Thermal ecology of the fiddler crab *Uca panacea*: Thermal constraints and organismal responses

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Abstract

Temperature is one of the primary environmental variables limiting organismal performance, fitness, and species distributions. Yet, understanding temperature effects requires thorough exploration of thermal constraints and organismal responses that can translate to fitness and non-lethal long-term consequences under both constant and changing thermal regimes. We examined the thermal ecology of the fiddler crab *Uca panacea*, including critical thermal limits, thermal sensitivity of locomotion, operative environmental temperatures, preferred body temperatures, and acclimation ability. Operative environmental temperatures frequently reached the critical thermal maximum ($41.8 \pm 0.8^{\circ}\text{C}$, mean $\pm$ s.e.m.), especially in unvegetated microhabitats, indicating the need for behavioral thermoregulation to maintain diurnal activity patterns. Preferred body temperatures ($21.1\text{--}28.6^{\circ}\text{C}$) were substantially below the thermal optimum ($30\text{--}40^{\circ}\text{C}$), although further research is needed to determine the driver of this mismatch. Critical thermal limits shifted $2\text{--}4^{\circ}\text{C}$ in response to exposure to low (20°C) or high (35°C) temperatures, with full acclimation occurring in approximately 9 d. This capacity for rapid acclimation, combined with the capacity for behavioral thermoregulation, is a strong candidate mechanism that explains the broad habitat use and could help explain the successful pantropical distribution of fiddler crabs.

Keywords: thermal ecology, thermal tolerance, acclimation, thermal physiology, fiddler crab, *Uca panacea*, intertidal

1. Introduction

Temperature affects biological processes at all levels of organization and is one of the primary environmental variables limiting organismal performance. Although organisms show lethal responses to extreme high and low temperatures, non-lethal responses (e.g., reductions in performance, changes in behavior) are observed with deviations from the optimum temperature. A number of performance traits show strong temperature dependence, including growth rate (e.g., Kingsolver et al., 2004), fecundity (e.g. Karlsson and Van Dyck, 2005), and locomotor performance (e.g., Gilchrist, 1996), although the optimum temperature often varies among traits (e.g., Allen et al., 2012; Angilletta et al., 2002; Herrel and Bonneaud, 2012; Van Damme et al., 1991). Responses of these traits to changes in temperature are often described using thermal performance curves (TPCs). For ectotherms, TPCs are generally highly asymmetric, with performance increasing gradually to a maximum at the optimum temperature and decreasing rapidly above that temperature (Angilletta, 2006; Martin and Huey, 2008). Such non-lethal performance responses to temperature can have importance consequences for fitness (Clark et al., 2013 and references within; Kingsolver et al., 2007; Pörtner and Farrell, 2008). Beyond the organismal level, environmental temperatures interact with thermal tolerance and sensitivity to determine species' ranges and geographic distributions (Cahill et al., 2013). Understanding such thermal effects, however, requires thorough exploration of thermal constraints and organismal responses that can translate to fitness and non-lethal long-term consequences under both constant and changing thermal regimes.

In ectotherms, the thermal niche is fundamentally defined by physiological tolerances and defines a population's potential response to changing climates (Deutsch et al., 2008; Huey et al., 2012; Sunday et al., 2011). Thermal tolerances are not fixed, however, but can shift through

acclimation based on the environment experienced by the organism (Anneli Korhonen and Lagerspetz, 1996; Claussen, 1977; Somero, 2005). Thermal acclimation can thus adjust this thermal niche to a wide range of body temperatures. On a population level, acclimation ability can buffer physiological impacts of changing temperatures as well as allow a species to extend its geographic range (Somero, 2010; Stillman, 2003). Additionally, behavioral thermoregulation can further reduce thermal stress by limiting direct exposure to temperature extremes (e.g., by retreats to burrows and shifts between microhabitats), thus allowing organisms to inhabit a greater range of thermal regimes while maintaining optimal body temperatures (Huey and Slatkin, 1976; Sunday et al., 2014). Thus, the realized thermal niche of an ectotherm is defined not only by physiological tolerances, but also by acclimation and thermoregulatory ability, modulated by behavioral responses to minimize stress. We must therefore integrate multiple mechanisms and levels of biological information to understand responses of organisms to thermal stress and the role of temperature in limiting species distributions.

Fiddler crabs (Crustacea: Decapoda: Ocypodidae) are an excellent system to study the strategies used to cope with thermal stress and the interactions between environmental conditions, thermal tolerances, behavior, and acclimation ability, and have been the subject of much recent research (e.g., Allen et al., 2012; Darnell et al., 2013; Jimenez and Bennett, 2007; Munguia et al., 2013). Although the fiddler crab genus (genus *Uca*, ~98 species) is pantropical, several species have successfully colonized the temperate zone and there is large variation in geographic distributions (Crane, 1975). Thermal tolerance (e.g., Allen et al., 2012; Edney, 1961; Vernberg and Tashian, 1959; Wilkens and Fingerman, 1965), preferred temperatures (Allen and Levinton, 2014), and body temperature relationships to environmental temperatures (Allen and Levinton, 2014; Smith and Miller, 1973; Thurman, 1998) have been described for a number of

