



## Size-dependent temperature and desiccation constraints on performance capacity: Implications for sexual selection in a fiddler crab

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### ABSTRACT

Reproductively active males of the sand fiddler crab *Uca pugnator* are routinely exposed to high body temperatures and desiccation while defending breeding-burrows from other males or displaying to attract females. Such males are generally larger than individuals in other parts of the marsh, in part, because large males win more contests and have greater energy stores. We propose an additional explanation: that higher thermal inertia and lower mass-specific water loss rates may make large males less susceptible to thermal and hydration stresses than small males. We experimentally investigated the effects of variation in body temperature ( $T_b$ ) and desiccation on physiological performance and behavior of male sand fiddler crabs as a function of body size. Treadmill endurance and sprint speed increased to a maximum before decreasing rapidly with further increases in  $T_b$ . Moderate dehydration (7–10% body water loss) resulted in significantly reduced locomotor performance, with small crabs exhibiting the greatest reductions in both body water and performance capacity. Fiddler crabs appear to be sensitive to the potentially conflicting demands of body temperature and hydration state. In a laboratory thermal gradient, crabs on wet sand chose  $T_b$ 's associated with high locomotor performance capacity. In contrast, crabs on dry sand selected lower  $T_b$ 's that presumably minimized water loss, with small crabs choosing the lowest  $T_b$ 's. In addition to providing empirical support for a general model of ectotherm locomotion, our results are consistent with the idea that larger individuals are better able to tolerate harsh environmental conditions above-ground, increasing the proportion of time they can spend engaging in fitness-enhancing reproductive activities rather than sheltering in a burrow.

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### 1. Introduction

The marine intertidal zone has been a model system for the experimental investigation of organismal responses to physical disturbance and physiological stress for decades (Bertness et al., 1999; Connell, 1961; Dayton, 1971; Menge, 1976). Characterized by steep gradients and high variability in physical conditions over small spatial and temporal scales, the utility of intertidal shores as a natural laboratory is due largely to the severity of the local environment. At low tide, marine organisms often experience physiological stress or even mortality from high body temperatures and desiccation associated with aerial exposure (Davison and Pearson, 1996; Helmuth et al., 2002; Somero, 2002). Although individuals can mitigate to some degree their vulnerability to extreme conditions through behavior (e.g. microhabitat selection; Huey, 1991) or physiological plasticity (e.g. expression of heat

shock proteins; Somero, 2002), temperature and desiccation stresses are widely viewed as perhaps the most significant abiotic factors influencing the performance and fitness of marine intertidal organisms (Helmuth et al., 2005; Hochachka and Somero, 2002).

Organismal body temperatures and water loss rates are strongly affected by ambient air temperature, wind speed and relative humidity at the time of low tide (Helmuth, 1998; Porter and Gates, 1969; Tracy, 1976). Subsequent effects of thermal and desiccation stresses on individuals are mediated both directly through physiological sensitivities (Deutsch et al., 2008; Huey, 1991; Somero, 2002) and indirectly through changes in species interactions (e.g. predation, competition, and facilitation) (Leonard, 2000; Pincebourde et al., 2008; Sanford, 1999). While the interactive effects of temperature and desiccation on the physiological and demographic performance of ectotherms have been well documented in terrestrial vertebrates (e.g. Crowley, 1985; O'Connor and Tracy, 1992; Preest and Pough, 1989) and arthropods (e.g. Carlson and Rowe, 2009; Herreid et al., 1981; Kingsolver, 1979), somewhat fewer studies have investigated the extent to which temperature and dehydration combine to limit the performance capacity of marine intertidal organisms, especially mobile animals (but see Weinstein, 1998; Weinstein et al., 1994). Thermal and hydration constraints are likely to be especially important for small intertidal

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organisms that have low thermal inertia and a water-permeable integument; as such, fiddler crabs in the genus *Uca* are excellent organisms for testing ideas about environmental constraints on physiology and behavior (Edney, 1961; Silbiger and Munguia, 2008; Smith and Miller, 1973; Thurman, 1998).

The sand fiddler crab, *Uca pugilator* Bosc (Fig. 1), is a small, highly active semi-terrestrial species that lives in sheltered areas of salt marshes along the Atlantic and eastern Gulf coasts of North America. Although non-breeding individuals are typically found foraging near the waterline or in simple refuge burrows within the marsh vegetation, reproductive activity is limited to open sand flats in the high intertidal zone (Christy, 1982, 1983; Croll and McClintock, 2000; Pratt and McLain, 2002). Environmental conditions are generally less stressful at lower levels in the marsh (Allen, 2007; Bortolus et al., 2002; Reinsel and Rittschof, 1995), however, females strongly prefer to mate with males controlling specialized breeding burrows high on the shore because of the reduced risk of burrow collapse due to tidal flooding. Males in these locations are exposed to air for long periods of time while using a single greatly-enlarged major claw as a weapon in agonistic contests with other males for control of burrows or in species-specific waving displays to attract receptive females for mating (Christy, 1978; Crane, 1975; Pope, 2000; Pratt et al., 2003). After mating, females stay sheltered in the breeding burrow for about two weeks, brooding their eggs before emerging to release planktonic larvae into the water (Christy, 1982, 1983). In contrast, males quickly return to the marsh surface to resume courting and fighting during low tide (Christy, 1978, 1982).

