-temperature seawater for 1 min before being placed into a dry cup at room temperature ($\sim 25^\circ\text{C}$) for 15 min. Each crab was then weighed and photographed against a white background. Carapace temperature, used as a proxy for internal body temperature, was measured with an infrared thermometer (model 42512, Extech Instruments, Waltham, MA).

Lamps containing 60-W soft-white incandescent bulbs provided a source of radiant heat and were positioned with the reflectors pointed directly downward, 21 cm above the surface of a table. Four clear plastic cups were placed under each lamp, with one crab in each cup. Cups were arranged such that each cup received a similar amount of light and heat. Irradiance at the position of the cups, which was measured with a CMP-3 pyranometer (Kipp & Zonen, Delft), was $\sim 400 \text{ W m}^{-2}$. Each set of four cups was considered as one block for statistical analyses and contained one crab from each of the four treatments. Every 10 min, each crab was weighed and body temperature was measured with the infrared thermometer. The positions of the four crabs under a lamp were rotated following each measurement. Each individual was exposed for 90 min. This time period was chosen on the basis of preliminary experiments and resulted in substantial increases in body temperature with minimal mortality. Behavior of crabs held in the cups was not quantified systematically. We did not, however, observe any obvious differences in behavior, posture, or claw orientation between the four treatments. At the conclusion of the experiment, the crabs were again photographed against a white background.

Fiddler crabs are able to change the shade of the carapace in response to temperature changes (Silbiger and Munguia 2008), and carapace shade likely has effects on the absorption of radiant energy and thus on body temperature. To test for differences in carapace shade and carapace color-change responses among the four treatments, carapace shade was determined for all crabs, using the methods described by Silbiger and Munguia (2008). Photographs were converted to grayscale and analyzed using ImageJ software (National Institutes of Health, Bethesda, MD). Using only the area of the carapace, a histogram was created for each image, showing the distribution of pixel intensities, ranging from 0 (black) to 255 (white). A gamma distribution was fitted to each histogram, generating a shape parameter γ that described the shade of the carapace, with higher γ values corresponding to a lighter shade and lower γ values corresponding to a darker shade. Carapace shade was analyzed using a two-way repeated-measures ANOVA testing for significant effects of treatment, time (before or after the 90-min experimental period), and a treatment \times time interaction.

Decreases in crab mass were nonlinear. To standardize

for the initial mass of each crab, masses were converted to percentages of the initial mass for desiccation rate analyses. An exponential decay function was fitted for each crab, with the form

$$M_b = a(e^{-bt}) + c,$$

where M_b is the percentage of initial body mass at time t and b is the desiccation-rate constant. The parameter a was held constant for all crabs. An exponential decay function was chosen because it produced the best fit to the data. Mean \pm SE R^2 value was 0.99 ± 0.001 . The percent change in total body mass over the full 90-min experiment was also calculated for each crab.

Body temperature increases were also nonlinear, and heating rate was determined for each crab using logarithmic regression. Logarithmic regression was chosen because it produced the best fit to the data. A regression line was fitted for each crab, with the form

$$T_b = m \ln(t + 0.1) + b,$$

where T_b is body temperature at time t and m is the heating-rate constant. In order to incorporate time zero into the regression, 0.1 min was added to each time measurement. R^2 values averaged 0.91 ± 0.01 . Additionally, the total change in T_b was calculated for each crab by subtracting the initial body temperature from the final body temperature.

Desiccation-rate constants, total changes in M_b , heating-rate constants, and total change in T_b were analyzed using mixed-effects ANCOVA, where treatment was the fixed effect, initial crab mass (after claw autotomy) was the covariate, and blocks were random effects. Each model also tested for a treatment \times mass interaction. In all cases, if ANCOVA indicated a significant effect of treatment, then a Tukey HSD test was used for all pairwise comparisons among treatments. Analyses were conducted in JMP, version 8.0.2 (SAS Institute, Cary, NC), and SigmaPlot 11.0 (Systat Software, Chicago, IL).

Results

Mass (mean \pm SE) of the major claw of male *Uca panacea* was $27.3\% \pm 0.42\%$ of crab mass (2.09 ± 0.07 g). One crab had a much smaller major claw (11.9% of crab mass), likely due to regeneration following autotomy that occurred in the field before collection, and so was excluded from further analyses. Major claw mass increased isometrically with body mass (major claw mass = $0.417 \times$ body mass $- 0.050$; $R^2 = 0.86$; fig. 2). Mass of the minor claw averaged $1.7\% \pm 0.01\%$ of total body mass.