fiddler crab species, both tropical and temperate. The majority of studies have focused singly on either thermal physiology, morphological effects on body temperature, or thermoregulatory behavior (but see Allen and Levinton, 2014; Allen et al., 2012), and in general have neglected acclimation ability (but see Vernberg, 1959; Vernberg and Vernberg, 1966). In this study, we examined thermal ecology and acclimation ability of the tropical-subtropical fiddler crab *Uca panacea* Novak and Salmon, with the goal of presenting a multi-faceted view of the thermal ecology of this species (Table 1), including the capacity to acclimate to rapid climatic shifts. Experiments were conducted encompassing not only thermal tolerance and sensitivity but also operative environmental temperatures, preferred body temperatures, and acclimation ability. Specific objectives were to (1) determine critical thermal limits and thermal sensitivity of locomotion in a fiddler crab, (2) compare preferred and optimum temperature ranges to operative environmental temperatures in the fiddler crab habitat, and (3) assess acclimation ability and rates of acclimation of crabs exposed to high and low temperatures.

2. Material and Methods

2.1. Study organism

The fiddler crab *Uca panacea* inhabits sandy shorelines of the Gulf of Mexico, from northwest Florida to Tabasco, Mexico (Barnwell and Thurman, 1984). Previous research on this species has focused on physiological and behavioral traits such as time activity budgets (Caravello and Cameron, 1987a, b, 1991; Darnell et al., 2013), osmoregulation (Thurman, 2002), circadian rhythms (Darnell, 2012), thermoregulation (Darnell and Munguia, 2011; Kronstadt et al., 2013), and interactions between sexual and natural selection (Darnell et al., 2013; Darnell and Munguia, 2011). The thermal tolerance, sensitivity, and acclimation ability of this species

has not been described.

In this study, adult *Uca panacea* (carapace width 15–20 mm) were collected from the southern shore of Stedman Island (27°53.137' N, 97°07.006' W) near Port Aransas, Texas, USA in June–August, 2012. Males and females of similar sizes were used and males selected for experimentation had full-sized, brachychelous (original, un-regenerated) claws. All crabs were held in shallow plastic pans containing seawater to a depth of 1.5 cm prior to experimentation to ensure similar hydration states. Water in the pans was changed daily and crabs were fed ad libitum with crushed flake fish food (Wardley Tropical Fish Flake Food).

2.2. Operative environmental temperatures in fiddler crab habitat

We estimated operative environmental temperatures at the fiddler crab collection site using physical models constructed from iButton dataloggers (Thermochron, Maxim Integrated Products, Inc., Sunnyvale, CA) with an accuracy and resolution of 0.5° and set to record temperature every minute. Each iButton was attached with acrylic caulk to a semi-circular copper base that held the iButton ~1 cm above the sediment, mimicking the legs of the crab. Claws were also constructed of copper wire and attached to the iButton. Both male (1 large claw, 1 small claw) and female (2 small claws) models were constructed (Figure 1). We acknowledge that there are many differences between an iButton-based model and a live fiddler crab, including differences in color and morphology and a lack of multiple physiological (e.g., coloration and color change: Darnell et al., 2013; Kronstadt et al., 2013; Munguia et al., 2013; evaporative water loss: Thurman, 1998) and behavioral (e.g., retreating into burrows or altering orientation relative to the sun: Smith and Miller, 1973) mechanisms determining body temperatures of live crabs. These models thus provide an approximation of expected body

temperatures based solely on morphology and environmental conditions. Such models have been used previously with fiddler crabs and closely approximate steady-state temperatures of live crabs (Allen and Levinton, 2014). Models were deployed in full sunlight or full shade areas (1 male and 1 female model in each microhabitat, for a total of 4 models deployed at a time) throughout the crab habitat in late July and early August 2012, during the peak reproductive and activity season for *U. panacea*. Six depolyments were conducted in total, with each model deployed for 8–34 h, depending on the weather. Data were binned hourly prior to calculations of summary statistics.

2.3. Critical thermal limits

Critical thermal limits were determined within 18 hours of collection for both male and female *U. panacea*. Each individual was tested for either critical thermal minimum ($CT_{\min}$) or maximum ($CT_{\max}$), and was tested only once. For both $CT_{\min}$ and $CT_{\max}$, crabs were placed in small glass bowls (10 cm diameter) containing seawater to a depth of 1.5 cm. These bowls were then placed in a temperature-controlled water bath. This depth was sufficient to cover the legs of the crab and the ventral portion of the crab's body to ensure that body temperatures followed water temperatures, but did not result in immersion of the crab. This procedure has been used previously for fiddler crabs by Allen et al. (2012). Crab body temperatures were monitored during experiments using copper-constantan thermocouples (0.23 mm diameter) implanted ~2 mm into the body cavity through the posterior margin of the carapace. Thermocouples were connected to a USB data acquisition system (Thermes USB, Physitemp Instruments Inc., Clifton, NJ) driven by a laptop computer and logged body temperatures every 2 s. Thermocouples were quite fragile and occasionally malfunctioned due to breakage of one of the two thermocouple

wires. In cases where thermocouples malfunctioned (<5% in each experiment), the water temperature as measured by a separate thermocouple was used instead of body temperature, as preliminary experiments indicated that body temperatures closely followed water temperatures.