Males in the high intertidal breeding areas, a small subset of the total population, are generally larger and have larger claws for their body size than males in other parts of the marsh (Christy, 1983; Pratt and McLain, 2002; Pratt et al., 2003). Large males win more contests, display with greater vigor, and are attractive to females (Christy, 1983; Hyatt and Salmon, 1978; Pratt and McLain, 2002). Presumably, small males are either quickly evicted from the breeding area by larger individuals (Jennions and Backwell, 1996; Pratt et al., 2003), run out of energy faster (Backwell et al., 1995; Jennions and Backwell, 1998; Kim and Choe, 2003; Pratt and McLain, 2002), or abandon the area after having little success in attracting a mate (Jennions and Backwell, 1998). In general, small organisms also have lower thermal inertia and higher mass-specific water loss rates than do large ones (Herreid, 1969; Stevenson, 1985; Yoder et al., 2007). Mating activity by *U. pugilator* occurs in mid-summer and previous work has shown that both thermal and desiccation stresses to surface-active crabs are potentially



**Fig. 1.** Male sand fiddler crab, *Uca pugilator*. The greatly enlarged major claw functions as both a weapon to defend specialized breeding burrows from other males and an ornament to attract females for mating. Photograph by D. DeLambert.

high at that time (Allen, 2007), suggesting an additional hypothesis to explain the skewed size distribution of males in the breeding area: small males are more susceptible to thermal and hydration stresses than large males and may therefore spend less time active on the marsh surface.

Here we experimentally investigate how body temperature and dehydration differentially affect the physiological performance and behavioral choices of male sand fiddler crabs as a function of individual body size. We address four specific questions: (1) how does locomotor performance (endurance capacity and sprint speed) vary as a function of crab body temperature; (2) how does desiccation rate vary as a function of crab body size; (3) how does locomotor performance (endurance capacity) vary as a function of crab body size and hydration state; and (4) how does crab body size influence behavioral choices made by fiddler crabs in response to environmental variation in temperature and water availability. We then evaluate our results in the context of the fiddler crab mating system.

## 2. Materials and methods

We collected surface-active male *U. pugilator* from Flax Pond, a *Spartina alterniflora* dominated salt marsh located on the northern shore of Long Island, New York, USA (40° 58' N, 73° 08' W) from June to September in 2004–2006, during the crab's reproductive season. Prior to experimentation, crabs were held in the laboratory at 20 °C in large aquaria with re-circulating seawater and fed TetraMarine fish flakes (Tetra, Blacksburg, VA) ad libitum. All crabs were held without food for 12 h immediately prior to data collection and no animals were kept for more than 10 days. For the initial experiment on locomotor performance, we used adult crabs similar in size to larger individuals displaying in the breeding areas of the marsh (carapace width =  $19.88 \pm 0.91$  mm; mean  $\pm$  SD). For subsequent experiments manipulating desiccation, we either used crabs of a range of body sizes (13.8–21.7 mm) or grouped individuals into two size classes: 'small' ( $16.79 \pm 1.05$  mm) and 'large' ( $21.24 \pm 0.77$  mm) that represent typical endpoints of the local body size continuum of reproductively active males (see also Pratt et al., 2003). For each crab, we measured carapace width to the nearest 0.01 mm with digital calipers and wet body mass to the nearest 0.001 g with a Sartorius LC 620 D balance.

### 2.1. Temperature and locomotor performance

Individual crabs were run on a motorized treadmill (Pro-Form 285T modified with a Dayton 4Z861 10:1 speed reducer) at a velocity of  $4 \text{ m min}^{-1}$  ( $0.24 \text{ km h}^{-1}$ ) at one of eight body temperatures ( $T_b = 5, 10, 15, 20, 25, 30, 35$  and  $40$  °C;  $n = 20$  crabs per  $T_b$ , 160 total). This velocity represents the mid-range of treadmill speeds used by Full and Herreid (1984) ( $0.06$ – $0.40 \text{ km h}^{-1}$ ) and is just above a performance threshold. Individuals running at this speed or higher lose stamina much faster than crabs running at slower velocities. The treadmill was located in a temperature-controlled environmental chamber set to produce the appropriate  $T_b$  for crabs in each trial (relative humidity was 40–60% as measured with a handheld hygrometer). Prior to being run to fatigue, crabs were given a 20-min habituation period on the motionless treadmill. Following the protocol of Full and 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 (see also Allen and Levinton, 2007). Each crab was subjected to a single trial. To minimize disturbance to experimental animals, we verified treatment temperatures by measuring  $T_b$ 's on a separate set of crabs in each treatment group that were otherwise handled identically to those described above ( $n = 5$  for each  $T_b$ , 40 total). Body temperatures were measured with a digital thermometer and penetrating hypodermic thermocouple probe (accuracy of  $\pm 0.1$  °C; 0.79 mm diameter) inserted laterally 3–4 mm into the carapace just forward of the tip of the flexed abdomen.

We determined the relationship between sprint speed and  $T_b$  for male *U. pugilator* by running individuals in a straight raceway at the same eight  $T_b$ 's ( $n=25$  crabs per  $T_b$ , 200 total). The wooden raceway measured 1.80 m long  $\times$  0.20 m wide  $\times$  0.24 m high, had a running surface of packed sand and was located in the environmental chamber described above. We released individual crabs at one end of the track and chased them to the other end. As above, each crab was subjected to a single trial. 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.