A total of 21 heating trials were conducted, resulting in 21 replicates for each of the four treatments and a total of 84 crabs (mass, 1.85 ± 0.04 g). Of the 84 crabs used,

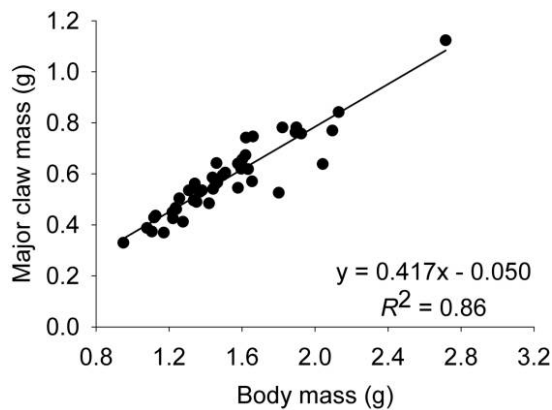


Figure 2: Major claw mass regressed against body mass (total mass minus major claw mass).

two died during the experiment, between 80 and 90 min after placement under the lamp, probably due to overheating (see below). One of these crabs was a female and the other was a male with the major claw removed. These two crabs were included in analyses of heating and desiccation rates but were excluded from analyses of total change in body temperature and mass.

Carapace shade, measured as a γ value, differed among the four treatments (table 2); males with the major claw removed had significantly higher γ values (indicating lighter shade) than did females or intact males, while males with the minor claw removed had intermediate γ values. Crabs in all four treatments became significantly lighter over the course of the experiment (table 2; fig. 3), with a mean change in γ of 0.057 ± 0.011 ($21.36\% \pm 4.51\%$). There was no significant treatment \times time interaction.

Crabs lost, on average, $7.64\% \pm 0.12\%$ of initial body mass over the 90-min experimental period (fig. 4A). Desiccation-rate constants (b) averaged 0.012 ± 0.0003 , and neither desiccation rate nor total change in M_b differed among treatments (table 2; fig. 4B). Both desiccation rate and total change in M_b varied with crab mass; body masses of larger crabs decreased more slowly than did those of smaller crabs, and larger crabs lost a smaller percentage of body mass than did smaller crabs (table 2; fig. 4C). There were no significant treatment \times mass interactions.

Body temperatures increased an average of $9.36^\circ \pm 0.21^\circ\text{C}$ over the 90-min experimental period for all treatments combined. Body-temperature increases were not linear over time but were characterized by a rapid increase over the first 10 min, after which the rate of increase slowed (fig. 5A). Heating-rate constants (m) averaged 1.40 ± 0.03 but differed among treatments (table 2). Females and males with the major claw removed had significantly higher heating rates than did intact males or males with

the minor claw removed (fig. 5B). Heating rate also varied with crab mass; body temperatures of larger crabs increased faster than did those of smaller crabs (table 2; fig. 5C). Additionally, there was a significant treatment \times mass interaction (table 2; fig. 5C).

Total change in T_b also varied among treatments (table 2). Body temperature increases in females ($11.08^\circ \pm 0.35^\circ\text{C}$) and in males with the major claw removed ($9.54^\circ \pm 0.35^\circ\text{C}$) were significantly greater than those in intact males ($8.81^\circ \pm 0.34^\circ\text{C}$) and in males with the minor claw removed ($8.08^\circ \pm 0.34^\circ\text{C}$). Total change in body temperature also varied with crab size; body temperatures of larger crabs increased more than did those of smaller crabs (table 2). There was no interaction between treatment and mass.

Discussion

The purpose of this study was to test the hypothesis that the enlarged male claw plays a role in thermoregulation of the fiddler crab *Uca panacea*. Removal of the major claw significantly affected the rate of increase in body temperature when a crab was exposed to a source of radiant heat; males lacking the major claw exhibited more rapid increases in body temperature and a greater total increase in body temperature than did intact males or males with the minor claw removed. These results complement previous findings on the importance of morphological traits

Table 2: Results of statistical analyses

Source	df	F	P
Carapace shade γ : ^a			
Treatment	3	6.349	<.001
Time	1	28.565	<.001
Treatment \times time	3	1.332	.270
Desiccation rate b :			
Treatment	3	2.5323	.065
Mass	1	9.4817	.003
Treatment \times mass	3	.3882	.762
Total change in M_b : ^b			
Treatment	3	2.445	.074
Mass	1	13.389	<.001
Treatment \times mass	3	.579	.631
Heating rate m :			
Treatment	3	59.028	<.001
Mass	1	71.938	<.001
Treatment \times mass	3	3.393	.023
Total change in T_b :			
Treatment	3	29.003	<.001
Mass	1	39.377	<.001
Treatment \times mass	3	1.802	.156

^a From the gamma distribution that described shade.

