Costs of Sexual Selection in the Sand Fiddler Crab, *Uca pugilator*

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Abstract of the Dissertation

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This dissertation investigates the costs and condition-dependence of sexually selected traits in the sand fiddler crab, *Uca pugilator*. Theory suggests that sexually selected structures and behavioral displays are honest signals of male quality to opponents and mates that are costly to produce and maintain. In mid-Atlantic salt marshes, reproductively active males use a single greatly enlarged major claw as both a weapon to defend specialized breeding burrows from other males and an ornament to attract females for mating. Carrying the major claw, which can comprise as much as 40% of the total body mass, imposes significant energetic and locomotor costs to male fiddler crabs. These costs are exacerbated by the location of breeding burrows in open areas high on the shore characterized by low food availability and high temperatures.

Using biophysical engineering methods I found that, from the perspective of a fiddler crab, the thermal environment of the mating area is quite harsh relative to other marsh microhabitats and that high temperatures and desiccation stress significantly constrain physiological performance and reproductive activity. Nevertheless, fiddler crabs can adjust their behavior in response to the magnitude of perceived benefits and costs. When the chance of successfully acquiring a mate is high, males will accept a higher body temperature (and concomitantly higher metabolic and water loss rates) than when the chances of mating are low. Likewise, experimentally lowering costs by adding food and reducing thermal stress in situ increased fiddler crab activity levels. Males in good condition (i.e., of high phenotypic quality) spend more time in the breeding area guarding a burrow and courting females than do males in poor condition. As a consequence, by selectively mating with only breeding area residents, females obtain mates of higher than average quality relative to males in other parts of the marsh. My results provide a possible mechanistic explanation for the maintenance of the sand fiddler crab mating system.

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Preface

My dissertation research benefited greatly from the generous assistance of numerous other people. In particular, Chapter 3 was the result of collaborative work between me, Dominique de Lambert and Jeff Levinton. Dominique was an undergraduate research assistant who helped collect much of the data in the initial field study characterizing the relationship between tenure in the breeding area and relative claw size for male fiddler crabs. Jeff made important contributions to the design of both that study and the estimation of fiddler crab body condition. My contributions to this chapter included experimental design, data collection and analyses for all components of the study and the writing. Chapter 3 will be submitted for publication as "Allen, B.J., de Lambert, D. & Levinton, J.S."

Similarly, Chapter 4 was the result of collaborative work between me, Brooke Rodgers and Jeff Levinton. Brooke was also an undergraduate research assistant who helped me collect the data in the treadmill experiment characterizing how endurance capacity of male fiddler crabs varied as a function of body size, temperature and hydration state. Again, Jeff contributed to both the design and interpretation of this particular experiment. My contributions to this chapter included experimental design, data collection and analyses for all components of the study and the writing. Chapter 4 will be submitted for publication as "Allen, B.J., Rodgers, B.S. & Levinton, J.S."

Appendix 1 was the result of collaborative work between me and Yuhao "Ram" Tuan, a visiting graduate student from National Taiwan Ocean University. Ram collected much of the data characterizing the relationship between fiddler crab locomotor performance and body temperature. My contributions to this work included experimental design, some data collection, analyses and the writing.

Funding for this research came in part from a grant from the American Museum of Natural History, Lerner-Gray Fund for Marine Research, a Grant-in-Aid-of-Research from Sigma Xi, a National Science Foundation Doctoral Dissertation Improvement Grant, a Graduate Council Fellowship from Stony Brook University and a Science to Achieve Results (STAR) Graduate Fellowship from the United States Environmental Protection Agency (EPA). EPA has not officially endorsed this publication and the views expressed herein may not reflect its views.

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The other individual who contributed the most to my intellectual growth at Stony Brook was Dianna Padilla. Dianna is unfailingly enthusiastic about doing science and consistently pushed me to stop planning things and start collecting data, analyzing my results or writing manuscripts. She was instrumental in the development of my ability to communicate science to different audiences via different formats. She also introduced Cheri and me to some of the best restaurants on Long Island – we would never have found them in the strip malls otherwise. I extend many thanks also to David Conover and Ray Huey, the other members of my committee. I was familiar with their work long before I met either one of them, as even a cursory glimpse at my dissertation will show. They challenged me to think in new ways; to integrate physiology, behavior, ecology and evolutionary biology, while always trying to understand the underlying mechanisms. I view the biological world differently than when I started the doctoral program and I am grateful to my entire committee for that.

The Department of Ecology and Evolution at Stony Brook is a wonderful community that I am sad to leave. I thank the departmental staff, Martha Nolan, Marilyn Pakarklis, Gwen Luke, Iris Roth, Donna DiGiovanni, Mike Doall and Fumio Aoki for all they did to make my life easier and better; I thank my officemates, Isabel Ashton, Paul Bourdeau and Sarah Gray for making it fun to come to work every day; I thank my research assistants, Dominique de Lambert, Brooke Rodgers and Yuhao "Ram" Tuan for making my dissertation far more interesting than it otherwise would have been; and I thank the other students and faculty of the department for creating such an exciting and engaging intellectual environment. I would especially like to thank Brendan Kelaher for demonstrating by example how to fully embrace a scientific and academic career while maintaining multiple outside interests – there is truly nothing wrong with arguing about experimental design while on a surfboard.

I also owe a tremendous amount to Susan Williams, who as my masters advisor at San Diego State taught me how to be a professional scientist. There's no doubt in my mind (nor in the mind of anyone else who knew me back then) that any academic success I have had since is due entirely to her. She took a SCUBA instructor from Club Med who had never been a serious student and taught me how to think critically, to construct and defend a logical argument and to integrate disparate ideas into a cohesive whole. She also gave me the basic practical skills I needed – grant writing, public speaking, experimental methodology and networking. She pushed me very hard to go to Stony Brook and work with Jeff and Dianna.

Finally, I want to thank my family. In particular, my wife Cheri, who gave up living at the beach in San Diego to come to Long Island, New York for ~~six~~ ~~seven~~ eight long years. Even though we are now moving back to the southern California coast, I expect to hear about how she was "Ripped from my homeland…" for the rest of my life. Nevertheless, I wouldn't have made it through the program without her love and support. Thanks to Jen Funk and Isabel Ashton for being such good friends to Cheri and me; we can't wait to join you in the OC. My parents, Jim and Karen Allen, and Cheri's parents, Dave and Peg Deutch, were incredibly supportive of us during my time at Stony Brook. Although this support was offered in many ways, perhaps the most obvious was the help they gave us in buying and (very extensively) renovating an old house. I promise that, at least for the next few years, coming to visit us won't involve hammers, paint or a ladder. Also, the many free cars were helpful (thanks to Chuck Deutch as well for that). I am eternally grateful to have Cheri, Boden and Emma to come home to every day – everyone should be so lucky!

Chapter 1: Introduction

A central premise of the theory of sexual selection is that the reproductive benefits of having an exaggerated secondary sexual trait are eventually offset by costs to fitness such as increased predation risk or reduced growth rate (Andersson 1994). Conditional handicap models (Zahavi 1975; Pomiankowski 1987; Grafen 1990) are among the currently favored hypotheses for the evolution of extreme sexual traits (Andersson 1994), suggesting that such ornaments, weapons and displays signal male phenotypic or genotypic quality to choosy females. Implicit in these models are three important assumptions: (1) that the degree of trait expression is dependent upon underlying male condition; (2) that traits are costly to produce or maintain; and (3) that the costs of an increase in trait size are smaller for males in good condition than for males in poor condition (reviewed in Kotiaho 2001). Linking the expression of sexual traits mechanistically to their associated costs and constraints is crucial to advancing our understanding of sexual selection. It is therefore surprising that several recent reviews of the literature have concluded there is far less empirical support for the condition-dependence and costliness of such traits than is generally assumed (Kotiaho 2001; Cotton *et al.* 2004). The inferences made in many of the studies evaluated in these reviews were judged to be circumstantial or correlational in nature, and therefore less than strongly conclusive. Sexually selected structures that have joint functions of combat and display complicate matters even more as they may not conform to simple hypotheses of trade-offs between the mating advantages of conspicuous traits and their disadvantages with respect to growth or survival (Berglund *et al.* 1996; Koga *et al.* 2001).

In this dissertation, I investigate the costs and constraints associated with sexual selection in the sand fiddler crab, *Uca pugilator* (Decapoda: Ocypodidae), a small, highly active semi-terrestrial crab found in temperate salt marshes. Fiddler crabs are an ideal system for studying sexual selection as they provide some of the most extreme examples of sexual dimorphism in the animal kingdom (Crane 1975). Whereas females of all species of *Uca* have two small (minor) feeding claws, males have one minor claw and one greatly enlarged major claw that can comprise nearly 50 percent of the total body mass. The major claw is used in agonistic contests with other males for control of breeding burrows in preferred locations and also is waved in species-specific displays to attract receptive females for mating (Crane 1975; Christy 1982, 1983; Pope 2000). Use of the major claw in both male-male combat and sexual display suggests that it is an honest signal of male quality and should therefore be condition-dependent and costly to produce and maintain (although development of low-mass regenerated claws and dishonest signaling has been found in at least one species; Backwell *et al.* 2000).

The fitness benefits that accrue to large male fiddler crabs with relatively large claws are well documented; such males are more likely to win contests for control of high-quality breeding burrows, display with greater vigor and are more attractive to females (Hyatt & Salmon 1978; Christy 1983; Jennions & Backwell 1998; Pratt & McLain 2002; Pratt *et al.* 2003). In contrast, the importance of potential costs and constraints associated with the development and display of the major claw or tenure in the mating area is much less well understood. Although a number of studies have looked for evidence of increased predation on males as evidence of a direct cost of the major claw due to conspicuous waving displays or reduced escape speed, the common conclusion is that large male crabs actually exhibit enhanced survival relative to juveniles or females (Bildstein *et al.* 1989; Johnson 2003; but see Koga *et al.* 2001). There is better evidence for the existence of a foraging cost borne by male *Uca*. Females have an advantage over males in food acquisition because the major claw is not used in feeding. Although they are able to compensate to a degree by modifying their feeding rate and amount of time spent foraging, males can never gain energy as quickly as females (Weissburg 1992, 1993). This discrepancy in energy acquisition presumably represents an indirect physiological cost of the major claw to males. Such a cost is likely exacerbated by the fact that females strongly prefer to mate with males controlling burrows high on the shore. As a general rule, temperature and desiccation stress increase while food availability decreases with increasing shore height across the intertidal zone, suggesting that the location and mid-summer timing of *U. pugilator* mating activity results in a potential trade-off between reproduction and growth for male crabs.

In Chapter 2, I explore the spatial distribution of food availability and thermal conditions across multiple salt marsh microhabitats used by *U. pugilator* and ask whether such patterns are consistent with the hypothesized trade-off between mating success and energy acquisition for reproductively active males. I then test directly whether environmental conditions constrain fiddler crab reproductive activity by experimentally manipulating food availability and thermal stress in the high intertidal breeding area.

In Chapter 3, I investigate whether variation in tenure at breeding sites by male fiddler crabs is positively correlated with individual competitive ability, so-called resource holding power (RHP), as predicted by current resource defense theory (Kokko 1999; Härdling *et al.* 2004) or negatively correlated as predicted by the hypothesized trade-off with energetic costs. I also ask whether RHP is, in turn, a function of underlying physiological condition. I first tested whether larger males or those with relatively large major claws spent more consecutive days in the breeding area. I then tested the correlations between individual RHP (defined as body size or relative claw length) and body condition. Finally, I experimentally manipulated males to be at one of three levels of condition before comparing time spent in the breeding area by crabs in each group.

In Chapter 4, I experimentally investigate whether body temperature (T_b) and hydration state differentially affect physiological and behavioral performance of sand fiddler crabs as a function of individual body size. Small individuals generally have lower thermal inertia and higher mass-specific water loss rates than large individuals (Herreid 1969; Stevenson 1985), suggesting an alternative (but not mutually exclusive) hypothesis to explain the skewed size distribution of males in the breeding area: small males are more susceptible to thermal and hydric stress than large males. I address three questions: First, what are the size-dependent consequences of simultaneous variation in T_b and hydration to locomotor performance? Second, does body size affect behavioral choices made by fiddler crabs in response to local thermal and hydric conditions? Finally, is size-specific variation in fiddler crab physiological and behavioral responses to temperature and hydric conditions in the laboratory relevant to environmental conditions in the field?

In Chapter 5, I summarize briefly the implications of this work and suggest several potential directions for future studies.