The upper endpoint on a thermal performance curve is set by the critical thermal maximum ( $CT_{max}$ ), the  $T_b$  at which locomotor performance is impaired to the point that an organism is effectively unable to move (Angilletta et al., 2002; Lagerspetz and Vainio, 2006). To determine  $CT_{max}$  of *U. pugilator*, we raised the  $T_b$ 's of ( $n=10$ ) fiddler crabs from 20 to 48 °C at a rate of 1 °C  $min^{-1}$  with a temperature-controlled water bath. This rate of heating is similar to what crabs experience in the field on warm sunny days (Smith and Miller, 1973; authors' unpublished data). Crabs were kept in a shallow glass dish containing filtered seawater to a depth of 1.5 cm (enough to half cover the crabs). Starting at 40 °C, crabs were removed from the water bath every minute, their  $T_b$ 's were measured as above and they were placed on their backs. Individuals that were able to right themselves were returned to the water bath to continue heating, whereas those that could not recover within the 1-min interval were removed. Crabs were typically out of the water for less than 15 s at a time. We calculated  $CT_{max}$  as the mean of the  $T_b$ 's at which individuals were unable to right themselves (Lagerspetz and Vainio, 2006).

## 2.2. Desiccation and locomotor performance

For this experiment, temperature in the environmental chamber was set at a constant 30 °C. Prior to being run to fatigue, crabs of different sizes (mass =  $2.74 \pm 0.79$  g; mean  $\pm$  SD) were given a 20-min habituation period on the treadmill either immediately following removal from seawater, or after a 2-h drying period during which they were exposed to ambient chamber air while sitting in a shallow open container. The treadmill was held motionless during this time. A preliminary study found that crabs typically lost 4–10% of their body mass over the 2 h period, depending upon their starting size and presumably representing water loss due to evaporation and respiration (Weinstein, 1998; Yoder et al., 2005, 2007). The order in which crabs were run was randomized with respect to body size and drying time ( $n=49$  'no drying', 36 '2 h drying').

Similar to the temperature experiment, we measured hydration state and  $T_b$  at the beginning of the endurance trials for a separate set of crabs in each treatment group (mass =  $2.89 \pm 0.81$  g) that were otherwise treated identically to those described above ( $n=40$  in both groups). Based on those results, percent water loss was assumed to be zero for crabs in the 'no drying' treatment groups. During the 20-min habituation period, crabs were enclosed in a small box under conditions of close to 100% relative humidity, limiting water loss to essentially nil over such a short time interval (Yoder et al., 2005). Dehydration rate for crabs in the '2 h drying' treatment groups was calculated as the difference in body mass before and after exposure to air, expressed in units of g  $H_2O$  lost per g crab mass per hour.

## 2.3. Selected body temperatures

To determine whether body size interacts with hydration state to influence the thermal preferences of fiddler crabs, we estimated the range of body temperatures selected by animals in the absence of associated ecological costs and constraints – so-called set-point or target  $T_b$ 's ( $T_{set}$ ; Hertz et al., 1993; Huey 1991; Huey and Slatkin, 1976; Huey et al., 1989) for small and large crabs on both wet and dry sand. We estimated  $T_{set}$  by allowing individual crabs to move about freely in a laboratory thermal gradient before taking their body temperature. The working section of the thermal gradient consisted of an open Plexiglas raceway (1.20 m long  $\times$  0.10 m wide  $\times$  0.10 m high) mounted on a solid aluminum bar (1.80 m long  $\times$  0.10 m wide  $\times$  0.05 m high) covered with a thin layer of sand. Each end of the aluminum bar was transited by four rigid copper pipes (1.27 cm (1/2 in.) diameter); heated water was circulated through the pipes at one end and chilled water at the other using recirculating water baths (Forma Scientific, Marietta, OH), resulting in substratum temperatures that changed linearly along the length of the bar. Crabs could easily choose a  $T_b$  from approximately 5 to 45 °C by changing their physical location in the thermal gradient. Individual male *U. pugilator* ( $n=20$  per treatment group, 80 total) were placed at random inside the Plexiglas raceway and allowed to adjust for 15 min before their body temperature was recorded with the digital thermometer described above; preliminary studies showed that this was enough time for them to explore the gradient and settle at a particular  $T_b$ . The thermal gradient was located behind an opaque screen to minimize external stimuli to the experimental crabs. We defined  $T_{set}$  as the range between the first and third quartiles of the distribution of all  $T_b$ 's selected in the gradient, a common metric in studies of thermal biology (Blouin-Demers and Weatherhead, 2001; Christian and Weavers, 1996; Hertz et al., 1993).

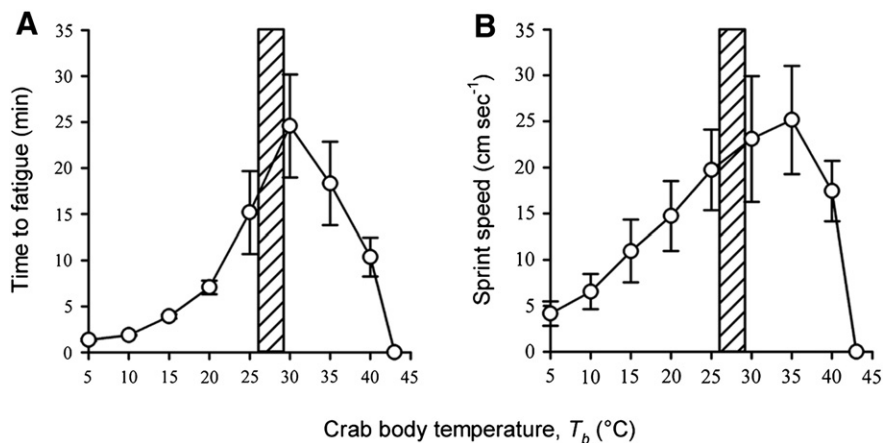


Fig. 2. Mean  $\pm$  SE locomotor performance of male *Uca pugilator* as a function of body temperature ( $T_b$ ): (A) endurance capacity; and (B) sprint speed. The hatched bars represent the mid-range of  $T_b$ 's selected by male fiddler crabs on wet sand in a laboratory thermal gradient ( $T_{set}$ ; see text for details).