For CT_{min} , temperature in the water bath was decreased from room temperature at a rate of $\sim 0.3^{\circ}\text{C min}^{-1}$. Every minute, crabs were placed on their backs and tested for the righting response. Under normal circumstances, a crab handled in this way will immediately right itself. The endpoint for determination of CT_{min} was the body temperature at which crabs were unable to right themselves (i.e., the loss of righting response [LRR]; Cuculescu et al., 1998; Lutterschmidt and Hutchison, 1997b). For CT_{max} , temperature in the water bath was increased from room temperature at a rate of $\sim 0.3^{\circ}\text{C min}^{-1}$. Crabs were observed continuously, and the endpoint for determination of CT_{max} was the loss of muscular coordination and onset of muscular spasms in the legs (Lutterschmidt and Hutchison, 1997a). Crabs were allowed to recover and were returned to their original field site after experimentation.

Because of space and equipment constraints, only 6 individuals could be tested for CT_{min} or CT_{max} simultaneously. Each set of 6 crabs tested included 3 males and 3 females and was considered one block for statistical analysis. A total of 8 blocks (48 crabs; 24 males, 24 females) were tested for each measurement (CT_{min} and CT_{max}). Data were analyzed using mixed-model ANOVAs with CT_{min} or CT_{max} as the response variable. Block as a random effect, and sex and carapace width as fixed factors. A second set of mixed-model ANOVAs were run for male crabs only to test for an effect of claw size on critical thermal limits. CT_{min} and CT_{max} were the response variables, block was a random effect, and relative claw size (claw length divided by carapace width) was a fixed factor.

2.4. *Thermal sensitivity of locomotion*

To determine the thermal sensitivity of locomotion and develop thermal performance curves for the species, we tested maximum sprint speed at body temperatures of 15, 20, 25, 30, 35, and 40°C. Body temperatures for a group of 6 crabs (3 male, 3 female) were adjusted from room temperature to the experimental temperature at a rate of 0.3°C min⁻¹ in a water bath (as above). Once body temperatures had reached the desired experimental temperature, each crab was placed at one end of a straight raceway (1 m long × 5 cm wide) and chased to the other end of the raceway (Allen et al., 2012). Each run was recorded from above with a digital video camera (Canon Powershot G10, 30 frames s⁻¹) and the maximum speed reached during the run was determined from the video. Each crab was tested three times with a minimum of 15 min between tests during which time they remained in the water bath at the experimental temperature. The fastest speed from the three runs for was used as the maximum sprint speed for each crab.

Crabs used for determination of thermal sensitivity of locomotion were collected on 6 nights in June and July. A total of 36 crabs (18 males, 18 females) were tested at each temperature. Data were analyzed with a mixed-model ANOVA with collection date as a random effect, temperature and sex as fixed factors, and maximum sprint speed as the response variable. A Tukey HSD test was used for post-hoc comparisons.

2.5. *Preferred body temperature range*

Set-point body temperatures (T_{set}) were determined in a laboratory thermal gradient. The working section (1 m long × 10 cm wide) was constructed of plexiglass walls mounted on an aluminum bar (6.4 mm thick) covered with a thin layer of moist sand. One end of the aluminum

bar rested on a hot plate while the other end was submerged in an ice water bath. Within the working section, crabs were able to select from a range of body temperatures. Preliminary experiments with crabs confined at various points along the gradient confirmed that the temperature gradient was approximately linear and crabs could select body temperatures from ~10–35°C. Crabs were placed individually in the gradient at haphazard locations (different starting point for each crab) and allowed 15 min to move throughout the gradient and select a temperature. Previous work suggests that this is enough time to settle at a particular body temperature (Allen et al., 2012). After 15 min, body temperature was measured with a hypodermic thermocouple thermometer inserted into the body cavity at the posterior margin of the carapace. All experiments were performed in a darkened room illuminated with dim red light. Fiddler crabs are generally insensitive to red light based on their visual pigments (Jordao et al., 2007), so this procedure approximates constant darkness. The orientation of the gradient was rotated 180° after every 15 crabs.

Thirty crabs (15 males, 15 females) were tested on each of three days for a total of 90 crabs. Day was considered a block and used as a random factor in a mixed-model ANOVA with sex as the fixed factor and preferred temperature as the response variable. T_{set} was defined as the range of temperatures bounded by the first and third quartiles of all selected body temperatures (Allen et al., 2012; Blouin-Demers and Weatherhead, 2001; Christian and Weavers, 1996; Hertz et al., 1993).