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Chapter 2: Sexual selection and the physiological consequences of habitat choice by a fiddler crab

Introduction

Life history theory provides a framework for understanding how organisms differentially allocate resources to survival, growth and reproduction. The ubiquity of trade-offs is a fundamental life history concept based on the assumption that resources are limited and those allocated to any particular trait are therefore unavailable for allocation to another (Roff 1992; Stearns 1992). Organisms must often balance multiple trade-offs simultaneously: for example, physiological trade-offs between energy allocated to current reproduction versus growth, storage, future reproduction or survival (Williams 1966), or within reproduction, between offspring number and size (Lack 1954); and behavioral trade-offs between foraging and predation risk (Stephens & Krebs 1986; Brown & Kotler 2004), predation risk and reproductive activity (Magnhagen 1991; Zuk & Kolluru 1998) and reproductive activity and foraging (Le Boeuf 1974; Clutton-Brock *et al.* 1982; Andersson 1994). In all cases, natural selection is expected to optimize allocation among competing life history traits in ways that maximize individual fitness (i.e., lifetime reproductive output) (Roff 1992; Stearns 1992).

Habitat choice can be a critical component of fitness maximization behavior in animals. Habitats offering reduced predation risk may be sub-optimal in terms of foraging efficiency (Lima & Dill 1990; Brown & Kotler 2004). Open areas offer optimal thermal and foraging opportunities to juvenile garden skinks, *Lampropholis guichenoti*, but, under threat of predation, lizards remain sheltered in safer habitats with fewer opportunities for basking and feeding; as a consequence, they grow more slowly, attain smaller body sizes at maturity and produce lighter clutch masses and offspring later in life (Downes 2001). Individuals may face a similar trade-off with respect to mating opportunities (Magnhagen 1991; Sih 1994). In the absence of predators, male three-spined sticklebacks, *Gasterosteus aculeatus*, prefer to court from open nest sites where their display behavior is highly visible to females; however, when predators are present males are much more likely to establish their nest in structurally complex vegetated habitat that offers them greater protection by reducing their visibility (Candolin & Voigt 1998). Although many studies have considered temporal trade-offs between growth and reproductive activity – mate-searching and guarding, fighting and courting displays all require time that is lost to foraging (Clutton-Brock *et al.* 1982; Robinson & Doyle 1985; Given 1988; Deutsch *et al.* 1991), the potential for spatial variation in habitat quality to drive such trade-offs is relatively unknown.

Fiddler crabs of the genus *Uca* are small, highly active semi-terrestrial crabs that typically live in sheltered areas of salt marshes and mangrove forests. Of the three sympatric species of *Uca* typically found in mid-Atlantic coastal marshes, the sand fiddler crab, *Uca pugilator*(Bosc), has the widest vertical distribution, from water's edge to the high intertidal zone. In the spring and early summer, the majority of fiddler crabs active in the marsh are found at low tide foraging on creek banks near the waterline in large aggregations of hundreds to thousands of individuals (Crane 1975, Christy 1982, 1983, McLain *et al.* 2003). When startled or in response to encroaching high tides, the crabs retreat to simple burrows in the nearby vegetation. By mid-summer, however, reproductively active males spend much of their time exposed in open sand flats high on the shore, guarding specialized breeding burrows from other males and engaging in courtship displays (Christy 1982, 1983; Christy & Salmon 1984). Males use a single greatly-enlarged major claw as both a weapon in agonistic contests with other males and an ornament waved in a species-specific display to attract receptive females for mating (Crane 1975; Christy 1978; Pope 2000; Pratt *et al.* 2003). Large males with relatively large claws are more likely to acquire and successfully defend breeding burrows in desirable locations (Hyatt & Salmon 1978; Christy 1983; Pratt & McLain 2002); such males are also in better physiological condition, display with greater vigor and are more attractive to females (Hyatt 1977; Jennions & Backwell 1996, 1998; Pratt *et al.* 2003; Pratt & McLain 2006). Females strongly prefer to mate with males controlling burrows high on the shore because of the reduced risk of burrow collapse due to tidal flooding (and subsequent egg loss during oviposition and brooding) (Christy 1983).

As a general rule, food availability decreases while temperature and desiccation stress increase with increasing shore height across the intertidal zone, suggesting that the timing and location of *U. pugilator* mating activity results in a potential trade-off between reproductive success and energy acquisition for male crabs. Fiddler crabs scoop sediment to their mouth with both claws if female, or the single small claw if male, where specialized mouthparts scour organic material (primarily benthic diatoms) from the mud or sand (Crane 1941; Miller 1961; Robertson & Newell 1982). Males compensate partially for the lack of a second feeding claw by increasing their feeding rate and overall foraging time, but they can never gain energy as quickly as females; their disadvantage increases when sediment food concentrations are low (Weissburg 1992, 1993). Bearing the major claw also imposes significant energetic costs to male fiddler crabs during both routine and reproductive activities (Weissburg 1993; Matsumasa & Murai 2005; Allen & Levinton 2007); such costs are exacerbated by high environmental temperatures that burden surface active crabs with increased body temperatures and associated metabolic rates (Teal 1959; Emmerson 1990). Finally, reproductively active males face significant opportunity costs of foraging and thermoregulating because any time spent feeding or sheltering underground is lost to courtship and potential mating (Caravello & Cameron 1987, 1991; Croll & McClintock 2000).

I investigated the spatial distribution of food availability and thermal conditions across multiple salt marsh microhabitats used by *U. pugilator* and ask whether such patterns are consistent with a hypothesized trade-off between mating success and energy acquisition for reproductively active males. I then tested directly whether environmental conditions constrain fiddler crab reproductive activity by experimentally manipulating food availability and thermal stress in the breeding area.

Methods

This study was conducted from June to September in 2003 and 2004, during the breeding season of *U. pugilator* at Flax Pond, a *Spartina alterniflora* salt marsh located on the northern shore of Long Island, New York, USA (40º 58’ N, 73º 08’ W).

(a) *Variation in microhabitat food availability*

I characterized spatial variation in food availability to fiddler crabs by sampling the surface sediment in creek bank, *Spartina* and sand flat salt marsh microhabitats on 15 and 29 July 2003. I took replicate cores from each microhabitat ($n = 9$ per sampling date, at least 1 m apart) to quantify chlorophyll *a* (chl *a*), percent carbon and water saturation – all factors known to influence fiddler crab foraging (Robertson *et al.* 1980; Weissburg 1992, 1993; Reinsel & Rittschof 1995). Samples for analyses of chlorophyll *a* and percent carbon were collected with a small syringe core (1.45 cm diameter; 0.5 cm deep) and water saturation with a larger box core (10 x 10 cm; the top 0.5 cm of sediment was removed and stored while the core was still *in situ*). Samples were immediately placed on ice in airtight plastic bags and stored in the dark until processed.

Chlorophyll *a* concentrations were determined by extracting samples with 10 mL of 90% acetone for 24 h at 4°C in darkness (Parsons *et al.* 1984); samples were centrifuged and the supernatant was analyzed in a narrow-beam spectrophotometer (Beckman Coulter, Inc., Fullerton, CA). Equations for estimating chl *a* in the presence of phaeopigments were taken from Parsons et al. (1984). After acetone extraction each sediment sample was dried at 80°C for 72 h, cooled in a desiccator and weighed; chl *a* concentrations were calculated as $\mu g\ g^{-1}$ sediment. Percent carbon was measured from samples dried at 60°C, ground into a coarse powder, weighed and analyzed with a Carlo Erba CHN autoanalyzer (Carlo Erba Instruments, Milan, Italy). Water saturation (reported as a percentage) was estimated by weighing the samples wet, drying them at 80°C before reweighing them and converting the mass of water lost to volume (assuming a density for water of 1 $g\ mL^{-1}$); samples were then ashed at 500°C for 4 h (after Reinsel & Rittschof 1995). Deionized water was added to 20 mL of ashed sediment until all empty space was filled; this volume of water was designated 100% saturation (Buchanan 1984). Saturation of field-collected sediment was calculated as the ratio of volume of water lost upon drying to that required to saturate to 100%. Values greater than 100% are indicative of standing water over the sediment when the samples were taken.

(b) *Variation in microhabitat thermal conditions*

The body temperatures of ectothermic organisms are often very different from the temperature of the surrounding air or substratum (Porter & Gates 1969; Stevenson 1985; Huey *et al.* 1989). For this reason, operative environmental temperatures (T_e) provide a more biologically useful measure of local thermal conditions. Operative temperature is defined as the temperature of an inanimate object of zero heat capacity with the same size, shape and radiative properties as an animal exposed to the same microclimate (Bakken 1992; Shine & Kearney 2001); in other words, operative temperature represents the expected body temperature (T_b) of an organism in a given environment. I estimated the distribution of fiddler crab T_e's among salt marsh microhabitats using small iButton temperature data loggers (Thermochron, 0.5 ºC resolution; Maxim Integrated Products, Inc., Sunnyvale, CA) embedded in models that approximated the crabs in size, shape and posture (Figure 1; Vitt & Sartorius 1999; Helmuth 1998; Dzialowski 2005). Each iButton (1.7 cm diameter) was attached with modeler's clay to a copper base formed from the semi-circular section of a 2.5 cm pipe strap (Nibco, Inc., Elkhart, IN); this design held the datalogger ~1 cm above the sediment surface, similar in height to the carapace of a live crab. Field validation trials showed that temperatures recorded by these thermal mimics closely approximated the steady-state body temperatures of live crabs (± 1.5 ºC under all conditions for crabs 18-22 mm in carapace width) and that more elaborate models (i.e., with greater morphological detail and painted to match the reflectance of live crabs) performed no better (author's unpublished data).

I measured operative temperatures available to *U. pugilator* in different salt marsh microhabitats on 10 days between 9 July and 27 August 2003 with 60 haphazardly-distributed models (creek bank, $n = 15$; *Spartina*, $n = 30$; and sand flat, $n = 15$). I deployed more models in the *Spartina* to better characterize the higher thermal heterogeneity I expected within the vegetative canopy. On each sampling date, T_e's were measured every 5 min from 0800 to 1800 hours. I concurrently sampled the body temperatures of male crabs active on the marsh surface ($n \geq 100$ each sampling date) using a digital thermometer with a hypodermic thermocouple probe (accuracy of ± 0.1°C).

Quantifying the relative thermal quality of a given microhabitat from the perspective of a fiddler crab also requires an estimate of the temperature range preferred by animals in the absence of associated ecological costs and constraints – so-called set-point or target T_b's (T_{set}) (Huey & Slatkin 1976; Hertz *et al.* 1993; Huey *et al.* 1989; Huey 1991). I estimated T_{set} of male fiddler crabs by allowing them to move about freely in a laboratory thermal gradient before taking their body temperature. Substratum temperature is an important factor determining equilibrium body temperatures of fiddler crabs in the field (Smith & Miller 1973; author's unpublished data). The working section of the thermal gradient consisted of an open plexiglass raceway (1.20 m long x 0.10 m wide x 0.10 m high) mounted on a solid aluminum bar (1.80 m long x 0.10 m wide x 0.05 m high) covered with a thin layer of sand. Each end of the aluminum bar was transited by four rigid copper pipes (1/2 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). Water flow was adjusted such that substratum temperatures changed linearly along the length of the aluminum bar. Crabs could easily choose a T_b from 5º to 45º C by changing their physical location in the thermal gradient. Individual male *U. pugilator* ($n = 48$) were placed at random inside the plexiglass 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 some particular T_b. I defined T_{set} as the central 50% of all T_b's selected in the gradient, a common metric in studies of thermal biology (Hertz *et al.* 1993; Christian & Weavers 1996; Blouin-Demers & Weatherhead 2001). T_{set} was determined separately for crabs on both wet and dry sand.

I calculated the thermal quality of each microhabitat as the mean of the absolute value of deviations between T_e and the crab's preferred temperature range (d_e). Analogously, I calculated the accuracy of T_b achieved by crabs in the field (relative to T_{set}) as the mean of the deviations of T_b from T_{set} (d_b) (after Hertz *et al.* 1993). Finally, I calculated the percent of T_e and T_b observations that fell within the preferred temperature range (i.e., d_e and $d_b = 0$, respectively). These numbers provide additional information about both the overall quality of the different microhabitats and the ability of fiddler crabs to effectively use their thermal environment.

The indices and other symbols used in this paper are listed in Table 1.