## 2.4. Statistical analyses

We tested for differences in fiddler crab locomotor performance as a function of  $T_b$  with one-way analyses of variance (ANOVA) with temperature as a fixed factor. Data were transformed with a  $\ln(x+1)$  function to correct for unequal variances and non-normality (Sokal and Rohlf, 1995). The relationships between fiddler crab body size and desiccation rate and locomotor performance were evaluated with linear regressions. Size-specific variation in selected  $T_b$ 's under different hydration conditions were compared with two-way

ANOVA with body size and sand hydration (wet or dry) as fixed factors on  $\ln(x+1)$  transformed data. Post-hoc multiple comparisons following the two-way ANOVAs were done with Tukey's HSD tests. All analyses were done with JMP 5.1.

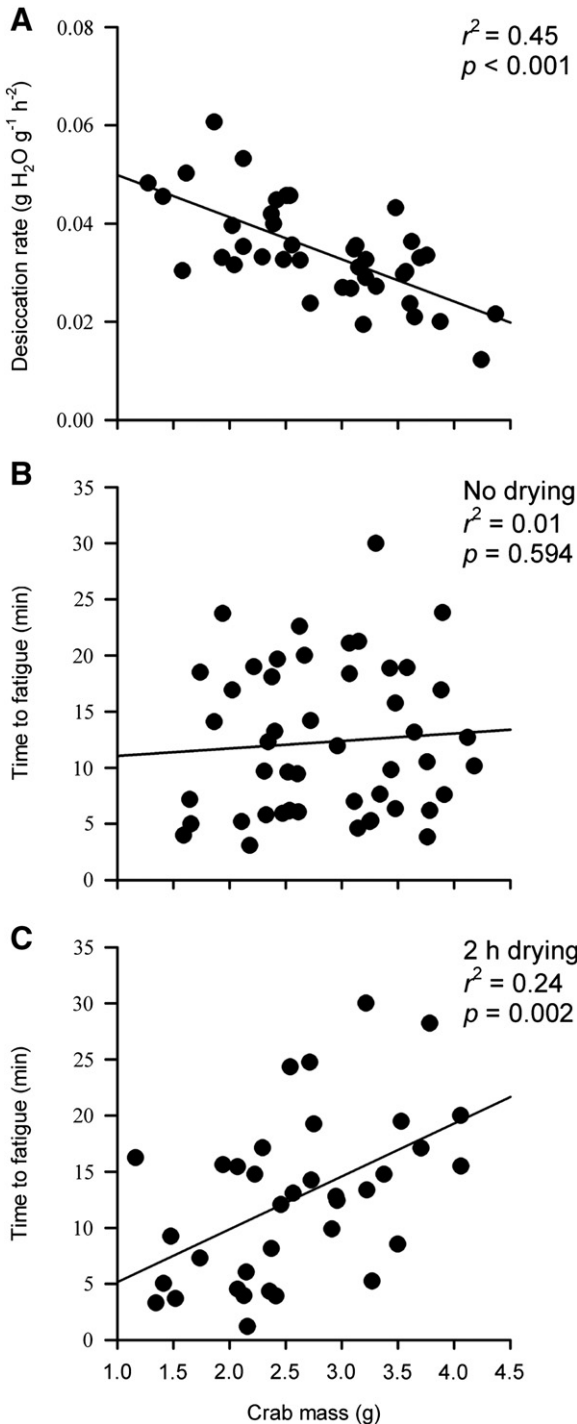
## 3. Results

### 3.1. Temperature and locomotor performance

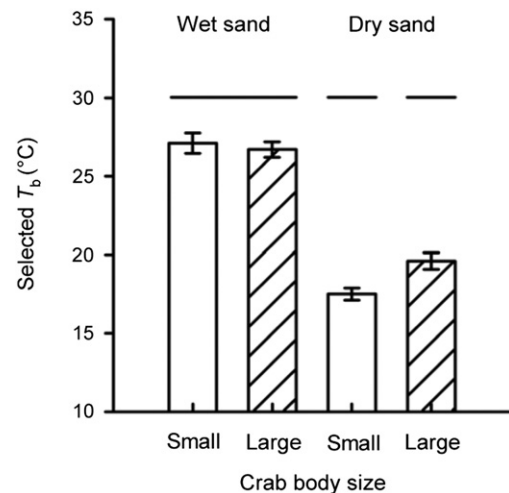
There were statistically significant differences in locomotor performance as a function of temperature (endurance:  $F_{7, 152} = 32.58$ ,  $p < 0.001$ ; sprint speed:  $F_{7, 192} = 130.40$ ,  $p < 0.001$ ). Fiddler crab endurance capacity was maximized at a  $T_b$  of 30 °C, while sprint speed was maximized at 35 °C (Fig. 2A, B). In both cases, locomotor performance initially improved with increasing  $T_b$ , was maximized at an intermediate  $T_b$ , and declined precipitously at  $T_b$ 's above this range.  $CT_{max}$  for male fiddler crabs in this study was  $43.1 \pm 0.41$  °C (mean  $\pm$  SE).