2.6. Acclimation to high and low temperatures

To determine the magnitude of acclimation of CT_{min} and CT_{max} when exposed to increased or decreased temperatures, crabs were randomly assigned to one of two treatments:

high temperature acclimation (35°C) or low temperature acclimation (20°C). Within 12 h of collection, crabs were placed in plastic pans (36.7 × 31.1 cm) containing seawater to a depth of 1.5 cm. These pans were placed in an environmental chamber at the acclimation temperature under a 14:10 LD cycle for 14 d. Following the 14 d acclimation temperature, $CT_{\min}$ or $CT_{\max}$ was tested for each crab (as above), for a total of 18 crabs (9 males, 9 females) for each acclimation treatment for each measurement. Because of space and equipment constraints, three separate acclimation experiments were conducted over a period of ~1 month. Data were analyzed using mixed-model ANOVAs with experiment number (1, 2, or 3) as the random effect, sex and acclimation treatment as fixed factors, and $CT_{\min}$ or $CT_{\max}$ as the response variable.

To further examine the acclimation response, we tested the time course of acclimation of $CT_{\min}$ and $CT_{\max}$ under high temperatures. Within 12 h of collection, crabs were placed in an environmental chamber at 35°C under a 14:10 LD cycle (as above). $CT_{\min}$ and $CT_{\max}$ were tested on subsets of crabs at 0, 3, 6, 9, and 12 d after placement in the environmental chamber. Because of equipment constraints, two separate experiments were conducted over a period of ~1 month. Only 6 individuals could be tested for $CT_{\min}$ or $CT_{\max}$ simultaneously due to space limitations in the water bath. Each set of 6 crabs tested included 3 males and 3 females and was considered one block for statistical analysis. Data were analyzed using mixed-model ANOVAs with experiment number (1 or 2) and block (nested within experiment) as random effects, sex and day (0, 3, 6, 9, or 12) as fixed factors, and $CT_{\min}$ or $CT_{\max}$ as the response variable. A Tukey HSD test was used for post-hoc comparisons.

3. Results

3.1. Operative environmental temperatures in the fiddler crab habitat

Operative environmental temperature (T_e) in the fiddler crab habitat ranged from 24.5–49.0°C in the shade and 25.5–51.5°C in the sun, and generally peaked between 13:00 and 14:00 each day (Figure 1). T_e during this time period averaged $42.1 \pm 1.7^\circ\text{C}$ (mean $\pm$ s.e.m.) in the sun and $37.9 \pm 1.5^\circ\text{C}$ in the shade. Over the full 24-h day, T_e recorded by male models in the sun averaged $33.0 \pm 0.5^\circ\text{C}$ while T_e recorded by female models in the sun averaged $33.5 \pm 0.5^\circ\text{C}$. In the shade, T_e recorded by male models averaged $31.6 \pm 0.4^\circ\text{C}$ while T_e recorded by female models averaged $31.9 \pm 0.4^\circ\text{C}$

3.2. Critical thermal limits

$CT_{\min}$ averaged $11.5 \pm 0.2^\circ\text{C}$, while $CT_{\max}$ averaged $41.8 \pm 0.1^\circ\text{C}$. Neither $CT_{\min}$ nor $CT_{\max}$ differed between males and females ($CT_{\min}$: $F_{1,37.47} = 0.678$, $P = 0.416$; $CT_{\max}$: $F_{1,37.42} = 0.028$, $P = 0.869$). Similarly, neither measurement was related to carapace width ($CT_{\min}$: $F_{1,42.29} = 0.334$, $P = 0.566$; $CT_{\max}$: $F_{1,43.29} = 0.211$, $P = 0.648$) and there was no interaction between sex and carapace width ($CT_{\min}$: $F_{1,41.42} = 2.098$, $P = 0.155$; $CT_{\max}$: $F_{1,42.7} = 0.547$, $P = 0.464$). When examining only male crabs, relative claw size (claw length/carapace width) was not a significant predictor of $CT_{\min}$ ($F_{1,19.77} = 0.047$, $P = 0.831$). There was, however, a significant positive correlation between $CT_{\max}$ and relative claw size ($F_{1,7.819} = 15.190$, $P = 0.005$); crabs with larger major claws relative to their body size generally had higher critical thermal maxima.

3.3. Thermal sensitivity of locomotion

Sprint speed differed significantly among the different temperatures ($F_{5,199} = 76.461$, $P < 0.0001$). Sprint speed generally increased as temperature increased from 15°C to 30°C, but remained similar at temperatures between 30°C and 40°C (Figure 2). In general, females sprinted

faster than males ($F_{1,199} = 13.549$, $P < 0.001$), although there was no significant temperature $\times$ sex interaction ($F_{5,199} = 1.909$, $P = 0.094$).

3.4. Preferred body temperature range

The average body temperature selected by crabs in the thermal gradient was $24.4 \pm 0.5^\circ\text{C}$ (Figure 2). Defining T_{set} as the range of temperatures bounded by the first and third quartiles of all selected body temperatures (Blouin-Demers and Weatherhead, 2001; Christian and Weavers, 1996; Hertz et al., 1993) results in a T_{set} range of $21.1\text{--}28.6^\circ\text{C}$. Set-point body temperatures did not differ between males and females ($F_{1,86} = 0.013$, $P = 0.909$).