(c) ***Environmental constraints on fiddler crab reproductive activity***

To test directly whether food availability or thermal conditions constrain reproductive activity by male *U. pugilator* in the breeding area, I transplanted crabs into enclosures in a high intertidal sand flat under different environmental conditions. Treatments consisted of: (1) ambient food availability and thermal stress (unmanipulated control); (2) increased food availability and ambient thermal stress; (3) ambient food availability and reduced thermal stress; and (4) increased food availability and reduced thermal stress and were randomly assigned to twelve circular enclosures arranged in three blocks of four (one replicate per treatment per block). Each enclosure (1.80 m diameter) was made from 60 cm high galvanized steel hardware cloth (6 mm mesh size), inserted 30 cm into the sediment. The top 7.5 cm of each cage wall was covered with smooth foil tape to prevent experimental crabs from escaping. In the food addition treatments, 20 g TetraMarine fish flakes (Tetra, Blacksburg, VA) in 1 L filtered seawater was distributed evenly across the sediment surface daily; enclosures that did not have food applied still received 1 L filtered seawater. Thermal stress was reduced in the appropriate enclosures by shades consisting of fiberglass window screening sewn onto a rigid plastic hoop (2 m diameter), supported 60 cm above the marsh surface on legs made of PVC pipe. Preliminary measurements showed that operative temperatures for fiddler crabs were reduced by as much as 8°C at midday under the shades.

On 27 July 2004 I transplanted twenty male *U. pugilator* into artificial burrows in each enclosure (one per crab). Burrows were created by pushing a 1.5-cm diameter wooden dowel 30 cm into the sediment, at an angle of approximately 40° (Christy 1982); males moved from naturally-occurring breeding burrows into artificial ones typically modify their new residence into a functional breeding burrow within one to two tidal cycles (author's personal observations). I used adult crabs similar in size to those already established and displaying in the breeding area (mean carapace width ± s.d. = 19.70 ± 1.02 mm; $n = 240$). Ten female crabs were also introduced to each enclosure to stimulate male courtship behavior (Pope 2000; Kim & Choe 2003). Crabs were given two days to adjust before any data were collected. During this time, males exhibited natural behaviors that included burrow maintenance, foraging, waving display and fighting. For five consecutive days I observed each enclosure for 25 minutes over a period of 3 h before to 3 h after low tide; I recorded both the number of males active on the marsh surface and the number of males waving. The order of observation among blocks and enclosures within blocks was randomized daily.

(d) ***Statistical analyses***

I compared environmental variables related to fiddler crab food availability among salt marsh microhabitats with two-way analyses of variance (ANOVA) with habitat and sampling date as fixed factors. Data were transformed using either a $\ln(x + 1)$ (chl a) or arcsine (percent carbon and water saturation) function to correct for unequal variances and non-normality (Sokal & Rohlf 1995). I calculated the mean percent of males active and percent waving for each experimental plot over the five-day observation period. I compared differences in reproductive activity among treatments by means of a three-way mixed model ANOVA with block as a random factor and food availability and shade as fixed factors; data were arcsine-transformed before analysis. Post-hoc multiple comparisons were done with Tukey's HSD test. All analyses were done with JMP 5.1.

Results

(a) *Variation in microhabitat food availability*

Sediment characteristics associated with food availability to *Uca pugilator* varied significantly among the different salt marsh microhabitats, generally decreasing with increasing tidal height (Figure 2). I pooled data over both sampling dates for all analyses because none of the interaction terms were significant (all $p \geq 0.298$) (Winer *et al.* 1991). Mean chlorophyll *a* concentration was highest in the creek bank and lowest in the high intertidal sand flat (Figure 2*a*; $F_{2, 51} = 146.6$, $p < 0.001$). In contrast, percent carbon was highest in the vegetated *Spartina* zone, although still lowest in the sand flat (Figure 2*b*; $F_{2, 51} = 169.6$, $p < 0.001$). Spatial change in percent water saturation of sediment mirrored that of chl *a* – highest in the creek bank and lowest in the sand flat (Figure 2*c*; $F_{2, 51} = 430.0$, $p < 0.001$). Food availability as assessed by all three variables was reduced by at least five-fold in the sand flat breeding area relative to the creek banks where crabs typically forage; values recorded for both percent carbon and water saturation in the sand flat were well below those previously found to stimulate feeding in this species (Reinsel & Rittschof 1995).

(b) *Variation in microhabitat thermal conditions*

I collected 72,600 T_e's from the fiddler crab thermal mimics and 1,258 T_b's from individual *U. pugilator* active on the marsh surface. Table 2 summarizes the data by habitat; the relative frequency distributions of operative and body temperatures are presented in Figure 3. As predicted, mean T_e was highest in the breeding area by several °C, however, mean T_b in the breeding area and creek bank were essentially the same, and only slightly higher than in *Spartina*. Even more surprisingly, maximum T_e and T_b were observed in *Spartina* and creek bank habitat, respectively, not in the high intertidal sand flat (Table 2). The mean T_b selected by crabs in the thermal gradient on wet sand was 27.6°C and the 25% and 75% quartiles defining T_{set} were 26.1°C and 29.3°C; T_{set} was significantly lower on dry sand ($F_{1, 94} = 316.1$, $p < 0.001$): the mean T_b was 20.8°C and the 25% and 75% quartiles were 19.2°C and 21.9°C.

Mean d_e provides a measure of the average thermal quality of the habitats available to *U. pugilator* – a higher value indicates thermal conditions farther from the preferred temperature range. Based on the observed variation in sediment percent water saturation among salt marsh microhabitats (Figure 2*c*), I calculated d_e and d_b (the deviations of T_e and T_b from T_{set}) using T_{set} measured on wet sand for crabs in the creek bank and *Spartina* microhabitats and on both wet and dry sand for crabs in the sand flat. Sediment in the breeding area will be wetted on several of the highest tides each month; nevertheless, for the most part this area of the marsh is quite dry relative to the *Spartina* and creek bank habitats lower on the shore. Mean d_e was highest in the sand flat using either metric and the percent of deviations equal to zero was correspondingly low (Table 2); together these data indicate that surface active crabs in the breeding area will have a difficult time maintaining T_b's within their preferred temperature range relative to crabs in *Spartina* or the creek bank (see also Figure 3). In contrast, while mean d_b was also highest in the breeding area when calculated using T_{set} for dry sand, mean d_b for all the habitats were quite similar when calculated using T_{set} for wet sand. In all cases, the percent equal to zero deviations of body temperatures from the preferred body temperature range were higher than the percent equal to zero deviations for operative temperatures, suggesting that fiddler crabs have the capacity to behaviorally regulate their body temperature by taking refuge in vegetation or protective burrows (Table 2; Figure 3).

(c) *Environmental constraints on fiddler crab reproductive activity*

Adding food to experimental plots in a high intertidal sand flat did not affect the proportion of males active on the marsh surface; however, the proportion of males present on the surface was significantly greater in shaded versus unshaded experimental plots(Figure 4*a*). The interaction between food and shade was not statistically significant (food: $F_{1,8} = 1.2$, $p = 0.306$; shade: $F_{1,8} = 62.6$, $p < 0.001$; food x shade: $F_{1,8} = 0.7$, $p = 0.414$). In contrast, both food addition and shade positively affected the proportion of males waving; again, the interaction term was not significant (Figure 4*b*; food: $F_{1,8} = 23.3$, $p = 0.001$; shade: $F_{1,8} = 8.5$, $p = 0.020$; food x shade: $F_{1,8} = 0.7$, $p = 0.417$). For both analyses I pooled data over the three blocks because those terms were not significant (both $p \geq 0.824$) (Winer *et al.* 1991).

Discussion

Food availability and thermal conditions for fiddler crabs are clearly worse in the breeding area compared to other salt marsh microhabitats. The overall lack of food, coupled with high thermal stress, means that males guarding burrows and courting females in high intertidal sand flats accept significantly reduced energy intake (and presumably growth) in exchange for the chance to mate. Studies of other species of fiddler crab have also found courtship behaviors that include waving displays and the construction of burrow hoods and pillars out of sediment to be constrained by energy availability (Backwell *et al.* 1995; Jennions & Backwell 1998; Kim & Choe 2003). That males in the breeding area spend significantly less time foraging compared to crabs in other salt marsh microhabitats merely compounds the problem (Caravello & Cameron 1987; Croll & McClintock 2000). Males can accumulate multiple females in a single burrow over time and male mating success is therefore positively correlated with tenure in the breeding area - a function of relative physiological condition (Christy 1978; Pratt & McLain 2002; Chapter 3). Given the reproductive advantages of large body size and good condition for male crabs, any trade-off between energy gain and current reproduction will almost assuredly involve future reproduction as well.

Fiddler crabs appear to be highly sensitive to the relative costs and benefits of alternative behavioral strategies. For example, non-reproductive foraging crabs employ a flexible energy-maximization strategy based upon both the concentration of food in the sediment and its relative ease of extraction. Individuals feeding in a given patch will leave at different threshold food concentrations depending on the sediment grain size (which affects intake rate) or will fail to feed altogether if the percent food or water is too low (Weissburg 1993; Reinsel & Rittschof 1995). The closely-related sand bubbler crab, *Scopimera inflata*, minimizes the distance traveled from its burrow while maximizing the total nearby area used for foraging (Zimmer-Faust 1987). Examples of fiddler crab behavioral adaptability are not, of course, limited to foraging. Risk-taking behavior in *Uca* is strongly context-dependent: when mating opportunities are increased, males will emerge from their burrow after a predator scare far more quickly than they would otherwise (Pratt *et al.* 2005; Reaney 2007). Smaller male *Uca annulipes* increase their rate of courtship waving relative to that of larger males late in the breeding cycle when less choosy females are more likely to accept a smaller mate (Jennions & Backwell 1998).

Fiddler crabs also seem able to effectively balance the potentially conflicting demands of body temperature and hydration state. In this study, fiddler crabs on wet sand in the laboratory chose T_b's that maximized locomotor performance (Weinstein 1998; Appendix 1) while on dry sand they accepted lower temperatures that presumably reduced their rate of dehydration due to evaporation. Nevertheless, the ability of fiddler crabs to make similar choices in the field is severely constrained. Although the high intertidal breeding area was the only salt marsh microhabitat with consistently dry sediment, it also provided the fewest opportunities for surface-active crabs to reach their preferred T_b. In contrast, crabs foraging in the lower marsh often had T_b's within their preferred range. Changing thermal and hydric conditions can have dramatic effects on organismal performance in a variety of contexts that include overall activity levels, locomotion; digestion, metabolism and heart rate (Huey 1982; Preest & Pough 1989; Tracy *et al.* 1993; Weinstein 1998); such effects will often be interactive. In American toads, *Bufo americanus*, the T_b yielding maximal locomotor performance is dependent upon hydration state – performance at all body temperatures is reduced as animals dehydrate, however, the magnitude of this decrease varies with T_b (Preest & Pough 1989). Similar results have been documented for the ghost crab, *Oypode quadrata*, a close relative of fiddler crabs (Weinstein 1998). Interestingly, the highest T_b's I observed during this study were from crabs in the creek bank habitat. Creek banks were typically covered by shallow standing water and the ability to remain fully hydrated may allow crabs to remain active even under thermal conditions that would be otherwise debilitating.

Thermal constraints on the activity patterns of animals have been well documented in a variety of taxa that include lizards (Porter & Gates 1969; Huey 1982; Grant & Dunham 1988), snakes (Huey *et al.* 1989; Blouin-Demers & Weatherhead 2001), mosquitos (Kingsolver 1979), quail (Goldstein 1984) and baboons (Hill 2006) and temperature and desiccation stress are widely viewed as perhaps the most significant abiotic factors influencing the performance and fitness of marine intertidal ectotherms (Connell 1972; Somero 2002; Helmuth *et al.* 2006). Thermal and hydric constraints are especially likely to be important for small organisms like fiddler crabs that have low thermal inertia and a water-permeable integument (Edney 1961; Smith & Miller 1973; Thurman 1998); such individuals are vulnerable to rapid shifts in microclimate conditions and should therefore make careful choices regarding habitat thermal and hydric quality (Stevenson 1985; Huey 1991; Yoder *et al.* 2005). Like many marine intertidal organisms (Helmuth *et al.* 2002; Somero 2002; Stillman 2003), fiddler crabs live close to their thermal tolerance limits (Teal 1959; Vernberg & Tashian 1959). This is particularly true for surface-active male *U. pugilator* in the high intertidal breeding area (this study; see also Bortolus *et al.* 2002). Although thermoregulatory capacity has been ascribed to a variety of behavioral and morphological characteristics of *Uca* such as basking, shuttling between sun and shade and color change (Crane 1943; Wilkins & Fingerman 1965; Powers & Cole 1976), taking refuge in a burrow appears to be the most effective way for fiddler crabs to simultaneously regulate both body temperature and hydric state (Smith & Miller 1973). Unfortunately for reproductively active males, such a strategy imposes significant opportunity costs with respect to foraging, burrow defense and courtship. When thermal and hydric costs of surface activity in the sand flat were reduced with shades, males spent less time in their burrows.