^b Relative body mass.

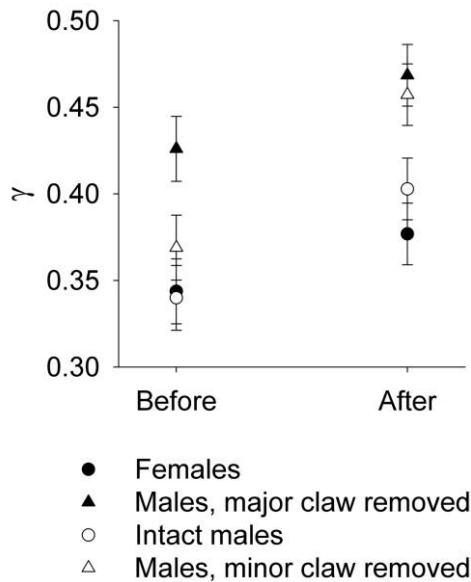


Figure 3: Mean γ values before and after the experiment for each of the four treatments (γ is the shape parameter from the gamma distribution describing shade). A higher value of γ represents a lighter shade. Crabs in all four treatments became lighter in color following exposure to heat. Error bars indicate \pm SE.

in ectotherm thermoregulation (e.g., Wasserthal 1975; Shepherd et al. 2008) and provide evidence supporting an alternative function of the major claw, a function that has potentially positive benefits for male crabs and that can ameliorate the energetic and foraging costs of enlarged claws.

Heating rates were similar between intact males and males with the minor claw removed. Heating rates for males with the major claw removed, however, were higher and similar to the rates observed for females (fig. 5B). Examining the total increase in body temperature confirmed these results. These data suggest that the major claw is involved in thermoregulation in *Uca panacea*. The major claw may function as a heat sink, moving heat away from the body and dissipating it into the surrounding air. Windsor et al. (2005) found that heat is rapidly transferred between the major claw and the body of the fiddler crab *Uca pugilator*, though further study is necessary to resolve the mode of heat transfer (passive conduction or an active physiological process) between the body and claw. The relative size of the major claw may also influence thermoregulatory ability, as a larger claw (relative to body size) should perform better as a heat sink.

Thermoregulatory mechanisms in ectotherms are generally behavioral, such as basking by reptiles (Bauwens et al. 1996) and altering wing orientation relative to the sun

in butterflies (Clench 1966). Similarly, fiddler crabs take refuge in their burrows, change their orientation relative to the sun, or move between surface microhabitats to maintain body temperature (Smith and Miller 1973; Pow-

