



Are crabs stressed for water on a hot sand flat? Water loss and field water state of two species of intertidal fiddler crabs



Jeffrey Levinton*, Shanna Lord, Yoshiaki Higeshide

Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA

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ABSTRACT

Field measures of stress are needed to understand the role of behavior in stress and how behavior trades off with overall fitness. Along Atlantic shores, displaying and reproductive burrow-occupying males of the fiddler crab *Uca pugilator* live in high intertidal dry sandy sediments, whereas *Uca pugnax* live in lower intertidal wetter muddy substrata. Water loss was examined in the lab for both species. Water loss of *U. pugilator* males was approximately linear with time and crabs regained water completely after 2 h of rehydration. Percent water loss was inversely correlated with body mass, irrespective of sex. Males of the higher intertidal *U. pugilator* lost proportionally less water over time than *U. pugnax*, which occupies muddier and wetter sediments. A field test of water state on a hot day demonstrated that males of either species seen at the surface next to mating burrows were not stressed for water, suggesting that behavior compensated adequately for water loss when displaying in the sun on the surface. Behavior can therefore compensate for what appears to be a stressful environment. However, such compensation likely comes at the cost of reproductive success, which depends upon remaining on the sediment surface in open stressful conditions. Large-sized males may be more successful in breeding territories owing to their proportionately lower water loss.

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1. Introduction

Organisms living in extreme edge environments appear to be continuously vulnerable to environmental extremes and likely succumb when a threshold such as an upper limit of high temperature is surpassed. An organism would appear to have three potential responses over different time scales to a physiological challenge: acclimate to the new condition, die in failure to function, or evolve a new accommodating response, assuming genetic variability is available (Helmuth et al., 2005). As climate changes, depending on success and failure in these responses, there might be winners and losers in a diverse community, which can be predicted based upon their respective vulnerabilities at the microhabitat, physiological, and molecular levels (Hofmann and Somero, 1995; Somero, 2010). In some cases, species can be ordered by their microhabitat occurrences, such as living at different tidal heights, and their expected vulnerability to temperature stress can be predicted by their time of exposure to low tide and temperature and desiccation stress (Ushakov, 1968). In species of porcelain crabs, the species that has evolved tolerance to the most extreme thermal condition has done so at the cost of susceptibility of heart function to sudden increases of temperature (Stillman, 2003).

Among ectotherms, an important additional factor in understanding organismal responses to climate extremes is the role of behavior in ameliorating thermal or other physiological stress (Chown et al., 2010; Kearney et al., 2009). At the end of a species range, behavior may reduce the range of environmental extremes, as an individual, for example, finds moist and shady microhabitats to avoid heat and water loss stress at the hot-temperature end of the range (Huey et al., 2003). A large-scale study of terrestrial vertebrate and arthropod ectotherms concluded that most species live with a relatively small thermal safety zone at higher temperatures (Sunday et al., 2014). To avoid otherwise, fatal stress from water loss or heat exposure fiddler crabs retreat to moist and cool burrows (Smith and Miller, 1973). Are such retreats successful in eliminating water stress, which is high at the sediment surface?

A useful approach to assessing stress would identify a physiological state that reflects environmental stress, examine the factors that influence this state, and then assess whether organisms in the field are living under stressful conditions. This could be done in two ways: (a) examining optimal preferences under laboratory or field conditions and observing whether individuals in the field are living under conditions that differ significantly from their preferences (Huey et al., 1989; Levinton and Mackie, 2013); (b) measuring a physiological state of organisms in the field, transferring individuals to more benign environmental conditions, and then assessing whether physiological state improves. This report takes the second approach. Under some distributions of performance as a function of environmental variation, conditions for optimal performance may not

* Corresponding author.

E-mail address: jeffrey.levinton@stonybrook.edu (J. Levinton).

exactly match organismal preferences (Allen et al., 2012; Martin and Huey, 2008).

Fiddler crabs (Arthropoda, Decapoda, family Ocypodidae, genus *Uca*) include about 100 species that live in tropical and subtropical intertidal flats throughout the world. Local diversity is strongly correlated with regional temperature (Crane, 1975; Levinton and Mackie, 2013). Fiddler crabs are strongly terrestrial, spending much time in air while moving, foraging, and mating (Crane, 1975). In many species, especially in the Americas, males construct burrows, within which they mate with females after attracting them to the burrow area (Crane, 1975). The eastern North American sand fiddler crab *Uca pugilator* occupies burrows in sand and larger more successful males occupy burrows in higher intertidal sites (Christy and Salmon, 1984). However, mating success at these burrows is traded off for food scarcity, temperature stress, and water stress (Allen and Levinton, 2014). Males at mating burrows alternate position between the sediment surface and within the burrow. When on the surface, males may move their greatly enlarged major claws in a stereotyped waving pattern, which attracts females by virtue of the size of male's major claw and other aspects of the male's behavior (Crane, 1975). An approach by an interested female may result in mating, which in this species occurs within the male's mating burrow. After a few days, males will desert the burrow and retreat to the lower intertidal for several days where they feed and perhaps gain water.