Given the poor opportunities for mating in most marsh microhabitats, male fiddler crabs have little choice but to defer feeding and growth in favor of reproductive activity in a physiologically stressful habitat (Crane 1975; Croll & McLintock 2000; Pratt & McLain 2002), however, individuals do not stay in the breeding area indefinitely. Residents must constantly defend their burrows against intruders trying to evict them (Jennions & Backwell 1996; Pratt & McLain 2002; Morrell *et al.* 2005; Pratt & McLain 2006) and combat and courtship displays are physiologically expensive (Matsumasa & Murai 2005). Males eventually either lose their burrow to a challenger or voluntarily abandon the breeding area to feed lower in the marsh (Christy 1978; Pratt & McLain 2002; Chapter 3). The degree to which crabs make their own choice to leave, versus having it made for them, is currently unknown; however, the underlying mechanism is clearly related to physiological condition. In an analogous example, male red deer, *Cervus elaphus*, significantly reduce the amount of time they spend foraging when holding a harem and can lose up to twenty percent of their body mass over time. Deteriorating body condition eventually contributes to the end of a stag's rut as previously sub-dominant males in better condition become more likely to win contests (Clutton-Brock *et al.* 1982; Andersson 1994). By reinforcing a relationship between residency and male condition, the very factors that make the breeding area so physiologically challenging may serve to filter out weaker competitors, allowing choosy females to pick among mates of higher than average phenotypic quality (Pratt & McLain 2002; Cotton *et al.* 2005; Chapter 3).

Environmental conditions in the breeding area clearly place male fiddler crabs outside their trophically- and thermally-defined optimal habitat. The degree to which individuals respond to food and thermal stress by appropriately allocating time in the breeding area against time foraging in the low marsh, and in the breeding area, time within burrows against time on the marsh surface, remains unknown. My results demonstrate that males can compensate to some degree for food and thermal stress, however, future work should focus on understanding the exact deployment of behaviors that make such accommodation possible.

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Table 1. Definitions of the indices and other symbols used in this paper (after Christian & Weavers (1996)).

index or symbol	**definition**
T_e	Operative temperature: the equilibrium temperature that a fiddler crab would attain in a given microclimate; calculated using physical models that mimic the thermal characteristics of live crabs.
T_b	Body temperature
T_{set}	Set-point range of T_b's: taken to be the central 50% of T_b's selected by fiddler crabs in a laboratory thermal gradient.
d_e	An index of the average thermal quality of a habitat as measured by the mean of the absolute value of the deviations of T_e from T_{set}.
d_b	An index of field body temperatures realtive to the set-point range as measured by the mean of the absolute value of the deviations of field active T_b's from T_{set}.

Table 2. Mean ± s.d., maximum and minimum operative environmental (T_e) and body (T_b) temperatures recorded in each salt marsh microhabitat used by *Uca pugilator* and mean ± s.d., maximum and percent equal to zero (% = 0) deviations of operative and body temperatures from the preferred body temperature range of fiddler crabs in each microhabitat. Sand flat deviations were calculated using preferred body temperature ranges on both dry and wet sediments; *deviation was in the negative direction, all other deviations were positive.

salt marsh		T_e				d_e	
microhabitat	**mean**	**max**	**min**		**mean**	**max**	**% = 0**
creekbank	29.6 ± 3.98	39.5	18.0		2.4 ± 2.28	10.2	27.4
Spartina	28.0 ± 4.00	46.0	17.5		1.9 ± 2.23	16.7	38.3
sandflat	33.1 ± 4.47	42.5	19.0	*dry*	11.1 ± 4.45	20.6	1.2
				wet	4.8 ± 3.43	13.2	14.9
		T_b				d_b	
	mean	**max**	**min**		**mean**	**max**	**% = 0**
creekbank	29.4 ± 2.63	37.2	21.5		1.3 ± 1.98	7.9	43.8
Spartina	27.0 ± 2.65	31.9	19.6		0.8 ± 1.63	6.5*	56.8
sandflat	29.8 ± 4.37	35.7	20.8	*dry*	7.8 ± 4.37	13.8	0.7
				wet	1.7 ± 3.53	6.4	35.7

Figure 1. A fiddler crab thermal mimic next to a burrow in the high intertidal sand flat breeding area of *Uca pugilator*.

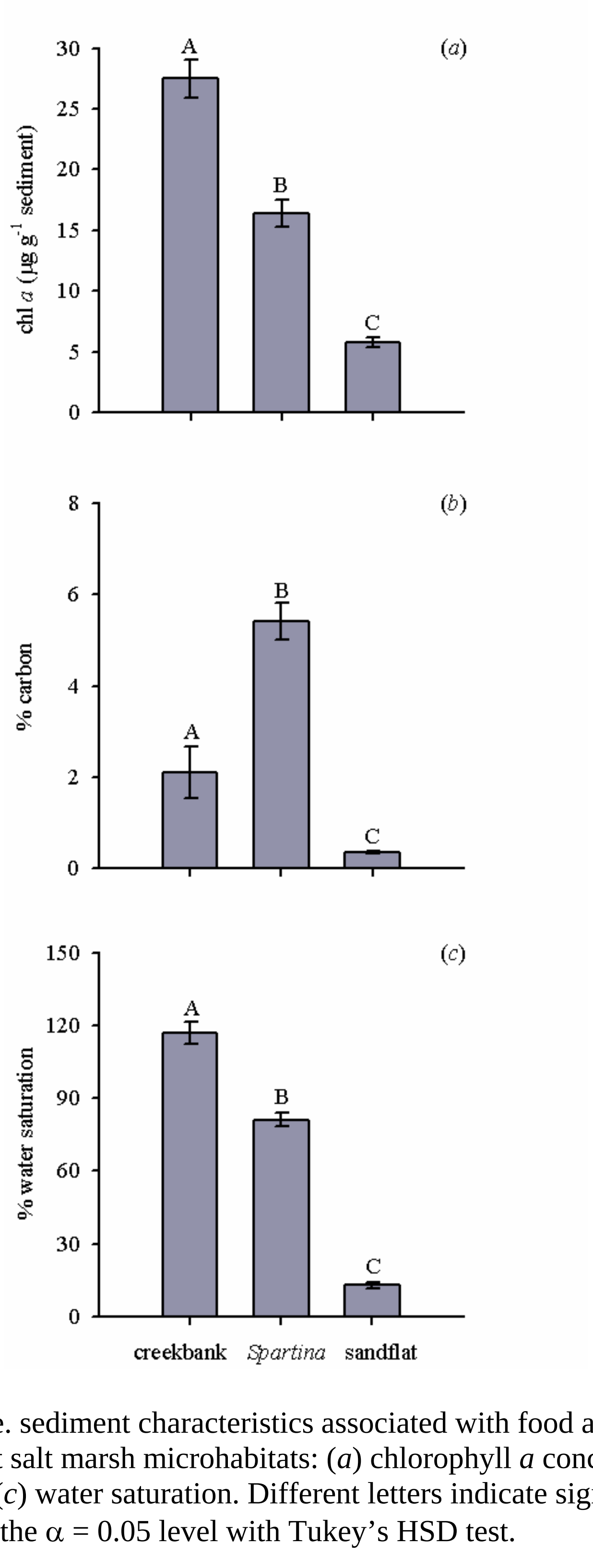

Figure 2. Mean ± s.e. sediment characteristics associated with food availability to *Uca pugilator* in different salt marsh microhabitats: (*a*) chlorophyll *a* concentration; (*b*) percent carbon; and (*c*) water saturation. Different letters indicate significant differences among treatments at the α = 0.05 level with Tukey's HSD test.

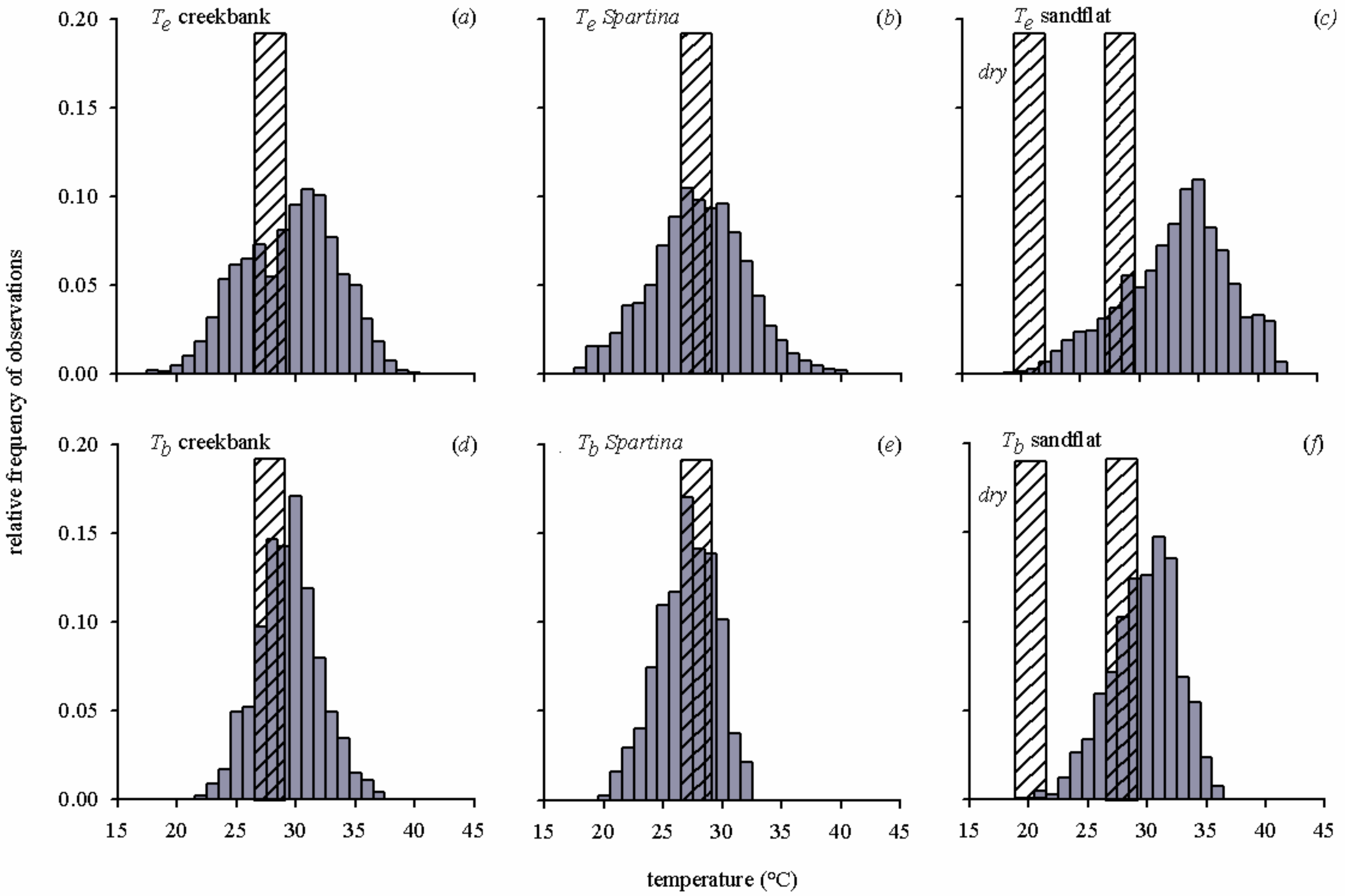

Figure 3. Relative frequency distributions of operative environmental temperatures (T_e; *a-c*) and body temperatures (T_b; *d-f*) of *Uca pugilator* in different salt marsh microhabitats. The hatched bars represent the range of preferred body temperatures (T_{set}) of male fiddler crabs in a laboratory thermal gradient on both wet (default) and dry sediments.