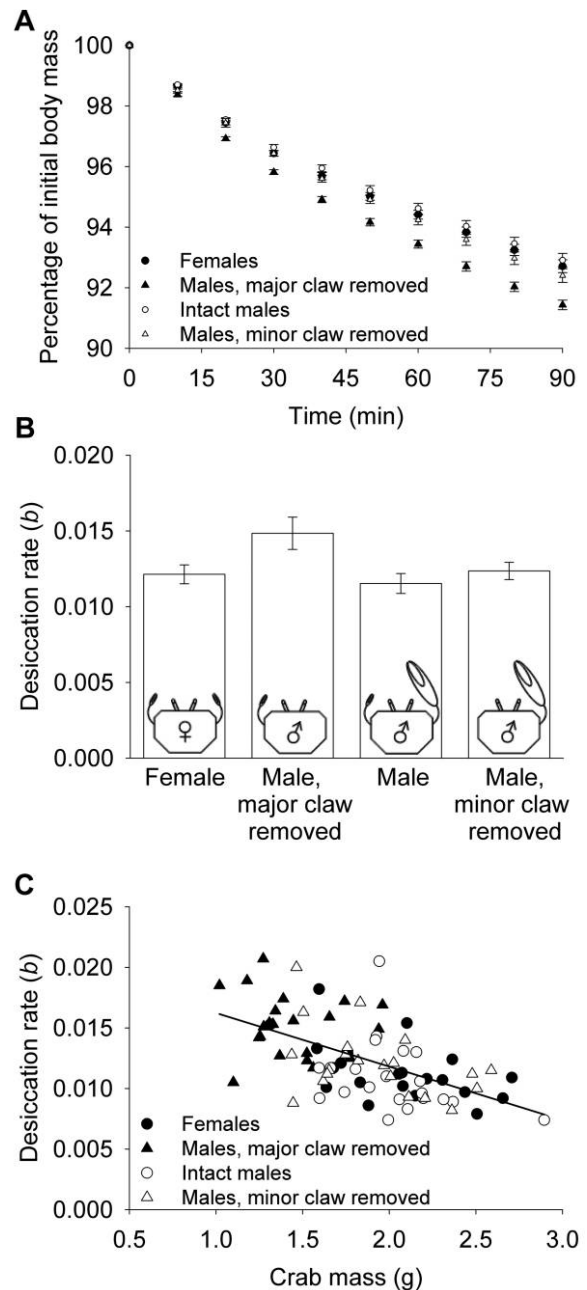


Figure 4: Results of body mass measurements: A, average relative body mass over the 90-min experimental period and B, least squares mean desiccation constants (b) for each treatment. Error bars indicate \pm SE. There were no significant differences among treatments. In C, desiccation-rate constants are regressed against crab mass; the line represents the overall regression.

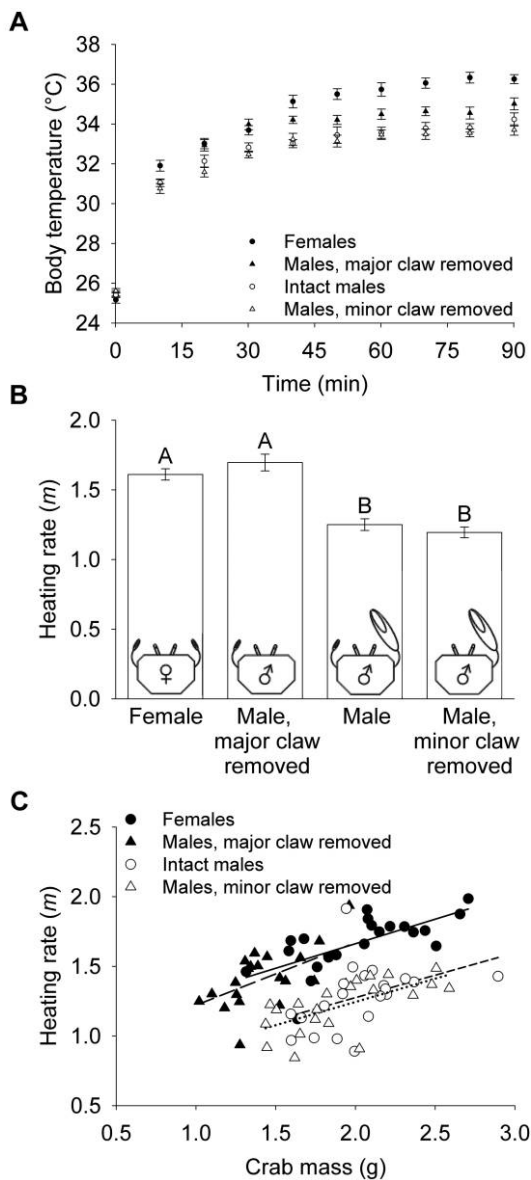


Figure 5: Results of body temperature measurements: A, average body temperatures over the 90-min experimental period and B, least squares mean heating-rate constants (m) for each treatment. Error bars indicate \pm SE. Different letters above bars indicate significantly different values at $P < .05$ with a Tukey HSD test. In C, heating-rate constants are regressed against crab mass for each of the four treatments. The solid line represents females, the long-dashed line represents males with the major claw removed, the short-dashed line represents intact males, and the dotted line represents males with the minor claw removed.

ers and Cole 1976; Thurman 1998). When presented with a temperature gradient, preferred temperatures are at or slightly below the body temperature at which locomotor performance is maximized (Allen 2007; B. J. Allen and J.

S. Levinton, personal communication). Fiddler crabs also change the shade and pattern of the carapace by dispersing or contracting chromatophores in response to temperature changes (Brown and Sandeen 1948; Silbiger and Munguia 2008). By blanching at high temperatures, fiddler crabs are able to increase the reflectance of the carapace and thus remain cooler (Wilkins and Fingerman 1965). We observed crabs in all four treatments becoming lighter after exposure to heat. Males with the major claw removed had the lightest coloration (fig. 3), perhaps indicating blanching of the carapace in response to induced claw autotomy. This difference in shade, however, does not explain the observed differences in heating rate, as males with the major claw removed had the greatest heating rate, and not a lower heating rate as predicted for a light-colored crab. There was no treatment \times time interaction, indicating that the change in carapace shade during the experiment did not differ among the four treatments.