3.5. Acclimation to high and low temperatures

Thermal limits of fiddler crabs shifted when exposed to increased or decreased temperature during the 14 d acclimation period (Figure 3). For crabs acclimated to 35°C , CT_{min} averaged $13.20 \pm 0.20^\circ\text{C}$ and CT_{max} averaged $45.12 \pm 0.14^\circ\text{C}$. For crabs acclimated to 20°C , CT_{min} averaged $9.07 \pm 0.24^\circ\text{C}$ and CT_{max} averaged $40.98 \pm 0.22^\circ\text{C}$. Both CT_{min} and CT_{max} differed significantly between the two acclimation treatments (CT_{min} : $F_{1,30} = 179.964$, $P < 0.0001$; CT_{max} : $F_{1,30} = 242.097$, $P < 0.0001$). Males and females responded similarly to both acclimation treatments (CT_{min} : $F_{1,30} = 1.197$, $P = 0.283$; CT_{max} : $F_{1,30} = 0.085$, $P = 0.772$), and there was no acclimation treatment $\times$ sex interaction for either CT_{min} or CT_{max} (CT_{min} : $F_{1,30} = 1.360$, $P = 0.253$; CT_{max} : $F_{1,30} = 0.392$, $P = 0.536$).

Following exposure to 35°C , both CT_{min} and CT_{max} shifted over the 12-d acclimation period (CT_{min} : $F_{4,14} = 10.935$, $P < 0.001$; CT_{max} : $F_{4,14} = 12.982$, $P < 0.001$). CT_{min} had increased significantly after 3 d, while CT_{max} did not increase until after 6 d of exposure (Figure 4). Full

acclimation of both $CT_{\min}$ and $CT_{\max}$ occurred after 9 d of exposure. No significant changes in either $CT_{\min}$ or $CT_{\max}$ occurred between 9 and 12 d. Males and females responded similarly ($CT_{\min}$: $F_{1,95} = 0.002$, $P = 0.970$; $CT_{\max}$: $F_{1,95} = 1.269$, $P = 0.263$), and there was no day $\times$ sex interaction for either $CT_{\min}$ or $CT_{\max}$ ($CT_{\min}$: $F_{4,95} = 2.040$, $P = 0.095$; $CT_{\max}$: $F_{4,95} = 1.231$, $P = 0.303$).

4. Discussion

Relationships between environmental temperatures, body temperatures, and organismal responses can have important consequences for individual fitness as well as population-level processes. Understanding these relationships, however, requires a comprehensive and integrative approach. Here, we examined the comprehensive thermal ecology of the fiddler crab *Uca panacea*, which included operative environmental temperatures in the fiddler crab habitat, thermal tolerance and sensitivity, preferred body temperatures, and acclimation ability.

4.1. Environment, tolerance, and acclimation

Fiddler crabs live in a highly variable and complex thermal environment. Measuring operative environmental temperatures allows one to set up expected hypotheses that can then be tested with live organisms to examine the relative roles of physiological and behavioral processes in determining body temperatures. We observed fluctuations in T_e of over 15°C over the course of a day (Figure 1). Even towards the northern end of their ranges, fiddler crab species experience stressful temperatures during the summer months, when activity and breeding peaks. Allen and Levinton (2014) found that in New York, *Uca pugilator* (sister-species to *U. panacea*; Rosenberg, 2011) frequently experiences operative environmental temperatures (T_e 's) above their

preferred temperature range, and occasionally experiences T_e 's above their critical thermal maximum, especially on open sandflats (Allen and Levinton, 2014; Allen et al., 2012). In South Texas, approximated T_e 's using iButton-based copper models were up to 5°C higher in direct sunlight than in shade during daylight hours, with peak temperatures in both microhabitats exceeding *Uca panacea*'s critical thermal maxima. In direct sunlight, this potentially deadly occurrence of $T_e > CT_{max}$ persists through much of the afternoon. Even when daytime temperatures did not exceed CT_{max} , however, they generally exceeded the preferred body temperature range, indicating that *U. panacea* live in a harsh thermal environment, and some form of thermoregulation is necessary to allow observed diurnal activity on the surface (Caravello and Cameron, 1991; Darnell et al., 2013). Indeed, Allen (2007) demonstrated by that fiddler crabs are able to reduce T_b to sublethal temperatures, even when T_e exceeded lethal temperatures. Fiddler crabs are able to reduce T_b below T_e through behavioral mechanisms, such as alternating time between the burrow and the surface (e.g., Smith and Miller, 1973), as well as physiological mechanisms including evaporative water loss, which further reduces body temperature (Thurman, 1998; Wilkens and Fingerman, 1965).

It should be noted that we deployed only a small number of models in two microhabitats. Thus, it is not possible to truly assess the thermal heterogeneity or fine-scale quality of the thermal environment of *Uca panacea* in this location. Future studies examining thermal heterogeneity and habitat quality will require a high number of models deployed throughout the habitat, as the intertidal and supratidal zone can be quite variable.