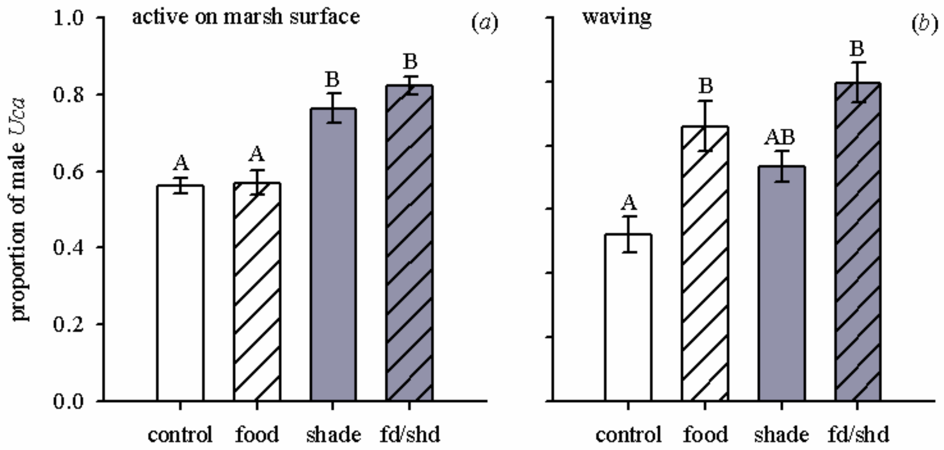

Figure 4. Mean ± s.e. proportion of male *Uca pugilator*: (*a*) active on the marsh surface; and (*b*) waving under different environmental conditions in the high intertidal sand flat breeding area [no food added (*open bars*); food added (*hatched bars*); no shade (*white bars*); and shade (*gray bars*)]. Differing letters indicate significant differences among treatments at the $\alpha = 0.05$ level with Tukey's HSD test.

Chapter 3: Condition-dependent tenure at breeding sites by male fiddler crabs

Introduction

Darwin (1871) proposed two alternative mechanisms to explain differential reproductive success among individuals: competition among males for access to females and female mate choice. It is often assumed that the winners of male-male contests are of higher quality and that females should therefore prefer them as mates (Berglund *et al.*1996; Wiley & Poston 1996). Although recent reviews have questioned the generality of this assumption (Qvarström & Forsgren 1998; Wong & Candolin 2005), the relationship between male dominance and female preference is particularly apt to be positive when males compete to control resources required by females for reproduction (e.g., food, mating or oviposition sites and refuge) (Emlen & Oring 1977; Andersson 1994). Females choosing to mate with dominant (i.e., competitively superior) males may guarantee themselves access to the best resources, increasing directly their fecundity or survival (Holm 1973; Andersson *et al.* 2002); they may also gain fitness indirectly via genetic benefits if traits that increase male competitive ability are heritable and increase the reproductive success of their male offspring (Montgomerie & Thornhill 1989; Alatalo *et al.* 1991). Resource defense mating systems are expected to evolve when critical resources are unevenly distributed in space or time such that competitively superior males have the potential to monopolize multiple mates (Emlen & Oring 1977). As the degree of resource control increases, so too does the variance in mating success among males.

The reproductive benefits to dominant males of resource defense are clear; however, such a strategy is often costly in terms of time, energy and survival. In addition to the risk of injury or even death associated with fights among males (Le Boeuf 1974; Clutton-Brock 1982), investment in territorial defense or courting displays may lead to reduced growth rate and energy storage or increased susceptibility to predators and parasites (Kirkpatrick 1987; Andersson 1994; Zuk & Kolluru 1998). As a consequence, the timing and duration of resource defense by males should be determined by both the quality of the defended resource and individual competitive ability, so-called resource holding power (RHP) (Parker 1974; Härdling *et al.* 2004). In many taxa, body size is a good indicator of RHP; however, other factors such as age, experience and physiological condition may also be important in determining an individual's ability to acquire and maintain control over resources (Andersson 1994). Especially when the frequency of resource turnover is low, males maximize their fitness by monopolizing high-quality resources for as long as possible; under such conditions theoretical models predict a positive relationship between individual RHP and the duration of resource control (Kokko 1999; Härdling *et al.* 2004).

Sand fiddler crabs, *Uca pugilator* (Bosc), are a model organism for testing theories about RHP and patterns of resource defense. *U. pugilator* are small, highly active semi-terrestrial crabs that live in sheltered areas of salt marshes along the Atlantic coast 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 & McClintock 2000; Pratt & McLain 2002). Males use a single greatly-enlarged major claw as a weapon in agonistic contests with other males for control of specialized breeding burrows, and wave it in a species-specific display to attract receptive females for mating (Crane 1975; Christy 1978; Pope 2000; Pratt *et al.* 2003). Mating, oviposition and egg-brooding all take place within the breeding burrows; burrows high on the shore are much preferred by females because of the reduced risk of burrow collapse (and subsequent egg loss) due to tidal flooding (Christy 1983). After mating, females remain underground for about two weeks before emerging to release their planktonic larvae into the water. In contrast, males quickly return to the marsh surface to resume courting and burrow defense (Christy 1978, 1982). Males are sequentially polygynous and can potentially accumulate multiple females in a single burrow; male mating success is accordingly correlated with tenure in the breeding area (Christy 1978; Pratt & McLain 2002).

Males with breeding burrows (residents) in desirable locations must engage repeatedly in agonistic interactions with both intruding males that attempt to displace them and burrow-holding neighbors that attempt to limit their courtship displays and other surface activities (Hyatt & Salmon 1978, 1979; Christy 1982, 1983; Pratt & McLain 2002, 2006). In general, body size, relative major claw length and residency status all influence the likelihood that a male will win an encounter with another male (Jennions & Backwell 1996; Pratt & McLain 2002; Morrell *et al.* 2005; Pratt & McLain 2006). Breeding area residents are both larger and have larger claws for their body size than crabs in other parts of the marsh and the frequency of burrow loss to intruding males is therefore low (Christy 1983; Pratt & McLain 2002; Pratt *et al.* 2003). Fighting and courtship displays by fiddler crabs are physiologically demanding, however, and bearing the major claw imposes significant additional energetic costs to male crabs even during non-reproductive activities (Weissburg 1993; Matsumasa & Murai 2005; Allen & Levinton 2007). Such costs are exacerbated by the location and timing (mid-summer) of mating activity by *U. pugilator*: temperature and desiccation stress are increased and food availability is reduced in high intertidal sand flats relative to nearby vegetation or locations lower on the shore (Reinsel & Rittschof 1995; Croll & McClintock 2000; Chapter 2). The length of time an individual male is able to maintain a burrow in the breeding area should therefore be a function of both short-term fighting ability and tolerance of cumulative energy loss, stress and damage from fighting over a more sustained period of time. These observations suggest that male fiddler crabs face a potential trade-off: the very characteristics that make one successful in combat, i.e., large body and relative claw size, are accompanied by significantly greater energetic costs that may limit the total time one can participate in reproductive activity.

I investigated whether variation in tenure at specialized breeding sites by male sand fiddler crabs, *Uca pugilator,* is positively correlated with individual resource holding power as predicted by current resource defense theory (Kokko 1999; Härdling *et al.* 2004) or negatively correlated as predicted by a hypothesized trade-off with energetic costs. I also asked whether RHP is, in turn, a function of underlying physiological condition. I first tested whether larger males or those with relatively large major claws spent more consecutive days in the breeding area. I then tested directly the correlations between individual RHP (defined as body size or relative claw length) and body condition. Finally, I experimentally manipulated males to be at one of three levels of condition before comparing the time spent in the breeding area by individuals in each group.

Methods

My study site, Flax Pond, is a *Spartina alterniflora* dominated salt marsh located on the northern shore of Long Island, New York, USA (40º 58' N, 73º 08' W). All experiments were conducted from June to September in 2006, during the breeding season of *U. pugilator*.

(a) ***Relationship between male tenure and resource holding power***

Daily, from 27 July to 28 August, I collected, measured and marked surface-active male *U. pugilator* as they moved into high intertidal breeding areas. I used a set of contiguous sand flats clearly delimited by the surrounding vegetation and unoccupied at the beginning of my study (prior to the start of the experiment a thick mat of dead *S. alterniflora* precluded males from establishing breeding burrows in these locations). I attempted to mark males on their first day in the breeding area by focusing on individuals establishing new burrows. I captured them by blocking the entrance to their burrow with a thin dowel after they emerged to deposit excavated sediment onto the marsh surface. I measured carapace width and (for approximately half the individuals) major claw length to the nearest 0.01 mm with digital calipers and marked each male with fingernail polish: crabs were given a unique combination of colors on their carapace and major claw and their burrows were marked with small wooden stakes painted to match that color scheme. Every day at low tide, after capturing, marking and replacing 5-15 newly-arrived males (the actual number on any given day was determined by how many new excavations I could identify), I spent several hours observing the rest of the crabs active in the area from a distance of several meters. Binoculars and a telephoto camera lens were used to facilitate the identification of individuals.

During each observation period, I noted whether a male crab emerged from a marked burrow to forage or display and if so, whether that individual bore markings that matched those on the appropriate wooden stake. Crabs were scored as either 'present' (crab and burrow colors matched), 'absent' (an unmarked crab was in the marked burrow) or 'displaced' (a marked crab was still in the breeding area but no longer in its original burrow). Burrows from which no crab emerged were re-checked on subsequent days until either an associated crab was finally seen or the burrow was determined to be abandoned. In the high intertidal zone in Flax Pond, burrows with no resident crab collapse within a few tidal cycles. Crabs that were unobserved for several days but later reappeared in the same burrow were assumed to be present during the intervening days as males typically stay underground for 1-3 days after mating before emerging to continue courting (Christy 1978). In total, I marked and monitored 136 individuals over the course of the study. I calculated correlations between tenure in the breeding area (the number of consecutive days each male was observed in the sand flat) and two measures of individual RHP: carapace width and relative claw length (standardized deviations from a least squares regression of major claw length on carapace width; Smith & Palmer 1994).

(b) *Relationship between RHP and condition*

Condition is generally understood to mean the relative size of energy stores compared to structural components of the body (i.e., a measure of ‘phenotypic quality’; Cotton *et al.* 2004) and is assumed to summarize the general health and vigor of an individual (Jakob *et al.* 1996; Green 2001). Measuring condition in live animals requires nondestructive methods that accurately reflect underlying variation in nutritional state. Residuals from an ordinary least squares regression of body mass on some linear measure of body size are a commonly-used metric of condition in the ecological literature (Jakob *et al.* 1996; Green 2001). The underlying goal of such an approach is to control for differences in overall body size when comparing body mass among individuals. To test whether individual RHP is related to condition in *U. pugilator*, I calculated correlations between both carapace width and relative claw length and the standardized residuals from a least squares regression of body mass on carapace width for a haphazardly collected sample of surface-active males (*n* = 90). I was able to explicitly separate carapace (body) mass from claw mass by inducing the crabs to autotomize (cast off) their major claw, a naturally-occurring phenomenon that does not appear to harm the crabs; fiddler crabs that have lost their major claw readily grow a new one (Crane 1975). Body mass was measured to the nearest 0.01 g with a Sartorius 2205 balance. Although using wet mass to estimate condition may confound inter-individual variation in energy reserves with water content if crabs replace lost lipids or somatic tissue with water (Fitzgerald *et al.* 1989; Jennions & Backwell 1998), I found qualitatively similar results estimating condition of male *U. pugilator* with wet or dry mass in a preliminary experiment (author’s unpublished data)).

(c) *Relationship between male tenure and condition*

To test directly whether variation in breeding site tenure by male *U. pugilator* is related to condition, I kept three groups of crabs at different levels of food availability before transplanting them into a high intertidal sand flat and compared the number of consecutive days they were observed engaged in reproductive behavior. I used adult crabs similar in size to those already established and displaying in the breeding area (mean carapace width ± s.d. = 20.45 ± 0.98 mm; *n* = 120). Prior to the experiment, crabs were held in six outdoor mesocosms (40 x 40 x 60 cm) exposed to natural light and air temperature, with flow-through filtered seawater at one end (10 cm depth; 20ºC) and a sloping beach of sand 30 cm high at the other. Crabs (*n* = 20 per mesocosm) exhibited natural behaviors that included burrow construction, foraging, waving display and fighting. I measured carapace width and major claw length for each crab before marking it with duplicate small plastic tags (Brushy Mountain Bee Farm, Moravian Falls, NC) attached to their carapace and major claw with cyanoacrylic adhesive (each crab bore a unique color/number combination). One of three feeding treatments was randomly assigned to each mesocosm (*n* = 2 mesocosms per treatment): high food availability (7.5 g TetraMarine fish flakes (Tetra, Blacksburg, VA) in 1 L filtered seawater distributed evenly across the sediment surface every day); medium food availability (food applied every third day); and low food availability (food applied every sixth day). On any given day, mesocosms that did not have food applied still received 1 L filtered seawater applied in the same way. Irrespective of treatment, I removed excess food daily from each mesocosm 10-12 hours after feeding by scraping away the upper few mm of sediment with a drywall knife (Jennions & Backwell 1998; Kim & Choe 2003). A preliminary experiment demonstrated that crabs fed less frequently were in significantly poorer condition (assessed as relative body mass) than crabs fed *ad libidum* (author's unpublished data).