### 3.2. Desiccation and locomotor performance

Although all crabs had similar hydration states immediately upon removal from seawater (100% hydrated), during a 2-h period of exposure to air small crabs lost water at a higher proportional rate than large crabs (Fig. 3A; desiccation rate =  $0.06 - 0.01 \times$  crab mass;  $r^2 = 0.45$ ,  $p < 0.001$ ,  $n = 40$ ). While hydrated crabs of all body sizes exhibited  $T_b$ 's that were 5–6 °C below ambient air temperature due to evaporative cooling ( $23.9 \pm 0.70$  °C; mean  $\pm$  SD), after 2 h of aerial exposure  $T_b$ 's of experimental crabs had increased closer to ambient ( $28.0 \pm 1.24$  °C), presumably due a reduction in the efficacy of such cooling over time. Given the strong temperature dependence of locomotor performance in *U. pugilator* (Fig. 2A, B; Weinstein, 1998), we decided to evaluate the relationship between time to fatigue and body size separately for the two groups. There was no effect of body size on endurance capacity of hydrated fiddler crabs (Fig. 3B; time to fatigue =  $10.23 + 0.72 \times$  crab mass;  $r^2 = 0.01$ ,  $p = 0.594$ ,  $n = 49$ ); in contrast, there was a positive effect of body size on endurance capacity of experimental crabs, with smaller crabs more strongly affected by drying time (Fig. 3C; time to fatigue =  $0.45 + 4.71 \times$  crab mass;  $r^2 = 0.24$ ,  $p = 0.002$ ,  $n = 36$ ), presumably due to their higher rate of dehydration.



**Fig. 3.** Relationships between mass of male *Uca pugilator* and (A) desiccation rate; (B) endurance capacity immediately following removal of crabs from seawater; and (C) endurance capacity after 2 h drying in an environmental chamber held at a constant 30 °C.



**Fig. 4.** Mean  $\pm$  SE body temperatures ( $T_b$ ) selected by male *Uca pugilator* in a laboratory thermal gradient ( $T_{set}$ ) as a function of body size [small crabs (open bars); large crabs (hatched bars)] and sediment water content (wet sand or dry sand). Small (carapace width =  $16.79 \pm 1.05$  mm; mean  $\pm$  SD) and large ( $21.24 \pm 0.77$  mm) size classes represent typical endpoints of the local body size continuum of reproductively active males. Non-overlapping horizontal bars indicate significant differences among treatment groups at the  $\alpha = 0.05$  level with Tukey's HSD test.

### 3.3. Selected body temperatures

On wet sand, the mean  $T_b$  selected by small crabs in the thermal gradient was 27.1 °C (the first and third quartiles defining  $T_{set}$  were 25.6 °C and 28.0 °C), similar to the 26.7 °C ( $T_{set}$  between 25.5 °C and 28.3 °C) selected by large individuals. In contrast, on dry sand the mean  $T_b$  selected by small crabs was 17.5 °C ( $T_{set}$  between 16.1 °C and 19.0 °C), compared with 19.6 °C ( $T_{set}$  between 17.7 °C and 20.7 °C) for large crabs. The interaction between body size and sediment hydration state (wet or dry) was statistically significant ( $F_{1, 76} = 6.84$ ,  $p = 0.011$ ). Large and small crabs chose similar high  $T_b$ 's under wet conditions. In contrast, while crabs of all sizes selected lower  $T_b$ 's under dry conditions, small crabs chose the lowest (Fig. 4).

## 4. Discussion

Fiddler crabs exhibited a pattern of locomotor performance as a function of  $T_b$  typical of many ectothermic organisms (e.g. Angilletta et al., 2002; Huey, 1982; Weinstein, 1998). Combined with the results of the thermal gradient experiment, these data suggest that in the absence of competing costs and constraints, fiddler crabs can and do select  $T_b$ 's that come reasonably close to optimizing their locomotor performance (see also Weinstein, 1998). The observation that fiddler crabs preferentially select  $T_b$ 's slightly below their measured performance optima is consistent with a new model of ectotherm temperature biology (Martin and Huey, 2008). Given that the thermal dependence of ectotherm performance is asymmetric, a  $T_b$  higher than the temperature at which performance capacity is maximized ( $T_{pmax}$ ) is generally expected to reduce performance more than would a  $T_b$  the same level below  $T_{pmax}$ . Ectotherms are imperfect thermoregulators that typically experience a range of body temperatures throughout the day. Under these conditions, the optimal body temperature (that which maximizes total fitness over time) should not be centered at  $T_{pmax}$  (which represents the maximization of instantaneous fitness), but rather, shifted to a somewhat lower temperature (Martin and Huey, 2008).

Hydration state and body size interacted strongly with fiddler crab body temperature to influence individual physiology and behavior. Variation in performance (e.g., endurance or sprint speed) presumably relates to variation in whole organism functional capability, influencing how an individual's phenotype interacts with their environment (Arnold 1983). Although locomotor performance of small crabs was comparable to that of large crabs when both groups were hydrated, they did far worse when moderately dehydrated (7–10% water loss) after 2 h of aerial exposure. Under similar environmental conditions, small crabs experienced greater water loss and presumably associated desiccation stress compared with large crabs. Darnell and Munguia (2011) reported a similar pattern of increasing dehydration rate with decreasing body size for the closely-related fiddler crab *U. panacea*. Studies of terrestrial locomotion in ghost crabs (*Ocypode quadrata*), crayfish (*Orconectes rusticus*), and isopods (*Porcellio laevis*) have found that locomotion is significantly reduced or even ceases when water loss approaches 10% (Claussen et al., 2000; Dailey et al., 2009; Weinstein et al., 1994). In ghost crabs (the sister taxon of *Uca*), water loss of only 3.6% initial body weight over a period of 90 min decreased maximum aerobic speed (the rate of locomotion at which maximum oxygen consumption is attained) by 32% relative to hydrated crabs; maximum aerobic speed was significantly correlated with endurance capacity (Weinstein, 1998; Weinstein et al., 1994). Effects of dehydration on locomotor performance are influenced by the rate of water loss: more rapid dehydration leads to a greater reduction in performance capacity, even if the total amount of water loss is the same (Weinstein, 1998). Under typical mid-summer conditions of high solar radiation and air temperatures and moderate winds, small fiddler crabs can lose 10% of their body water in less than 20 min (authors' unpublished data), suggesting that in the exposed breeding area

surface-active crabs without access to a burrow for refuge might be at significant risk of impairment on many days.

