



Thermal constraints on microhabitat selection and mating opportunities



Pablo Munguia^{a, *}, Patricia R. Y. Backwell^b, M. Zachary Darnell^{c, 1}

^a School of Biological Sciences, The University of Adelaide, Adelaide, Australia

^b Research School of Biology, The Australian National University, Canberra, Australia

^c Department of Biological Sciences, Nicholls State University, Thibodaux, LA, U.S.A.

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Hot tropical environments constrain ectotherm mating opportunities when mate selection occurs on the surface. Thus, microhabitats and refugia can become a qualitative trait in mate selection. In fiddler crabs, the enlarged claw of males can act as a heat sink, which becomes advantageous when surface temperatures reach 50 °C during the day and crabs are actively seeking to mate. *Uca mjoebergi* females prefer male burrows found in the shade; therefore, we investigated the thermal constraints imposed on males and females in shaded and unshaded habitats. Crab surface activity decreased and body temperature increased as the day progressed, with more crabs active in shaded than sunny microhabitats. Body temperature was lower in male crabs found in burrows relative to crabs on the surface. Male claw size explained 10% of body temperature. Our results add further support to the hypothesis that thermal constraints imposed on males can be overcome by the large claw acting as a heat sink and the burrow acting as a refuge from heat. Classic sexually selected traits, including ornaments and behaviours, can have a secondary purpose in thermoregulation.

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The tropics are hot, yet many tropical species exhibit diurnal activity patterns and are active in direct sunlight, exposed to extreme heat stress (Sinervo et al., 2010). Species that court and mate during the hottest part of the day would be particularly stressed; selection therefore favours individuals that endure adverse environmental conditions in exchange for mating opportunities. Sexual selection via endurance rivalry should favour extended presence at the breeding site, which is often associated with an increase in the number of mating opportunities (Banks & Thompson, 1985; Darnell, Fowler, & Munguia, 2013; Salvador, Díaz, Veiga, Bloor, & Brown, 2008). Across both tropical and temperate zones, high temperature, solar radiation and desiccation risk can limit time spent in these stressful breeding areas, as has been shown for both endotherms (Campagna & Leboeuf, 1988) and ectotherms (Darnell et al., 2013; Monaco, Wethey, Gulledge, & Helmuth, 2015), and thus environmental conditions may modulate mating behaviour and mating opportunities. This is expected to

be of greater importance in the tropics, where temperature and solar radiation are at a maximum.

In ectotherms, behavioural thermoregulation can buffer individuals from thermal stress associated with extreme or rapidly changing temperatures (Huey et al., 2012; Kearney, Shine, & Porter, 2009; Smith & Miller, 1973). Mobile species can exploit the thermal heterogeneity of the environment to regulate body temperatures and reduce exposure to thermal extremes. Yet because behavioural thermoregulation often involves a retreat from breeding or display sites to more thermally innocuous habitats, it may come at a cost to mating opportunities. Thermoregulatory microhabitat selection can thus limit activity periods involved in mate searching and display (Darnell et al., 2013). Sexually dimorphic traits can also influence thermoregulatory ability and body temperature, as morphology alters rates of heat transfer between the organism and the environment. A number of sexually dimorphic traits have thermoregulatory effects including bills (Greenberg & Danner, 2013; Luther & Greenberg, 2014), horns (Shepherd, Prange, & Moczek, 2008) and claws (Darnell & Munguia, 2011).

Fiddler crabs are often studied in the context of sexual selection and sexual dimorphism. Male fiddler crabs have an enlarged claw that is used in courtship (Detto, 2007; Murai & Backwell, 2006; Pope, 2000), intrasexual combat (Hyatt & Salmon, 1978) and thermoregulation, transferring heat away from the body and

* Correspondence: P. Munguia, School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia.

E-mail address: pablo.munguia@adelaide.edu.au (P. Munguia).

¹ Present address: Division of Coastal Sciences, School of Ocean Science and Technology, The University of Southern Mississippi, Ocean Springs, MS, U.S.A.

dissipating it to the environment (Darnell & Munguia, 2011). Differential selective pressures on males and females due to sexual selection via endurance rivalry on males results in sex-specific thermal constraints on behaviour (Darnell et al., 2013). Male fiddler crabs perform a waving display on the surface to attract females and because signal competition occurs during this time, endurance rivalry favours increased time on the surface. Yet while on the surface performing the waving display, males endure extreme thermal conditions, with operative environmental temperatures often exceeding preferred and even lethal temperatures (Allen & Levinton, 2014; Darnell, Nicholson, & Munguia, 2015). Surface activity of female fiddler crabs does not seem to be constrained by temperature (Darnell et al., 2013; Milner, Detto, Jennions, & Backwell, 2010), but female mate choice can be influenced by temperature, as mate-searching females preferentially approach males that are in the shade regardless of whether the females are released in the sun or shade (Kerr & Backwell, 2016). The challenge is to understand how mating strategies and structures (i.e. claws and burrows) aid in thermoregulation. The extent to which claw size affects body temperature and burrows can serve as thermal refugia is still unknown.