After 21 days I transplanted the experimental crabs (*n* = 40 males per treatment) into artificial burrows in a high intertidal sand flat. Burrows were made by pushing a 1.5-cm diameter wooden dowel 30 cm into the sediment, at an angle of approximately 40° (Christy 1982). Males moved from naturally-occurring breeding burrows into artificial ones typically modify their new residence into a functional breeding burrow within one to two tidal cycles (author's personal observations). The artificial burrows were located among the existing breeding burrows in the sand flat, evenly dispersed within a 1 x 12 m strip parallel to the shoreline. Crabs were randomly assigned to burrows marked with small wooden stakes carrying a matching tag. I monitored the experimental burrows for 4-6 hours daily, scoring each associated crab as either 'present', 'absent' or 'displaced' as described above. I ended the experiment after 11 days, when no marked crabs had been seen for four consecutive days. I then calculated tenure in the breeding area and resource holding power for each male as in the initial field experiment.

(d) *Statistical analyses*

To evaluate the relationship between male tenure in the breeding area and individual resource holding power, I calculated Spearman correlation coefficients between tenure and both carapace width and relative claw size for those crabs for which I had complete data (Sokal & Rohlf 1995). To test whether individual RHP was related to condition, I calculated Pearson correlation coefficients between relative body mass (not including claw mass) and both carapace width and relative claw length (these data better met the parametric assumptions of the Pearson coefficient than did the tenure data above; Sokal & Rohlf 1995). Treatment-specific differences in tenure among crabs in the food manipulation experiment were evaluated with failure-time statistics (PROC LIFETEST; SAS 2004). Tenure functions were compared with Wilcoxon's signed ranks test followed by pairwise multiple comparisons to determine specific differences between treatment groups (Allison 1995). Significance levels were corrected with the sequential Bonferroni technique with an experiment-wise error rate of $\alpha = 0.05$ (Dunn-Sidák method; Sokal & Rohlf 1995). I investigated within-treatment individual variation in tenure and resource holding power by calculating Spearman correlation coefficients between tenure and both carapace width and relative claw size by treatment group. All analyses were done with SAS 9.0.

Results

(a) *Relationship between male tenure and resource holding power*

Of the 136 newly-arrived male *U. pugilator* I marked in the high intertidal breeding area, I observed 90 on subsequent days who stayed for an average of 6.1 ± 3.82 d (mean ± s.d.), with a minimum of 1 d and a maximum of 15 d. I may be overestimating average tenure by excluding from my analysis crabs that spent less than one day in residence, however, I have no way to determine what proportion of the missing crabs left as a result of disturbance associated with capture and marking (and should therefore not be counted). Likewise, if the assumption that males were captured as they first arrived in the breeding area was wrong, my estimate of mean tenure is too low and the power to detect a relationship between tenure and individual resource holding power would be reduced. Nevertheless, data from a thorough study of *U. pugilator* reproductive behavior by Christy (1978) show that tagged males inside a large enclosure spent an average of 5.3 ± 2.88 consecutive days participating in reproductive activity in high intertidal breeding sites, with a minimum of 1 d and a maximum of 11 d. The concordance between Christy's (1978) study and this one suggests that my measurements of male tenure are probably reasonable. I found no relationship between number of consecutive days in the breeding area and carapace width (Figure 2*a*); however, there was a significant positive correlation between tenure and relative claw length (Figure 2*b*). My data do not allow me to differentiate between males that were evicted from their burrow by an intruder and those that voluntarily abandoned the breeding area to feed (e.g., Christy 1978; Pratt & McLain 2002); however, both mechanisms put an end to male participation in reproductive activity.

(b) *Relationship between RHP and condition*

I found no relationship between relative body mass (not including claw mass; a direct measure of nutritional state) and carapace width for male *U. pugilator* (Figure 1*a*). This is not particularly surprising given that I calculated condition as standardized residuals from a least squares regression of body mass on carapace width; nevertheless, such a result is not necessarily a foregone conclusion. In contrast, condition was significantly positively correlated with relative claw length (Figure 1*b*). These data suggest that relative claw size is an honest signal of underlying male condition and that males producing larger claws have had greater recent access to food resources or are more efficient at obtaining and storing energy (Weissburg 1993; Jennions & Backwell 1998; Pratt & McLain 2002).

(c) *Relationship between male tenure and condition*

Well-fed males, in putative good condition, stayed in the breeding area for significantly more time than did males fed less frequently (Table 1; Figure 3). I found no relationship between tenure and carapace width among crabs within treatments (Figure 4*a-c*); however, as in the observational study above, there were significant positive correlations between tenure and relative claw length (Figure 4*d-f*). Clearly, both absolute and relative condition influence the amount of time reproductively active male fiddler crabs can spend in the high intertidal breeding area. Although not statistically different from one another (test for common correlation coefficient, $p > 0.05$; Sokal & Rohlf 1995), correlations between tenure and relative claw size (but not carapace width) increase monotonically as food availability decreases (Figure 4*a-f*).

Discussion

My results clearly demonstrate that variation in breeding area tenure by male *Uca pugilator* can be explained, at least in part, by differences in individual resource holding power and that RHP is, in turn, related to underlying physiological condition. Resource holding power is often thought to be a function of body size as larger males are more likely to win fights in a variety of animal taxa (Andersson 1994) and fiddler crabs are no exception (Jennions & Backwell 1996; Pratt & McLain 2002; Morrell *et al.* 2005; Pratt &

McLain 2006). Nevertheless, I found no direct relationship between absolute carapace width and tenure among male *U. pugilator* in Flax Pond. Instead, relative measures of fitness such as body condition and relative claw length were better descriptors of RHP.

Competitive superiority in combat does not necessarily lead to longer periods of resource control of course. When dominant males can easily usurp resources from weaker individuals the duration of resource control for the best competitors may be short, particularly when resource defense is costly and males seek to minimize their exposure to these costs (Härdling *et al.* 2004). Alternatively, if resource quality is highly variable, dominant males may trade increased mating success for duration of control while a resource is theirs exclusively by contesting for only the best resources against other strong competitors (Koenig 1990; Alcock 2000). In any event, neither of these conditions applies to *U. pugilator* as residents are rarely supplanted by intruders (Pratt & McLain 2002, 2006). Rather, it appears as though absolute body size may not be the best predictor of RHP in this species.

This conclusion is limited to males within the size range I observed (18-24 mm carapace width); males of this size can all be considered ‘large’ relative to the total population (author’s unpublished data). Based on qualitative observations at this site, I suspect that had I included more small males (12-18 mm c.w.) in my study I would have found significantly reduced breeding area tenure for those individuals. Small males are more likely to lose their burrow to an aggressive intruder (Pratt & McLain 2002, 2006) and may also have greater difficulty tolerating the harsh physiological conditions of open sand flats compared to larger crabs (e.g., water loss rates are relatively higher for small crabs exposed to the sun; Chapter 4). Even so, because larger males tend to dominate high intertidal areas during the breeding season, the size range of individuals I observed is generally representative of the reproductively active population (see also Pratt & McLain 2002).

In contrast, individuals with relatively large major claws for their carapace width (an alternative measure of RHP) *did* spend more time in the breeding area guarding a burrow and courting females, as predicted by resource defense theory (Kokko 1999; Härdling *et al.* 2004). Coupled with the observation that males with relatively longer claws were also in better condition (Figure 2*b*), these data suggest that relative energy reserves, rather than absolute body size, are a primary determinant of individual RHP in *U. pugilator* (see also Jennions & Backwell (1998)). Relative claw size in fiddler crabs presumably provides an integrative measure of recent foraging success or efficiency at energy assimilation and expenditure, factors likely to be important in determining an individual’s ability to tolerate cumulative energy loss, stress and damage from fighting while in the breeding area (Andersson 1994). Similarly, male northern elephant seals fast during the breeding season while engaging in fierce contests with one another for access to groups of females and can lose more than one third of their body mass over a period of several months (Le Boeuf 1974); large dominant males are better able to tolerate the long-term energetic costs of participating in reproductive activity and gain the majority of all matings (Deutsch *et al.* 1990). Correlations between condition and reproductive tenure have also been found in a variety of other taxa that include red deer, *Cervus elaphus*, (Clutton-Brock *et al.* 1982), damselflies, *Calopteryx maculate*, (Marden & Waage 1990) treefrogs, *Hyla gratiosa*, (Murphy 1994) and sand gobies, *Pomatoschistus minutus*, (Lindström 1998).

In addition to staying in the breeding area longer, large male fiddler crabs with relatively large major claws also win more contests, display with greater vigor and may be more attractive to females (Hyatt & Salmon 1978; Christy 1983; Jennions & Backwell 1998; Pratt & McLean 2002; Pratt *et al.* 2003). My results suggest that all of these attributes may be linked to better physiological condition (see also Jennions & Backwell 1998). Development and growth of the major claw represents a significant energetic investment by male fiddler crabs (Hopkins 1982; Backwell *et al.* 2000; Allen & Levinton 2007) and the allocation of resources by an organism to any particular life-history trait implies that those resources are unavailable to others: a trade-off (Williams 1966; van Noordwijk & de Jong 1986). Nevertheless, all of the observed relationships between relative claw size and the fitness-enhancing traits described above are positive, not negative as expected. These data are consistent with the idea that if extravagant morphological characters or behavioral displays are costly to produce and maintain (Kirkpatrick 1987; Andersson 1994; Zuk & Kolluru 1998), then body size, weapons and signals of fighting ability should function as reliable cues of male quality to potential opponents and choosy females (Grafen 1990; Johnstone 1995; Berglund *et al.* 1996).

The positive relationship I found between individual RHP and male breeding site tenure in *U. pugilator* also fits this pattern. Although infrequent tidal inundation of the breeding area is good from the perspective of female crabs sequestered in underground burrows (Christy 1982, 1983), such sites are characterized by low food availability and high temperature and desiccation stress that pose significant problems for males active on the marsh surface (Croll & McClintock 2000; Henmi 2003; Chapter 2). Previous studies have demonstrated that waving and fighting associated with courtship by fiddler crabs can be limited by both food availability (Backwell *et al.* 1995; Jennions & Backwell 1998; Kim & Choe 2003; Chapter 2) and temperature (Smith & Miller 1973; Chapter 2). Bearing the enlarged major claw (which can comprise as much as 40% of the total body mass) compounds the problem for males by increasing the proportion of striated muscle tissue in large individuals, leading to higher mass-specific metabolic rates (Weissburg 1993; Levinton & Judge 1993; Allen & Levinton 2007). Nevertheless, males with relatively large claws actually spend *more* time in the breeding area and correlations between tenure and relative claw size may even increase as food availability decreases. Such a result, while certainly not definitive, at least suggests that males in relatively poor condition (i.e., individuals with small major claws given their body size) are more negatively affected by physiological stress and food limitation than males in good condition.

Conditional handicap models of sexual selection propose that secondary sexual traits such as ornaments and displays are honest signals of male quality because their associated costs are higher for lower-quality individuals (Zahavi 1975; Cotton *et al.* 2004). I would argue that condition-dependent tenure in the breeding area by male fiddler crabs provides an analogous example. Although some experimental evidence suggests that claw size alone may increase male attractiveness to females (Oliveira & Custodio 1998), it is not entirely clear whether female *U. pugilator* prefer larger males or those with relatively larger claws directly, or are instead choosing mates indirectly based on the location and quality of the breeding burrow they control (the strong positive correlation between the two variables confounds easy interpretation) (Hyatt & Salmon 1978; Christy 1983). Regardless, given that males in good condition (i.e., of high phenotypic quality) exhibit longer tenure, even females mating at random among breeding area residents will obtain mates of higher than average quality relative to males in other parts of the marsh. The relationship between greater relative claw length and longer breeding area tenure constitutes a positive feedback system that accords increased reproductive success (i.e., fitness) to these males, providing a possible mechanistic explanation for the maintenance of the sand fiddler crab mating system.