Critical thermal limits can be quite sensitive to experimental methodology, including rates of temperature change (Terblanche et al., 2007). For both CT_{min} and CT_{max} , temperature was ramped at a rate of $\sim 0.3^\circ\text{C min}^{-1}$. Although a temperature change of $0.3^\circ\text{C min}^{-1}$ is greater than

rates of change of air temperature or operative environmental temperature observed in the field (Figure 1), this rate of thermal ramping is similar to rates of body temperature change previously observed in the field for the fiddler crab *Uca rapax* in a similar climate (Smith and Miller, 1973) and would be expected when a fiddler crab emerges from a cool, dark burrow into the high intertidal breeding area (Darnell et al., 2013; Powers and Cole, 1976) or retreats into a burrow after sustained surface activity (Smith and Miller, 1973).

Thermal tolerance limits and thermal sensitivity can shift through acclimation to recent environmental experience (Anneli Korhonen and Lagerspetz, 1996; Claussen, 1977; Somero, 2005), thus altering organismal responses to changes in body temperature. Thermal acclimation can adjust the thermal performance curve allowing organisms to tolerate a wider range of body temperatures or by shifting thermal tolerance towards warmer or cooler temperatures. For example, acclimation can result in shifts in the thermal performance curve (TPC) after exposure to high or low temperatures (Huey et al. 2012) or a broadening or narrowing of the TPC after exposure to a highly variable or consistent thermal regime, or in the context of differential adaptation of life history stages to thermal variability (Pelosse et al., 2007). We observed acclimation of both $CT_{\min}$ and $CT_{\max}$ following sustained exposure to low (20°C) or high (35°C) temperatures. Acclimation as observed here did not result in a broadening of the TPC, but rather a shift. Acclimation to high temperature (35°C) resulted in a gain of high-temperature tolerance and a loss of low-temperature tolerance, while acclimation to low temperature (20°C) resulted in a gain of low-temperature tolerance and a loss of high-temperature tolerance. Acclimation occurred quite rapidly, with $CT_{\min}$ beginning to shift after 3 d of exposure and $CT_{\max}$ beginning to shift after 6 d of exposure to the new temperature and complete acclimation occurred after 9 d of exposure to the new thermal regime. This rapid acclimation ability has the potential to reduce

thermal stress and buffer physiological impacts arising from rapid changes in climatic conditions. *Uca pugilator*, sister-species to *U. panacea*, exhibits a distinct periodic habitat shift, spending on average 5–6 d in the high intertidal breeding area before retreating to less stressful habitats such as the low intertidal zone or within the marsh vegetation (Allen, 2007; Christy, 1978). Such an alternation of habitats would repeatedly create new conditions for acclimation over a relatively short timescale. Further study is necessary to determine if *U. panacea* exhibits a similar periodic shift among habitats.

Given the diversity of latitudinal ranges found within the genus *Uca*, we would expect thermal tolerance and acclimation ability to vary among species as a function of both the thermal stability of their environment as well as the breadth of their latitudinal (thermal) range. Species living at higher latitudes or spanning broad latitudinal ranges are expected to have broader thermal tolerances and greater acclimation ability compared to species with narrow latitudinal ranges or inhabiting the tropics, where the thermal regime is relatively stable. A recent study with a wide-ranging (latitudinal range: 23°N to 30°S) Indian Ocean fiddler crab, *Uca urvillei*, found that the species is a thermal generalist, with a wide thermal tolerance range. Future studies are necessary to determine if these patterns, are often seen in other taxa (e.g., Addo-Bediako et al., 2000; Brattstrom, 1968; Deutsch et al., 2008; Sunday et al., 2011), are present across the genus *Uca*.

4.2. Temperature preference and performance

Behavioral thermoregulation allows an organism to exploit thermally heterogeneous habitats (both spatial and temporal) to maintain a preferred body temperature or reduce their exposure to stressful thermal extremes (Clench, 1966; Cowles and Bogert, 1944; Kearney et al.,

2009; McGaw, 2003). Foraging and performing claw-waving displays (for males) on the surface exposes fiddler crabs to stressful high temperatures, but individuals are able to regulate body temperatures by moving between surface microhabitats (Darnell et al., 2013) or retreating into burrows (Smith and Miller, 1973). Because of the burrow's role as a refuge from predators (Koga et al., 2001; Reaney, 2007), a refuge from desiccation (Thompson et al., 1989; Thurman, 1984, 1998; Wolcott, 1992), and a mating site (Christy, 1982; Christy and Salmon, 1984), fiddler crabs are primarily central-place foragers and remain relatively close to their burrows (Land and Layne, 1995; Layne et al., 2003). This central place foraging behavior limits their ability to shuttle between open and vegetated surface areas to regulate body temperatures, and fiddler crabs rely primarily on retreats into burrows to reduce body temperature. Such a retreat into the burrow is a highly effective means of regulating body temperature and can reduce body temperatures by up to 10°C over a short time period (Smith and Miller, 1973).