Claw waving has the potential to increase the thermoregulatory function of the major claw, as increased airflow over the claw during waving would increase the rate of heat dissipation. Waving was not observed in this study, likely because of the continuous presence of the experimenter. Additionally, altering the orientation of the large claw relative to the sun could be an important behavioral mechanism for heat gain following emergence from burrows. Although orientation was not systematically examined in this experiment, no obvious differences in posture or claw orientation were observed among the four treatments. Thus, in nature, the thermoregulatory benefit of the major claw may be greater than that observed here, because of behavioral mechanisms. Heat gain is also likely to vary on the basis of the water content of the crab. Here we attempted to standardize water content among the four treatments by immersing each crab in seawater for 1 min, followed by a 15-min period in a dry cup. In the field, however, fiddler crabs may have substantially lower water contents, leading to differences in heating rates and heat gain.

In contrast to the general observation that larger organisms are better able to maintain stable body temperature than are smaller organisms, we observed that both heating rate and total change in body temperature increased with increasing body size. We hypothesize that these relationships are the result of differences in the rate of heat loss between large and small crabs, driven by differences in evaporative cooling rates based on body size. Our observation that the *U. panacea* desiccation rate was inversely related to crab mass (fig. 4) is consistent with the general observation that smaller organisms generally lose water faster than do larger organisms because of increased surface area relative to body volume. Thus, body temperatures likely remained lower in smaller crabs than

in larger crabs because of heat loss from evaporative cooling. Fiddler crabs are generally able to lower their body temperature several degrees below the ambient environmental temperature through this mechanism (Edney 1961; Wilkens and Fingerman 1965; Thurman 1998). There was also a significant treatment \times mass interaction in the analysis of heating rate. The heating rates of males with the major claw removed were more sensitive to body size than were the heating rates of the other three treatments, as indicated by the increased slope of the heating rate by mass regression (fig. 5C). Neither desiccation rate nor percent change in body mass differed among the four treatments, indicating that differences in evaporative cooling did not underlie the observed differences in heating rates among the four treatments.

While these observations support the hypothesized thermoregulatory function of the enlarged male claw, further experiments are necessary to conclusively demonstrate this function. We have demonstrated here that the major claw confers a thermal benefit to male fiddler crabs when they are exposed to high temperatures; this study is the first step toward a better understanding of the ecological role of the sexually selected major claw. Future research should resolve whether active or passive processes are responsible for this thermal benefit, focus on the roles of mechanisms such as evaporative cooling and convective heat transfer in heat loss through the major claw, examine hemolymph flow between the body and claw, and assess the effects of behavioral mechanisms on the thermal benefit provided by the major claw. Our observations, while they do not provide conclusive evidence of a thermoregulatory function, should stimulate further research on the ecological and physiological functions of the major claw, a structure previously considered only in the context of sexual selection.

By exploring ecological functions of sexually selected traits, we can better quantify costs and benefits associated with trait function. Furthermore, such an approach can be enhanced by examining the relationship of form and function in the context of both sexual and natural selection. Here we present evidence that the major claw of male fiddler crabs functions not only to attract mates and in male-male competition, as previously shown, but also as a thermoregulatory organ. We hypothesize that the major claw functions as a heat sink, moving heat away from the body and dissipating heat to the environment. Similar morphological heat sinks are present in other organisms and include the horns of horned beetles (Shepherd et al. 2008), the large ears of jackrabbits (Hill and Veghte 1976; Hill et al. 1980) and elephants (Phillips and Heath 1992; Weisenböck et al. 2010), the bills of toucans (Tattersall et al. 2009), and the horns of goats (Taylor 1966; Picard et al. 1999). In fiddler crabs, a thermoregulatory function of the

major claw would allow male crabs to remain at the surface longer to compensate for their reduced feeding efficiency and would also allow the crab to perform the waving display longer before having to retreat into the burrow. Thus, while sexual dimorphism is the product of sexual selection, these traits can still have physiological advantages beyond mating. Fiddler crabs have long been used as a lens through which to explore mating behavior and sexual selection (table 1) and thus provide an ideal opportunity to investigate the ecological importance of a sexually selected trait, the male's enlarged major claw.

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Male fiddler crab *Uca panacea* at the entrance to its burrow. Photograph by Moisés A. Bernal.