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Table 1. Pairwise multiple comparisons of tenure curves for male *Uca pugilator* in the food manipulation experiment. To keep the experiment-wise error rate $\alpha = 0.05$, comparisons were done with a sequential Bonferroni approach (Dunn-Sidák method; Sokal & Rohlf 1995) following Wilcoxon's signed ranks tests. Individual comparisons marked with an asterisk (*) were statistically significant.

food manipulation experiment	
treatment group	**significance**
high v medium	*
high v low	*
medium v low	*

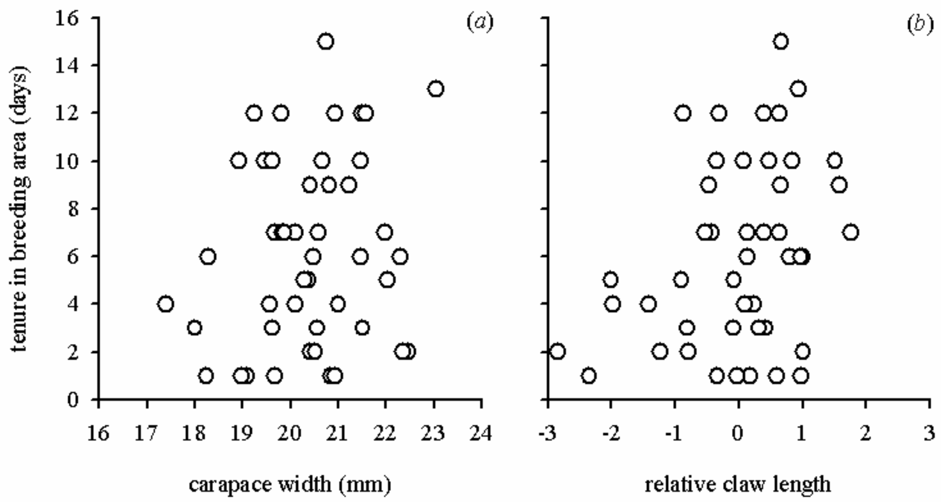

Figure 1. Relationship between the number of consecutive days spent in the breeding area by male *Uca pugilator* and individual resource holding power defined by: (*a*) carapace width ($r_s = 0.161$, $p = 0.285$, $n = 46$); (*b*) relative claw length ($r_s = 0.303$, $p = 0.041$, $n = 46$).

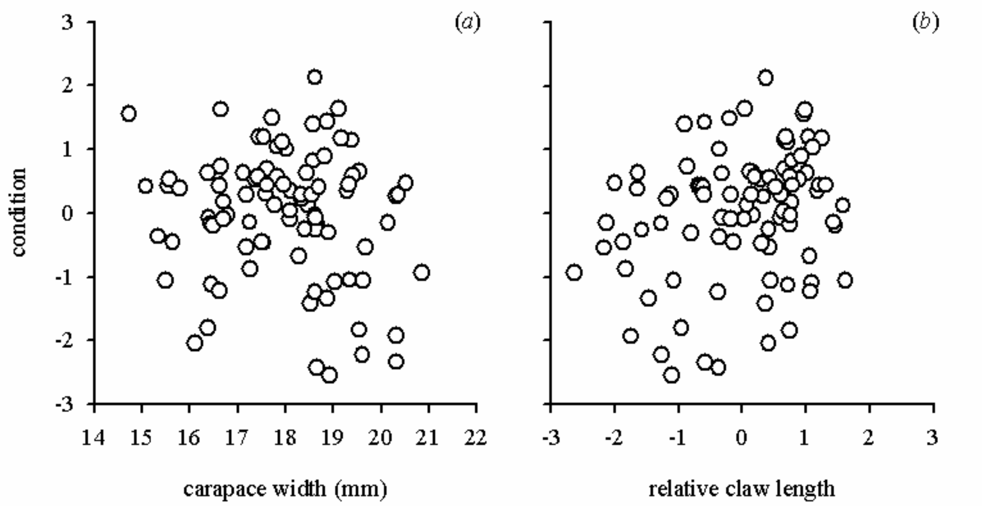

Figure 2. Relationship between condition (standardized residuals from a least squares regression of body mass (not including claw mass) on carapace width) of male *Uca pugilator* and: (*a*) carapace width (r = -0.004, p = 0.972, n = 90); (*b*) relative claw length (standardized residuals from a least squares regression of major claw length on carapace width) (r = 0.260, p = 0.013, n = 90).

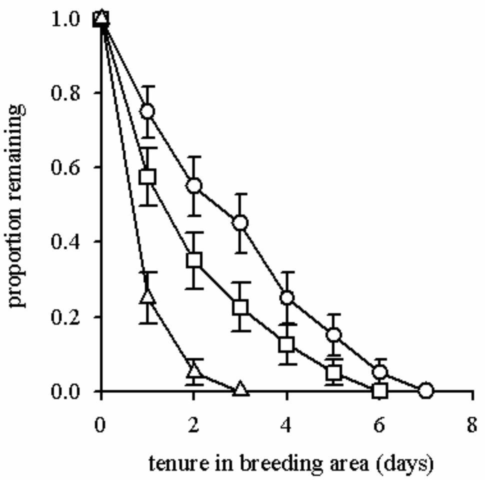

Figure 3. Proportion (± s.e.) of tagged male *Uca pugilator* in high (*circle*), medium (*square*) and low (*triangle*) food availability treatment groups remaining in the breeding area each day following transplantation into artificial burrows ($p < 0.001$, $n = 40$).

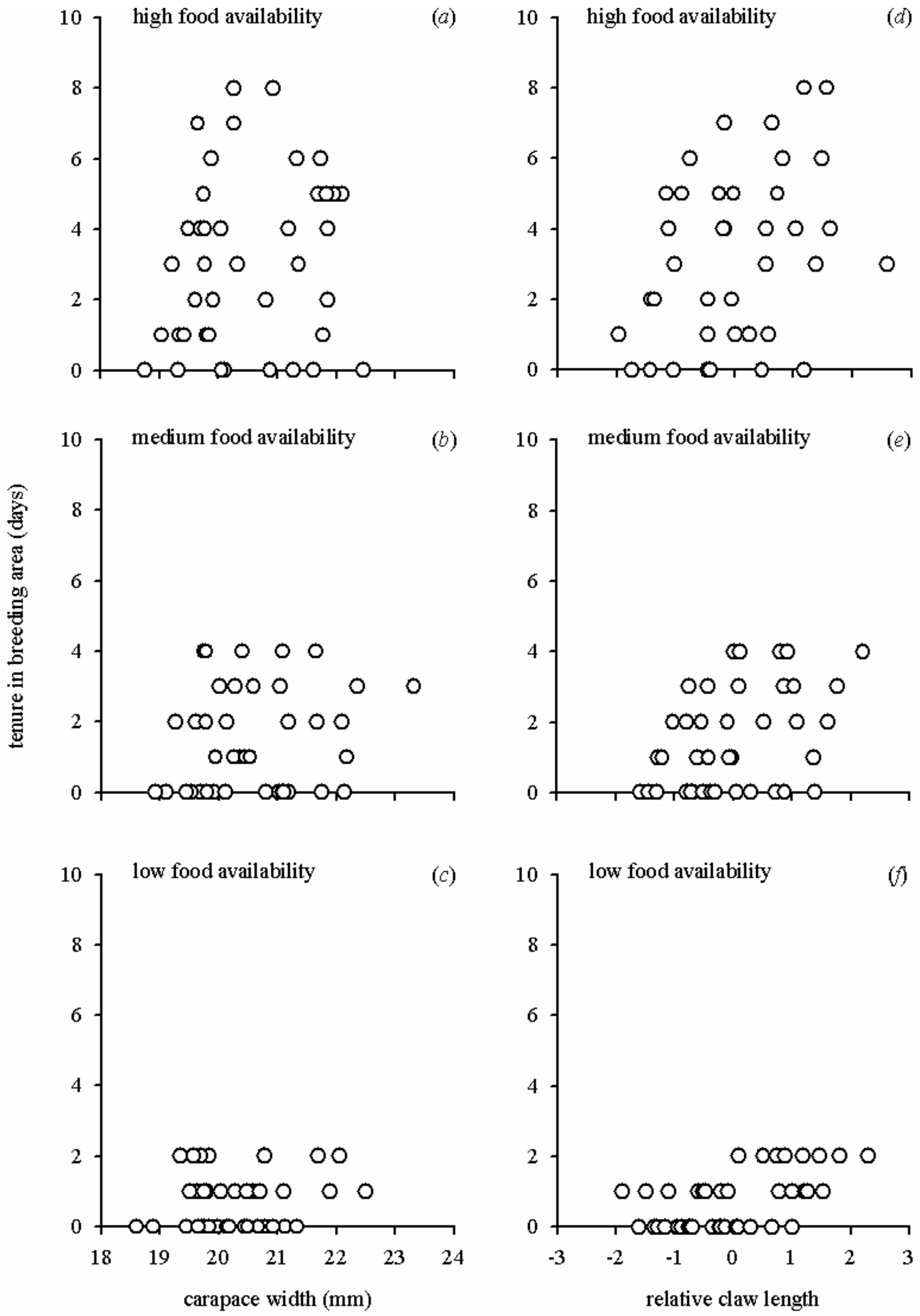

Figure 4. Relationship between consecutive days spent in the breeding area by male *Uca pugilator* and individual resource holding power: (*a*) carapace width, high food availability ($r_s = 0.192$, $p = 0.235$, $n = 40$); (*b*) carapace width, medium food availability ($r_s = 0.166$, $p = 0.306$, $n = 40$); (*c*) carapace width, low food availability ($r_s = 0.161$, $p = 0.322$, $n = 40$); (*d*) relative claw length, high food availability ($r_s = 0.367$, $p = 0.020$, $n = 40$); (*e*) relative claw length, medium food availability ($r_s = 0.406$, $p = 0.009$, $n = 40$); (*f*) relative claw length, low food availability ($r_s = 0.530$, $p < 0.001$, $n = 40$).

Chapter 4: Size-dependent thermal and hydric constraints on performance capacity of a fiddler crab

Introduction

The marine intertidal zone is generally considered to be a stressful environment, with steep environmental gradients and high variability in physical conditions over small spatial and temporal scales. At low tide, marine organisms experience physiological stress or even mortality from extreme temperatures and desiccation associated with aerial exposure (Lewis 1954; Helmuth 1998; Bertness *et al.* 1999; Somero 2002; Williams & Dethier 2005). Both body temperature (T_b) and water loss rate are strongly affected by ambient air temperature, wind speed and relative humidity at the time of low tide (Porter & Gates 1969; Tracy 1976; Helmuth 1998). The interactive effects of temperature and desiccation on the physiological and behavioral performance of ectotherms have been well documented in reptiles (Crowley 1985; Wilson & Havel 1989), amphibians (Gatten 1987; Preest & Pough 1989; O'Connor & Tracy 1992) and insects (Kingsolver 1979), however, relatively fewer studies have investigated the extent to which temperature and hydration combine to limit the performance capacity of marine intertidal organisms, especially mobile animals (but see Helmuth 1998; Weinstein 1998).

The sand fiddler crab, *Uca pugilator*, is an excellent organism for testing ideas about environmental constraints on physiology and behavior. *U. pugilator* are small, highly active semi-terrestrial crabs that live in sheltered areas of salt marshes along the Atlantic coast of the United States. 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 & McClintock 2000; Pratt & McLain 2002). Males 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 specialized breeding burrows or in species-specific waving displays to attract receptive females for mating (Crane 1975; Christy 1978; Pope 2000; Pratt *et al.* 2003). Environmental conditions are generally less stressful lower in the marsh (Reinsel & Rittschof 1995; Bortolus *et al.* 2002; Chapter 2), however, females strongly prefer to mate with males controlling burrows high on the shore because of the reduced risk of burrow collapse due to tidal flooding. After mating, females stay sheltered in the breeding burrow for about two weeks, brooding their eggs before emerging to release their planktonic larvae into the water (Christy 1982, 1983). In contrast, males quickly return to the marsh surface to resume courting and burrow defense during low tide (Christy 1978, 1982).

Males in the breeding area are generally larger and have larger claws for their body size than males in other parts of the marsh (Christy 1983; Pratt & McLain 2002; Pratt *et al.* 2003). This has often been interpreted as the result of differential combat success among males for control of burrows in desirable locations, variation in body condition and female preference. Large males win more contests, display with greater vigor and are attractive to females (Hyatt & Salmon 1978; Christy 1983; Jennions &

Backwell 1998; Pratt & McLain 2002; Pratt *et al.* 2003). Presumably, small males are either quickly evicted from the breeding area by larger individuals (Jennions & Backwell 1996; Pratt *et al.* 2003), run out of energy faster (Hurst & Conover 2003) or they abandon the area after having little success in attracting a mate (Jennions & Backwell 1998). Mating activity by *U. pugilator* occurs in mid-summer, and previous work has shown that both thermal and desiccation stress are higher in the breeding area compared to other salt marsh microhabitats (Chapter 2). Small individuals generally have lower thermal inertia and higher mass-specific water loss rates than do large individuals (Herreid 1969; Stevenson 1985). These observations suggest an alternative, but not mutually exclusive, hypothesis to explain the skewed size distribution of males in the breeding area: small males are more susceptible to thermal and hydric stress than large males.