Although we did not explicitly examine behavioral thermoregulation, we assessed preferred (set-point) body temperatures (T_{set}) in a laboratory thermal gradient. The set-point body temperature range (21.1–28.6°C) was below the optimum temperature (T_{opt}) for locomotion (30–40°C). The upper limit of T_{set} observed here was similar for that observed for *Uca pugilator* on wet sand by Allen et al. (2012). Mismatches between T_{set} and T_{opt} are quite common, and multiple hypotheses have been proposed (Gvoždík, 2015), including (1) the asymmetry model of Martin and Huey (2008), where due to the asymmetric nature of thermal performance curves, a deviation of body temperature (T_b) above T_{opt} results in a greater decrease in performance than an equal deviation of T_b below T_{opt} , (2) the “hotter-is-better” model of Asbury and Angilletta (2010), where selection favors a mismatch between T_{set} and T_{opt} if maximum performance is greater in individuals with a higher T_{opt} , and the multiple thermal optima model of Angilletta et al. (2002),

where due to variation in T_{opt} among multiple performance traits, T_{set} lies in a range representing a compromise among multiple thermal optima, and (4) the evolutionary pace hypothesis of Gvoždík (2015), where the mismatch between T_{set} and T_{opt} is due to a difference in evolutionary rates of T_{set} and T_{opt} . The difference between T_{set} and T_{opt} is greater than the maximum of 3°C predicted by Martin and Huey (2008), although further research is necessary to distinguish among the remaining three hypotheses. Interestingly, T_{set} observed here represents a temperature range that is almost exclusively observed at night in the natural habitat during the peak activity season (summer). Yet *U. panacea* exhibits both diurnal and nocturnal activity (Caravello and Cameron, 1987b; Darnell et al., 2013), further highlighting the importance of thermoregulatory mechanisms.

Evaporative water loss and hydration state must be considered when examining thermal preferences and thermal performance curves. For example, Allen et al. (2012) observed a decrease in T_{set} with decreased hydration state, and hydration state interacted with body temperature and body size to influence performance. We conducted all our experiments under conditions of full hydration, as crabs were held in shallow pans containing seawater to a depth of ~1.5 cm between collection and experimentation (6–18 h).

4.3. Sexual selection and thermal ecology

Fiddler crabs provide extreme examples of sexual dimorphism, with males possessing a single small feeding (minor) claw and a greatly enlarged major claw that can comprise up to 50% of total body mass (Christy and Salmon, 1984; Crane, 1975). This claw serves a number of functions including mate attraction (Pope, 2000a, b) and combat with other males over breeding burrows (Hyatt and Salmon, 1978). Additionally, the major claw of male fiddler crabs serves a

425 thermoregulatory function, reducing male body temperatures (Darnell and Munguia, 2011). This
426 thermoregulatory function likely results from both passive (morphological) and active
427 (physiological) mechanisms, with the large claw functioning as a heat sink, drawing heat away
428 from the body and dissipating heat into the surrounding air through convective heat loss (Darnell
429 and Munguia, 2011). Male and female fiddler crabs differ not only morphologically, however,
430 but also ecologically and physiologically due to differing selective pressures on the sexes (e.g.,
431 Allen and Levinton, 2007; Darnell et al., 2013; Gerald and Thiesen, 2014; Valiela et al., 1974;
432 Weissburg, 1993). *Uca pugilator* males and females differ in their ability to change color in
433 response to changes in temperature, with males showing a greater color changing ability than
434 females (Munguia et al., 2013; Silbiger and Munguia, 2008). However, *U. panacea* only exhibits
435 color change differences between males and females under specific combinations of temperature
436 and background coloration (Kronstadt et al., 2013). We observed no differences in critical
437 thermal limits, thermal sensitivity of locomotion, preferred body temperature range, or
438 acclimation ability between males and females. These results suggest that physiologically, males
439 and females respond similarly to thermal stress. Differences in behavioral responses to thermal
440 stress observed previously (Darnell et al., 2013; Kronstadt et al., 2013) are not due to differences
441 in physiological tolerances, but rather in the relative ecological and sexual costs and benefits of
442 such behaviors. We did, however, observe a difference in sprint speed between males and
443 females, with females sprinting significantly faster than males. This likely reflects a cost
444 associated with possession of the greatly enlarged major claw. In other fiddler crab species,
445 sprint speed on horizontal surfaces does not differ between the sexes (Allen and Levinton, 2007;
446 Gerald and Thiesen, 2014), although Gerald and Thiesen (2014) did observe a decrease in sprint
447 speeds on both uphill and downhill inclines associated with possession of the major claw. These

differences may reflect morphological or biomechanical differences between species.