Our results support a general model of ectotherm terrestrial locomotor performance that predicts performance capacity will increase with  $T_b$  at moderate temperatures up to a point, decrease with increasing dehydration, and that the magnitude of this decrease will change depending on  $T_b$  (Preest and Pough, 1989; Weinstein, 1998). Mass-specific water loss rates are inversely related to body size in aquatic and semi-terrestrial crabs and larger individuals contain more water overall (Grant and McDonald, 1979; Yoder et al., 2010). As a consequence, under similar environmental conditions, large crabs stay hydrated longer and therefore perform better, than small crabs. Whereas small males can quickly reach  $T_b$ 's and desiccation levels detrimental to physiological performance, larger males approach those limits more slowly. Hyatt (1977) observed that large reproductively-active male *U. pugilator* spent less time in their burrows than small individuals and suggested that this might be due to reduced tolerance to thermal and desiccation stresses of small crabs. Our data are consistent with this hypothesis. Similarly, Darnell and Munguia (2011) showed that the major claw of fiddler crabs can function as a heat sink, transferring heat away from the body such that large males with relatively larger claws will gain heat more slowly than small individuals.

Of tropical origin, fiddler crabs are very permeable and exhibit high net water loss rates (Crane, 1975; Thurman, 1998; Yoder et al., 2005, 2010). The associated high rates of evaporative cooling can be extremely effective at lowering fiddler crab body temperatures in hot, dry environments such as the high intertidal breeding area (Edney, 1961; Powers and Cole, 1976; Smith and Miller, 1973; Thurman, 1998). The primary limitation of such a strategy is the availability of free water to replace that lost to evaporation. Non-reproductive crabs foraging on creek banks low in the marsh have easy access to shallow standing water. Crabs in this microhabitat are typically active even on hot days when fiddler crabs in other parts of the marsh are in their burrows (Allen, 2007), suggesting that an ability to remain fully hydrated extends the range of environmental conditions over which crabs can remain on the marsh surface. In contrast, the main source of water to fiddler crabs in the breeding area is likely to be interstitial water in the burrow. Fiddler crabs, and the closely-related ghost crab, *O. quadrata*, use hydrophilic tufts of setae located at the base of their walking legs to efficiently extract water from damp sand (Thompson et al., 1989; Wolcott, 1984). When surface sediments become dry (as is common in the breeding area; Allen 2007) crabs can still hydrate effectively within their burrows. Nevertheless, the need to remain below-ground to do so presents an opportunity cost to crabs that need to rehydrate frequently, as they will consequently spend less time participating in reproductive or foraging activities.

Fiddler crabs appear to be sensitive to the potentially conflicting demands of body temperature and hydration state. Crabs on wet sand in the laboratory chose  $T_b$ 's associated with high locomotor performance capacity (Allen, 2007; Weinstein, 1998), while on dry sand they accepted lower temperatures that presumably reduced their rate of dehydration due to evaporation. Small crabs, with the highest mass-specific water loss rates, selected the lowest  $T_b$ 's on dry sand. Our results suggest that fiddler crabs may be choosing combinations of body temperature and hydration state that optimize the joint function of the two variables, rather than either one separately (Huey, 1991; Huey and Slatkin, 1976; Huey and Stevenson, 1979). While this may be relatively easy to do in the laboratory in the absence of associated ecological costs and constraints, the ability of fiddler crabs to make similar choices in the field will often be limited by other factors. The high intertidal breeding area is the only salt marsh microhabitat with consistently dry sediment and high environmental temperatures, a combination that provides relatively few opportunities for surface-active crabs to reach their preferred  $T_b$ . In

contrast, crabs foraging in the lower marsh often have  $T_b$ 's within that range (Allen, 2007). Our data suggest that larger individuals may be better able to tolerate environmental conditions further from their optimal state, increasing the proportion of time they can spend participating in fitness-enhancing behaviors such as foraging, burrow defense, and courtship, rather than sheltering underground.

We are certainly not suggesting that existing mechanistic explanations for the observed surfeit of large males in the sand fiddler crab breeding area are incorrect. The importance of competitive dominance, energy stores, and attractiveness to females is well documented (Christy, 1983; Crane, 1975; Jennions and Backwell, 1996, 1998; Pratt and McLain, 2002; Pratt et al., 2003). Rather, we wish to raise the possibility that in addition to the factors listed above, physiological and behavioral responses to local environmental conditions might play an additional and even important role in structuring fiddler crab populations in space and time. These constraints may modulate allocation of time by male fiddler crabs to mating activities while in the breeding area, and of time spent in the breeding area versus rehydrating and feeding in other less physiologically stressful habitats in the marsh. For example, is it better for a smaller male to attempt to court in hotter, drier areas where they will encounter more females when they are on the surface even though the total amount of time they can spend on the surface is limited by temperature and desiccation stresses, or to take a burrow in a cooler and wetter peripheral location where the female encounter rate is lower? Experimental manipulations of fiddler crab social context (e.g., male size distributions) and environmental parameters (e.g., levels of solar radiation, air and sediment temperatures, and water availability) will likely prove to be tractable and informative with respect to understanding the potential importance of ecological constraints on mating behavior and sexual selection.