The time spent by males in the open at their burrows is a time of highly reduced available food, very low water content of the surface sediment and apparent thermal and water loss stress (Allen and Levinton, 2014; Reinsel and Rittschof, 1995). More males are found to be displaying if shade is experimentally provided or if food is experimentally added around the burrow (Allen and Levinton, 2014). In *U. pugilator*, larger males are generally found in burrows in higher parts of the sandy intertidal. Dominance by larger males at the highest part of the shore is related to success in mating and combat of larger males over smaller males (Christy and Salmon, 1984; McLain and Pratt, 2007). However, large body size also confers physiological advantages. Larger males have greater endurance after being subjected to desiccation stress (Allen et al., 2012). Water loss is proportionally less in larger males, presumably because of their smaller surface area/volume ratios (Herreid, 1969). In *U. mjoebergi*, smaller males waved less than larger individuals (Callandar et al., 2011), which may have been influenced by their poorer performance in physiologically stressful conditions and contributed to their poorer mating success.

This report focuses on water loss, which is a major source of stress in fiddler crabs, which have permeable carapaces. Crabs do not replenish water from the atmosphere so water loss can only be compensated by direct contact with moist sediment or water (Yoder et al., 2005). The rate of water loss is inversely related to body size (Allen et al., 2012; Herreid, 1969), which varies over the geographic range of *U. pugilator* (Munguia et al., 2013; Yoder et al., 2007). The degree of carapace permeability also differs at different sites (Yoder et al., 2007). In general, species living farther from predictable immersion tend to be less permeable to water loss (Edney, 1961; Smith and Miller, 1973), but other factors may make it difficult to make a simple ordering among species (Thurman, 1998).

Field studies focused on mating males of the high-dry-sandy fiddler crab *Uca pugilator* and the low-wet-muddy fiddler crab *U. pugnax* on salt marsh flats in Long Island Sound. These two species coexist in salt marsh environments in Long Island, New York waters. Adult *U. pugilator* tend to occur in sandy sediments and have maxillary appendages adapted to feeding on sand grains (Teal, 1958). Larvae of *U. pugnax* recruit to muddier sediments (Brodie, 2005; O'Connor, 1993), whereas *U. pugilator* tends to recruit among vegetation perhaps to hide from predators (Brodie, 2005).

Using water loss as a trait, two main hypotheses are tested:

Hypothesis 1. The high-dry-sand species *U. pugilator* suffers from water stress, whereas the low-wet-muddy species does not.

Hypothesis 2. The high-dry-sandy *U. pugilator* loses water more slowly than the low-wet-muddy *U. pugnax*, owing to adaptation of the former to drier conditions. We also present data on water loss patterns and the possibility of rapid rehydration when crabs in air are returned to water. A field-based test of water stress is developed to test hypothesis 1.

2. Methods

Individuals of *U. pugilator* and *U. pugnax* were collected from a site in Flax Pond, Old Field, New York. Crabs were collected by hand, transported immediately to the lab, and maintained in a recirculating seawater aquarium at 20 °C at a salinity of 28.

Drying experiments were performed in a temperature-regulated environmental chamber with fluorescent lights, maintained at 30 °C. Water loss was approximated by the change in mass over the time period of drying (Herreid, 1969). This loss included internal water (Yoder et al., 2007) and water adsorbed to surfaces that we failed to blot away with a dry paper towel. Relative humidity in the environmental chamber was measured with a Cole-Parmer thermohygrometer and ranged to 30–40% humidity. To examine the relation of percent water loss, crabs were placed in individual cups in air for a period of 2 h, after which they were reweighed to estimate water loss. Crabs were blotted dry for 3–5 min and then weighed using a Sartorius MC1 balance, weighed to an accuracy of 0.001 g. We studied water loss as a function of body mass, sex (*U. pugilator*), and between species (males of *U. pugilator* and *U. pugnax*).

To follow the course of water loss over time, crabs were weighed every 15 min for a total time of 135 min. In one experiment, male *U. pugilator* were placed again in water for another 2 h, in order to estimate the degree of rehydration on the same time scale as our water loss experiments. During rehydration, mass could not be measured every 15 min because that would involve frequent removing of crabs from water, blotting, and reentry, which was likely physiologically disruptive. We also measured carapace length, width, and major claw length to the nearest 0.01 mm using a Mitutoyo digital caliper, interfaced to a laptop computer. There was no mortality in any of these experiments.

To test for the degree of water stress of *U. pugilator* and *U. pugnax* under field conditions, male crabs were collected at the Flax Pond field site. A male was collected if it was seen out of its burrow on the sediment surface waving its major claw and could be collected less than a minute after it retreated to its burrow when we approached. Males were then taken immediately to the lab (this took less than 2 min generally), brushed off to remove sand and weighed to the nearest 0.001 g. Males were then immersed in a cup of seawater (salinity was approximately 28) for 2 h, removed, blotted thoroughly on paper toweling and reweighed.

3. Results

3.1. Water loss and rehydration of *Uca pugilator* over time

Fig. 1A shows body mass over time in air at 30 °C. Water loss was approximately linear. To see if this loss was immediately reversible, Fig. 1B shows water gain over 2 h, following 2 h of water loss. The average mean fraction remaining after 2 h of dehydration was 0.941 ± 0.009 SD, $N = 17$). Gain of mass lost in air was nearly recovered when the animals were returned to water (mean = 0.992 ± 0.002 , $N = 17$).

3.2. Water loss of male and female *U. pugilator*.

Fig. 2A shows initial mass for *Uca pugilator* males and females as a function of carapace length. The obvious difference in mass between sexes is mainly a reflection of the large major claws of males. Water loss of males and females as a function of initial blotted dry mass is shown in Fig. 2B. A significant negative regression of percent water

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