The greatly enlarged major claw of male fiddler crabs has traditionally been considered primarily in the context of sexual selection, but recent evidence indicates an additional thermoregulatory function of the large claw (Darnell and Munguia, 2011). We observed that in male fiddler crabs, major claw size is also related to thermal tolerance, as a larger claw (relative to body size) was associated with a greater CT_{max} . We do not believe this effect is simply due to differences in body mass and thus differences in rates of heat exchange, as internal body temperatures were measured directly. Instead, a larger claw relative to body size may indicate a male in greater physiological condition, as has been previously observed for *Uca pugilator* (Allen, 2007). Additionally, males with larger claws relative to body size may have greater access to food resources than males with smaller claws, again contributing to a greater physiological condition. New research directions are needed to confirm the mechanism through which the upper thermal limit is related to major claw size.

Future Directions

Temperature is a fundamental factor determining a wide range of organismal traits across a range of spatial scales from microhabitats to determination of geographic range. The diverse latitudinal ranges within the genus *Uca*, extreme sexual dimorphism, and complex intertidal habitats make fiddler crabs an excellent invertebrate body system in which to investigate responses to temperature on the organism, population, and species levels. The mating system of fiddler crabs, imposes tradeoffs between thermally stressful mating activity and thermoregulatory behaviors, as retreating into the burrow reduces body temperature but reduces time for the sexual claw-waving display. Integrating the organismal responses observed here with these sexual

tradeoffs will shed light on the factors driving body temperatures, behavioral decisions, and degrees of thermal stress experienced in the natural environment.

Plastic responses to temperature stress (as evidenced by rapid acclimation ability), combined with the ability for behavioral thermoregulation (Kronstadt et al., 2013; Silbiger and Munguia, 2008; Smith and Miller, 1973) is a strong candidate mechanism that explains the broad habitat use of these species and could help explain the successful pantropical distribution of fiddler crabs. Multi-population and multi-species comparative studies will clarify the relative importance of thermal tolerance, acclimation, and behavioral thermoregulation in driving species distributions under both current conditions and future climate change.

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673 **Tables**

674 Table 1. Thermal physiology concepts used in this study.

Concept	Definition
Body temperature (T_b)	The internal temperature of a live organism.
Thermal sensitivity	The degree to which an organism's performance depends on body temperature ¹
Thermal performance curve (TPC)	Thermal reaction norms for performance, describing the change in performance over a range of body temperatures ^{1,2}
Critical thermal limits	Minimum (CT_{min}) and maximum (CT_{max}) body temperatures that permit performance ^{1,3}
Thermal tolerance range	The range of temperatures bounded by CT_{min} and CT_{max} .
Thermal acclimation	A shift in thermal physiology occurring after long-term (generally days to weeks) exposure to novel thermal conditions, often including a shift in the TPC ^{1,4,5}
Operative environmental temperature (T_e)	The steady-state temperature of an inanimate object approximating an organism's size, shape, and radiative properties in the appropriate microhabitat, representing the expected body temperature of an organism in the absence of physiological or behavioral thermoregulation ^{6,7}
Set-point body temperature range (T_{set})	The temperature range preferred by an organism in the absence of ecological costs ⁷
Optimum temperature (T_{opt})	T_b at which some performance metric is maximized ²

675 ¹Angilletta, 2009; ²Huey and Stevenson, 1979; ³Luttershmidt and Hutchinson, 1997; ⁴Bowler,
676 2005; ⁵Sinclair and Roberts, 2005; ⁶Bakken, 1992; ⁷Hertz et al. 1993

677

Figure captions

Figure 1. Operative environmental temperatures in *U. panacea* habitat. (A) iButton-based physical models used to measure T_e . (B) T_e in the sun (solid line) and shade (broken line) over the course of a day, averaged from multiple iButton-based models over 6 days in July–August, 2012 and binned into 5-min intervals. Standard deviations are indicated by the shaded areas, with the light gray shading representing s.d. in the sun and the medium gray shading representing s.d. in the shade. Dark gray shading represents overlapping s.d. (C) Distribution of T_e in full sunlight. Black bars represent nighttime (20:30–06:30) temperatures while white bars represent daytime (06:30–20:30) temperatures. (D) Distributions of T_e in the shade, with bar coloration as in panel C.

Figure 2. Thermal performance curve of sprint speed as a function of body temperature for male (solid line) and female (broken line) *Uca panacea*. Error bars indicate ± 1 s.d. Different letters above means represent statistically significant differences among overall means (combining both sexes) for each temperature at $P < 0.05$. The curve is bounded by $CT_{\min}$ and $CT_{\max}$. Bar graph represents distribution of body temperatures selected by *Uca panacea* in a thermal gradient. The set-point body temperature range, bounded by the first and third quartiles of all selected body temperatures was 21.1–28.6°C.

Figure 3. $CT_{\min}$ and $CT_{\max}$ immediately upon collection (no acclimation), after 14 d acclimation to 20°C, and after 14 d acclimation to 35°C. Error bars indicate ± 1 s.d.

701

702 **Figure 4.** The timecourse of acclimation to high temperature in *U. panacea*. $CT_{\min}$ (bottom) and

703 $CT_{\max}$ (top) tested every 3 d after initiation of exposure to 35°C. Error bars indicate ± 1 s.d.

704 Different letters above means represent statistically significant differences at $P < 0.05$.

Figure 2

Figure 3

Figure 4