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## References

- Allen, B.J., 2007. Costs of sexual selection in the sand fiddler crab, *Uca pugilator*. PhD thesis, Stony Brook University, Stony Brook, NY.
- Allen, B.J., Levinton, J.S., 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. *Funct. Ecol.* 21, 154–161.
- Arnold, S.J., 1983. Morphology, performance and fitness. *Am. Zool.* 23, 347–361.
- Angilletta, M.J., Niewiarowski, P.H., Navas, C.A., 2002. The evolution of thermal physiology in ectotherms. *J. Therm. Biol.* 27, 249–268.
- Backwell, P.R.Y., Jennions, M.D., Christy, J.H., Schober, U., 1995. Pillar building in the fiddler crab *Uca beebei*: evidence for a condition-dependent ornament. *Behav. Ecol. Sociobiol.* 36, 185–192.
- Bertness, M.D., Leonard, G.H., Levine, J.M., Bruno, J.F., 1999. Climate-driven interactions among rocky intertidal organisms caught between a rock and a hot place. *Oecologia* 120, 446–450.
- Blouin-Demers, G., Weatherhead, P.J., 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82, 3025–3043.
- Bortolus, A., Schwindt, E., Iribarne, O., 2002. Positive plant–animal interactions in the high marsh of an Argentinian coastal lagoon. *Ecology* 83, 733–742.
- Carlson, B.E., Rowe, M.P., 2009. Temperature and desiccation effects on the antipredator behavior of *Centruroides vittatus* (Scorpiones: Buthidae). *J. Arachnol.* 37, 321–330.
- Christian, K.A., Weavers, B.W., 1996. Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecol. Monogr.* 66, 139–157.
- Christy, J.H., 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: a hypothesis. *Science* 199, 453–455.
- Christy, J.H., 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Anim. Behav.* 30, 687–694.
- Christy, J.H., 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behav. Ecol. Sociobiol.* 12, 169–180.
- Claussen, D.L., Hopper, R.A., Sanker, A.M., 2000. The effects of temperature, body size, and hydration state on the terrestrial locomotion of the crayfish *Orconectes rusticus*. *J. Crust. Biol.* 20, 218–223.
- Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31, 61–104.
- Crane, J.C., 1975. Fiddler Crabs of the World. Princeton University Press, Princeton.
- Croll, G.A., McClintock, J.B., 2000. An evaluation of lekking behavior in the fiddler crab *Uca* spp. *J. Exp. Mar. Biol. Ecol.* 254, 109–121.
- Crowley, S.R., 1985. Insensitivity to desiccation of sprint running performance in the lizard, *Sceloporus undulatus*. *J. Herpetol.* 19, 171–174.
- Dailey, T.M., Claussen, D.L., Ladd, G.B., Buckner, S.T., 2009. The effects of temperature, desiccation, and body mass on the locomotion of the terrestrial isopod, *Porcellio laevis*. *Comp. Biochem. Physiol. A* 153, 162–166.
- Darnell, M.Z., Munguia, P., 2011. Thermoregulation as an alternate function of the sexually dimorphic fiddler crab claw. *Am. Nat.* 178, 419–428.
- Davison, I.R., Pearson, G.A., 1996. Stress tolerance in intertidal seaweeds. *J. Phycol.* 32, 197–211.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Nat. Acad. Sci. U.S.A.* 105, 6668–6672.
- Edney, E.B., 1961. The water and heat relationships of fiddler crabs (*Uca* spp.). *Trans. R. Soc. S. Africa* 36, 71–91.
- Full, R.J., Herreid II, C.F., 1984. Fiddler crab exercise: the energetic cost of running sideways. *J. Exp. Biol.* 109, 141–161.
- Grant, J., McDonald, J., 1979. Desiccation tolerance of *Eurypanopeus depressus* (Smith) (Decapoda: Xanthidae) and the exploitation of microhabitat. *Estuaries* 2, 172–177.
- Helmuth, B., Kingsolver, J.G., Carrington, E., 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu. Rev. Physiol.* 67, 177–201.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., Blanchette, C.A., 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298, 1015–1017.
- Helmuth, B.S.T., 1998. Intertidal mussel microclimates: predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* 68, 51–74.
- Herreid II, C.F., 1969. Water loss of crabs from different habitats. *Comp. Biochem. Physiol.* 28, 829–839.
- Herreid II, C.F., Full, R.J., Prawel, D.A., 1981. Energetics of cockroach locomotion. *J. Exp. Biol.* 94, 189–202.
- Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.
- Hochachka, P.W., Somero, G.N., 2002. Biochemical Adaptation: Mechanism and Process in Physiological Evolution. Oxford University Press, London.
- Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles. In: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia: Physiology C. Physiological Ecology*, 12. Academic Press, New York, pp. 25–91.
- Huey, R.B., 1991. Physiological consequences of habitat selection. *Am. Nat.* 137, S91–S115.
- Huey, R.B., Slatkin, M., 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51, 363–384.
- Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19, 357–366.
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944.
- Hyatt, G.W., 1977. Field studies of size-dependent changes in waving display and other behavior in fiddler crab, *Uca pugilator* (Brachyura, Ocypodidae). *Mar. Behav. Physiol.* 4, 283–292.
- Hyatt, G.W., Salmon, M., 1978. Combat in fiddler crabs *Uca pugilator* and *Uca pugnax*: a quantitative analysis. *Behaviour* 65, 182–211.
- Jennions, M.D., Backwell, P.R.Y., 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* 57, 293–306.
- Jennions, M.D., Backwell, P.R.Y., 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behav. Ecol.* 9, 605–611.
- Kim, T.W., Choe, J.C., 2003. The effect of food availability on the semilunar courtship rhythm in the fiddler crab *Uca lactea* (de Haan) (Brachyura: Ocypodidae). *Behav. Ecol. Sociobiol.* 54, 210–217.
- Kingsolver, J.G., 1979. Thermal and hydration aspects of environmental heterogeneity in the pitcher plant mosquito. *Ecol. Monogr.* 49, 357–376.
- Lagerspetz, K.Y.H., Vainio, L.A., 2006. Thermal behaviour of crustaceans. *Biol. Rev.* 81, 237–258.
- Leonard, G.H., 2000. Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81, 1015–1030.
- Martin, T.L., Huey, R.B., 2008. Why “suboptimal” is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* 171, 102–118.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46, 355–393.
- O'Connor, M.P., Tracy, C.R., 1992. Thermoregulation by juvenile toads of *Bufo woodhousi* in the field and laboratory. *Copeia* 1992, 865–876.
- Pincebourde, S., Sanford, E., Helmuth, B., 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnol. Oceanogr.* 53, 1562–1573.