Here, we were interested in understanding the thermal constraints imposed on a highly dimorphic intertidal species. We asked (1) how does crab activity and body temperature differ between microhabitats? We defined shaded and unshaded sections of mangrove forests where crabs are mostly active. (2) Is male surface activity constrained by temperature? (3) How does the large male claw affect body temperature and thermoregulation? (4) How does use of the burrow help buffer temperatures? If burrow depth or claw size affects body temperature, then these structures, coupled with shifts in behaviour, can help explain how organisms can reconcile mating strategies in adverse environments.

METHODS

Study Site and Species

Uca mjoebergi is a small (<15 mm carapace width, <1.2 g wet mass) fiddler crab that is endemic to Australian intertidal mudflats. As in other fiddler crab species, sexual dimorphism is extreme. Females possess two small feeding claws, while males possess a single small (minor) feeding claw and a greatly enlarged major claw. In male *U. mjoebergi*, the major claw accounts for $35.6 \pm 0.007\%$ (mean \pm SE) of total body mass (we measured $N = 28$ males using a balance).

Individual male and female *U. mjoebergi* defend burrows and surrounding territories (ca. 10 cm diameter) on the mudflat surface (Crane, 1975). The burrow is used as a refuge from predation (Reaney, 2007), heat stress (Darnell et al., 2013; Smith & Miller, 1973) and desiccation stress, as well as a mating site (Reaney & Backwell, 2007). The surrounding territory is used for feeding and courting (Reaney, 2007). Time spent on the surface also influences feeding, and females can generally feed faster than males (Weis & Weis, 2004); yet the number of males feeding on the surface does not differ between shaded and unshaded habitats (Kerr & Backwell, 2016). Mating in *U. mjoebergi* occurs during a 7–9-day period around neap tides, when the mudflat is exposed throughout the tidal cycle. Sexually receptive females leave their own burrows and wander the mudflat surface searching for a mate. Males perform a species-specific waving display on the surface near their burrows to attract the attention of nearby females. Females typically sample multiple burrows before selecting a mate (Clark & Backwell, 2015). Mating occurs in the male's burrow, and males then guard females until oviposition (1–2 days). The male return to the surface to resume courting, feeding and mating, while the female remains in

the burrow for the ca. 20 day incubation period until she re-emerges on a nocturnal spring tide to release larvae (Reaney & Backwell, 2007).

This study was conducted over 6 days in a single mating cycle during November 2015 at East Point Reserve, Darwin, Australia (12°24.53'S, 130°49.85'E). This population of *U. mjoebergi* resides in the high intertidal zone where the mudflat represents a heterogeneous matrix of microhabitats, with open unshaded areas interspersed with areas shaded by mangroves. To characterize the temperature profile, we placed five iButton dataloggers (Thermochron, Maxim Integrated Products, Inc., Sunnyvale, CA, U.S.A.) 1 cm below the surface in shaded and unshaded habitats of the mudflat and recorded temperature every 10 min for the duration of the study. Three Hobo pendant temperature dataloggers (Onset Computer Corporation, Bourne, MA, U.S.A.) were suspended from mangrove branches and recorded air temperature every 5 min for the duration of the study.

Population Level Surface Activity in Different Microhabitats

Surface activity was quantified in both unshaded and shaded microhabitats throughout the day as the number of crabs active on the surface within 0.33 m² plots. Each plot was monitored for 5 min every hour from 0900 to 1300 hours and the maximum number of male and female crabs active on the surface during the 5 min observation time was recorded. A total of six plots in each microhabitat were monitored each day, and the experiment was conducted over 4 days. Plots were moved each day to a new random location, for a total sample size of 36 plots (2 microhabitats \times 6 plots \times 4 days). Data were analysed using a linear mixed-effects REML-fitted model with number of crabs active on the surface as the response variable. Microhabitat, sex and time were included as fixed effects, and date was included as a random effect.

Surface Activity, Body Temperatures and Thermal Limits

The duration of surface activity was measured for individual male and female crabs. Individual focal crabs were observed and timed from the time they emerged from the burrow until the next retreat to the burrow. Observations were made from 1–2 m away to reduce the risk of disturbance, and data were discarded if crabs were startled into the burrow. Durations of surface activity were measured throughout the day, from ca. 0800 to 1400 hours, in both shaded and open microhabitats. A total of 172 individual crabs were observed for the duration of surface activity.

Body temperatures of surface-active fiddler crabs were measured using a hypodermic copper-constantan thermocouple (Model MT-29/1, 0.1 °C accuracy, Physitemp Instruments Inc., Clifton, NJ, U.S.A.) connected to a thermocouple thermometer (Microtherma 2T, 0.2 °C accuracy, ThermoWorks, American Fork, UT, U.S.A.) inserted into the body cavity through the posterior margin of the carapace. Body temperatures were only measured if the crab could be captured on the surface or within 30 s of entering the burrow, and were taken within 5 s of capture. We measured body temperature for 205 individual surface-active crabs, both male and female, in both shaded and unshaded microhabitats, from ca. 0800 to 1400 hours.

The critical thermal maximum (CT_{max}), which represents the maximum temperature at which performance is possible, was estimated under natural conditions using the loss of righting response as the endpoint (Allen, Rodgers, Tuan, & Levinton, 2012; Cuculescu, Hyde, & Bowler, 1998; Lutterschmidt & Hutchison, 1997). Prior to experimentation, crabs were held in the shade in a shallow plastic pan containing ca. 1 cm of water to ensure full hydration. Male crabs were then tethered on the mudflat surface

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