- Pope, D.S., 2000. Testing function of fiddler crab claw waving by manipulating social context. *Behav. Ecol. Sociobiol.* 47, 432–437.
- Porter, W.P., Gates, D.M., 1969. Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* 39, 227–244.
- Powers, L.W., Cole, J.F., 1976. Temperature variation in fiddler crab microhabitats. *J. Exp. Mar. Biol. Ecol.* 21, 141–157.
- Pratt, A.E., McLain, D.K., 2002. Antisymmetry in male fiddler crabs and the decision to feed or breed. *Funct. Ecol.* 16, 89–98.
- Pratt, A.E., McLain, D.K., Lathrop, G.R., 2003. The assessment game in sand fiddler crab contests for breeding burrows. *Anim. Behav.* 65, 945–955.
- Preest, M.R., Pough, F.H., 1989. Interaction of temperature and hydration on locomotion of toads. *Funct. Ecol.* 3, 693–699.
- Reinsel, K.A., Rittschof, D., 1995. Environmental regulation of foraging in the sand fiddler crab *Uca pugilator* (Bosc 1802). *J. Exp. Mar. Biol. Ecol.* 187, 269–287.
- Sanford, E., 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283, 2095–2097.
- Silbiger, N., Munguia, P., 2008. Carapace color change in *Uca pugilator* as a response to temperature. *J. Exp. Mar. Biol. Ecol.* 355, 41–46.
- Smith, W.K., Miller, P.C., 1973. The thermal ecology of two south Florida fiddler crabs, *Uca rapax* Smith and *Uca pugilator* Bosc. *Physiol. Zool.* 46, 186–207.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, 3rd ed. W. H. Freeman and Co., New York.
- Somero, G.N., 2002. Thermal physiology of vertical zonation on rocky intertidal shores: optima, limits, and costs of living. *Int. Comp. Physiol.* 42, 780–789.
- Stevenson, R.D., 1985. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *Am. Nat.* 125, 102–117.
- Thompson, W.E., Molinaro, P.J., Greco, T.M., Tedeschi, J.B., Holliday, C.W., 1989. Regulation of hemolymph volume by uptake of sand capillary water in desiccated fiddler crabs, *Uca pugilator* and *Uca pugnax*. *Comp. Biochem. Physiol. A* 94, 531–538.
- Thurman, C.L., 1998. Evaporative water loss, corporal temperature and the distribution of sympatric fiddler crabs (*Uca*) from south Texas. *Comp. Biochem. Physiol. A* 119, 279–286.
- Tracy, C.R., 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecol. Monogr.* 46, 293–326.
- Weinstein, R.B., 1998. Effects of temperature and water loss on terrestrial locomotor performance in land crabs: integrating laboratory and field studies. *Am. Zool.* 38, 518–527.
- Weinstein, R.B., Full, R.J., Ahn, A.N., 1994. Moderate dehydration decreases locomotor performance of the ghost crab, *Ocypode quadrata*. *Physiol. Zool.* 67, 873–891.
- Wolcott, T.G., 1984. Uptake of interstitial water from soil: mechanisms and ecological significance in the ghost crab *Ocypode quadrata* and two gecarcinid land crabs. *Physiol. Zool.* 57, 161–184.
- Yoder, J.A., Reinsel, K.A., Welch, J.M., Clifford, D.M., Rellinger, E.J., 2005. Herding limits water loss in the sand fiddler crab, *Uca pugilator*. *J. Crustac. Biol.* 25, 141–145.
- Yoder, J.A., Tank, J.L., Rellinger, E.J., Moore, B.E., Gribbins, K.M., 2007. Differences in body size and water balance strategies between North Carolina and Florida populations of the sand fiddler crab, *Uca pugilator*. *J. Crust. Biol.* 27, 560–564.
- Yoder, J.A., Bosley, J.W., Chambers, M.J., Hart, C.E., Gribbins, K.M., Collier, M.H., 2010. Reduced cuticular permeability promotes inland habitat expansion and freshwater survival in the fiddler crab *Uca minax* but not in its less terrestrial counterparts *U. pugilator* and *U. pugnax*. *Crustaceana* 83, 481–492.