I experimentally investigated whether body temperature and hydration differentially affected physiological and behavioral performance of sand fiddler crabs as a function of individual body size. I addressed three questions: First, what are the size-dependent consequences, in terms of locomotor performance, of simultaneous variation in temperature and hydration state? Second, does body size affect behavioral choices made by fiddler crabs in response to varying thermal and hydric conditions? Finally, is size-specific variation in fiddler crab physiological and behavioral responses to temperature and hydric conditions in the laboratory relevant to environmental conditions in the field?

Methods

I 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 (40º 58’ N, 73º 08’ W) from June to September in 2005-2006, during the breeding season of *U. pugilator*. Prior to experimentation, crabs were held in the laboratory at 20 ºC in large aquaria with re-circulating seawater and fed TetraMarine Marine fish flakes (Tetra, Blacksburg, VA) *ad libidum*. I grouped individuals into two size classes: ‘small’ (mean carapace width ± s.d. = 16.92 ± 1.09 mm; *n* = 131) and ‘large’ (20.63 ± 0.96 mm; *n* = 134), which represent typical endpoints of the body size continuum of reproductively active males in this marsh (see also Pratt *et al.* 2003). For each crab, I measured carapace width to the nearest 0.01 mm with digital calipers and, when appropriate, wet body mass to the nearest 0.001 g with a Sartorius LC 620 D balance.

(a) *Size-specific effects of desiccation on locomotor performance*

I exercised male fiddler crabs from each size class individually on a motorized treadmill (Pro-Form 285T modified with a Dayton 4Z861 10:1 speed reducer) at a velocity of 4 m min^{-1} (0.24 km h^{-1}). This velocity represents the mid-range of *U. pugilator* running speeds studied by Full & Herreid (1984) (0.06 – 0.40 km h^{-1}), and is just above a performance threshold for males. Individuals running at this speed or higher lose stamina much faster than crabs running at slower treadmill-paced velocities. The treadmill was kept in an environmental chamber set at 30 °C (relative humidity ≈ 40%). Prior to being run to fatigue, crabs were given a 20-min acclimation period on the treadmill either immediately following removal from seawater, or after a 2 h delay in which they were exposed to chamber air in a shallow open container. A preliminary experiment found that crabs typically lost 5-8 % of their body mass over this 2 h period, presumably representing water loss due to evaporation and respiration (Weinstein 1998; Yoder *et al.* 2005). Treatment groups therefore consisted of: (1) small males, no delay ($n = 23$); (2) large males, no delay ($n = 26$); (3) small males, 2 h delay ($n = 18$); and (4) large males, 2 h delay ($n = 18$). Following the protocol of Full & Herreid (1984), I 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 & Levinton 2007).

To minimize disturbance to experimental animals on the treadmill, I measured hydration state at the beginning of the endurance trials for a separate set of crabs in each treatment group that were otherwise treated identically to those described above (all $n = 20$). Percent water loss was assumed to be zero for crabs in the 'no delay' treatment groups. During the 20 min acclimation 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; author's unpublished data). Percent water loss for crabs in the '2 h delay' treatment groups was calculated as the difference in body mass before and after the exposure to air, expressed as a percentage of initial mass. After weighing each crab, I also measured its body temperature (T_b) with a digital thermometer and hypodermic thermocouple probe (accuracy of ± 0.1°C).

(b) *Size-specific effects of desiccation on preferred body temperature range*

To determine whether body size interacts with hydration state to influence the thermal preferences of fiddler crabs, I estimated the range of body temperatures preferred by animals in the absence of associated ecological costs and constraints – so-called set-point or target T_b's (T_{set}) (Huey & Slatkin 1976; Hertz *et al.* 1993; Huey *et al.* 1989; Huey 1991) for small and large crabs on both wet and dry sand. I 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 plexiglass raceway (1.20 m long x 0.10 m wide x 0.10 m high) mounted on a solid aluminum bar (1.80 m long x 0.10 m wide x 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). Water flow was adjusted such that substratum temperatures changed linearly along the length of the aluminum bar. Crabs could easily choose a T_b from 5 to 45 ºC by changing their physical location in the thermal gradient. Individual male *U. pugilator* ($n = 48$) were placed at random inside the plexiglass 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 some particular T_b. I defined T_{set} as the central 50 % of all T_b's selected in the gradient, a common metric in studies of thermal biology (Hertz *et al.* 1993; Christian & Weavers 1996; Blouin-Demers & Weatherhead 2001).

(c) *Size-specific variation in desiccation rate and body temperature in the field*

I tested how body size affected the thermal and hydric state of crabs exposed on the marsh surface under semi-natural conditions adjacent to the Flax Pond Marine Laboratory. On several hot sunny days in July 2006 between 1200 and 1400 hours, I held crabs in shallow open trays covered with a thin layer of sand collected from the high intertidal breeding area; individuals were unable to burrow or otherwise shelter themselves from the sun and wind. Air temperatures (T_a) measured with a shaded thermocouple ranged from 30.4 – 33.1 ºC, relative humidity measured with a handheld hygrometer ranged from 52 – 66 % and wind speeds measured 2 cm above the sediment surface with a rotating-vane anemometer ranged from 0 – 2 m sec^{-1}. I moved crabs from 20 ºC seawater (corresponding to ambient water temperature in the marsh) to the experimental trays for 20 min each, measuring body mass before and after the trial and body temperature after. Initial T_b's of all crabs were equal to water temperature. As described above, I calculated percent water loss as the difference in body mass before and after aerial exposure, expressed as a percentage of initial mass.

(d) *Statistical analyses*

I tested the relationship between fiddler crab body size and locomotor performance, percent water loss and body temperature with two-way analyses of variance (ANOVA) with body size (small and large) and start time (no delay and 2 h delay) as fixed factors. Data were transformed with either a ln(x + 1) (time to fatigue and body temperature) or arcsine (percent water loss) function to correct for unequal variances and non-normality (Sokal & Rohlf 1995). Size-specific differences in preferred T_b's under different hydric 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. Size-specific differences in percent water loss and body temperature under field conditions were tested with one-way ANOVAs on arcsine (percent water loss) or ln(x + 1) (body temperature) transformed data. Post-hoc multiple comparisons were done with Tukey's HSD test. All analyses were done with JMP 5.1.

Results

(a) *Size-specific effects of desiccation on locomotor performance*

There was a statistically significant interaction between crab body size and the presence or absence of a 2 h delay before individuals were run on the treadmill ($F_{1, 84}$ = 4.41, $p = 0.034$; Figure 1*a*). In other words, the effect of body size on locomotor performance was dependent upon whether a given individual had first been subjected to a period of aerial exposure. While small and large crabs ran for similar lengths of time when exercise began shortly after their removal from seawater, large crabs ran for significantly longer after a 2 h delay (Figure 1*a*). Presumably, this difference in performance capacity is related to the degree of desiccation experienced by crabs of different body size: small crabs lost water at a significantly higher rate than did large crabs (Figure 1*b*). Given that both small and large crabs had similar hydration states immediately upon removal from seawater (100 % hydrated), this resulted in a significant interaction term in the analysis ($F_{1, 79}$ = 6.11, $p = 0.016$). Contrary to my expectations, instead of negatively affecting fiddler crab endurance, desiccation appeared at first glance to actually enhance it (Figure 1*a*). Nevertheless, I believe that this apparent contradiction can be resolved by comparing the body temperatures of crabs among the different treatment groups. Immediately after removal from seawater, hydrated crabs of both body sizes exhibited similar T_b's that were several degrees below ambient air temperature (T_a) (Figure 1*c*); after 2 h of aerial exposure, however, T_b's of experimental crabs had increased towards T_a. Again, the interaction term was statistically significant ($F_{1, 79}$ = 5.63, $p = 0.020$). Locomotor performance of *U. pugilator* is positively related to T_b in this temperature range (Weinstein 1998; Appendix 1) and I suggest that the observed increase in endurance capacity of dehydrated crabs is due to concomitantly higher T_b's.

In a separate study, I characterized the change in endurance capacity of hydrated male *U. pugilator* as a function of T_b from 5 – 40 ºC (Appendix 1). When the performance of dehydrated crabs (this study) is compared to that of hydrated crabs at the same T_b, it is clear that not only does desiccation have strong negative effects on crab locomotion, but that those effects are size-dependent. While desiccation reduced the endurance capacity of large crabs by almost 20 %, the performance decrement exhibited by small crabs was much greater – more than 50 %. This result is driven by the fact that under similar environmental conditions, small crabs experienced greater water loss and putative hydric stress compared to large crabs, while simultaneously exhibiting higher T_b's (with associated increased expectations for performance capacity).

(b) *Size-specific effects of desiccation on preferred body temperature range*

On wet sand, the mean T_b selected by small crabs in the thermal gradient was 27.1 °C (the 25 % and 75 % 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 to 19.6 °C (T_{set} between 17.7 °C and 20.7 °C) for large crabs. The interaction between body size and sediment hydric state (wet or dry) was statistically significant ($F_{1, 79}$ = 6.84, $p = 0.011$); although all crabs chose lower T_b's under dry conditions, smaller crabs preferred to be at the coolest temperatures (Figure 2).

(c) *Size-specific variation in desiccation rate and body temperature in the field*

Under field conditions, small crabs exposed to sun and wind for 20 min exhibited significantly higher water loss rates ($F_{1, 18}$ = 10.58, $p = 0.004$) and body temperatures ($F_{1, 18}$ = 20.14, $p < 0.001$) compared to large crabs (Figure 3).

Discussion

Body temperature and hydration state strongly interact with fiddler crab body size to affect individual physiological and behavioral performance. Although locomotor performance of small crabs was comparable to that of large crabs when both groups were hydrated, they did far worse under conditions of increased water loss and associated higher T_b's after 2 h of aerial exposure. My results are consistent with 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 & 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 (Herreid 1969; Grant & McDonald 1979; Turra & Denadai 2001). As a consequence, under similar environmental conditions, large crabs stay hydrated longer, and therefore perform better, than small crabs. Larger males also had an advantage over smaller males when both were held, without access to shelter, under field conditions similar to those in the high intertidal breeding area. Whereas small males quickly reached

T_b's and desiccation levels detrimental to physiological performance and even survival (Vernberg & Tashian 1959; Weinstein 1998), larger males approached those limits more slowly. Hyatt (1977) observed that larger *U. pugilator* spent less time in their burrows than small crabs and suggested that this might be due to reduced tolerance to thermal and desiccation stress of small individuals.

Consistent with their tropical origin, sand fiddler crabs are very permeable and exhibit high net water loss rates (Crane 1975; Thurman 1998; Yoder *et al.* 2005). The associated high rates of evaporative cooling can be extremely effective at lowering fiddler crab body temperatures in hot dry environments, such as the exposed breeding area (Edney 1961; Wilkins & Fingerman 1965; Smith & Miller 1973; Powers & Cole 1976; Thurman 1998). The primary limitation of such a strategy, of course, is the availability of free water to replace that lost to evaporation. Non-reproductive crabs foraging on creek banks low in the marsh typically have 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 (Chapter 2), suggesting that the ability to remain fully hydrated extends the range of environmental conditions over which crabs can remain active 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, *Ocypode quadrata*, use hydrophilic tufts of setae located at the base of their walking legs to efficiently extract water from damp sand (Wolcott 1984; Thompson *et al.* 1989).

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 that would maximize locomotor performance (Weinstein 1998; Appendix 1), 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, preferred the lowest T_b's. 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 & Slatkin 1976; Huey & Stevenson 1979; Huey 1991). Although this may 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 is certainly reduced. Taking refuge in a moist burrow may be the most effective way for fiddler crabs in the breeding area to simultaneously regulate both body temperature and hydric state (Smith & Miller 1973). Nevertheless, such a strategy imposes significant opportunity costs to reproductively active crabs. 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.

I am certainly not suggesting that existing mechanistic explanations for the observed surfeit of large males in the sand fiddler crab breeding area are inadequate. The importance of competitive dominance, physiological condition and attractiveness to females are well documented (Crane 1975; Christy 1983; Jennions & Backwell 1996, 1998; Pratt & McLain 2002; Pratt *et al.* 2003). Rather, I wish to raise the possibility that in addition to the biological factors listed above, physical conditions might also play a 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.

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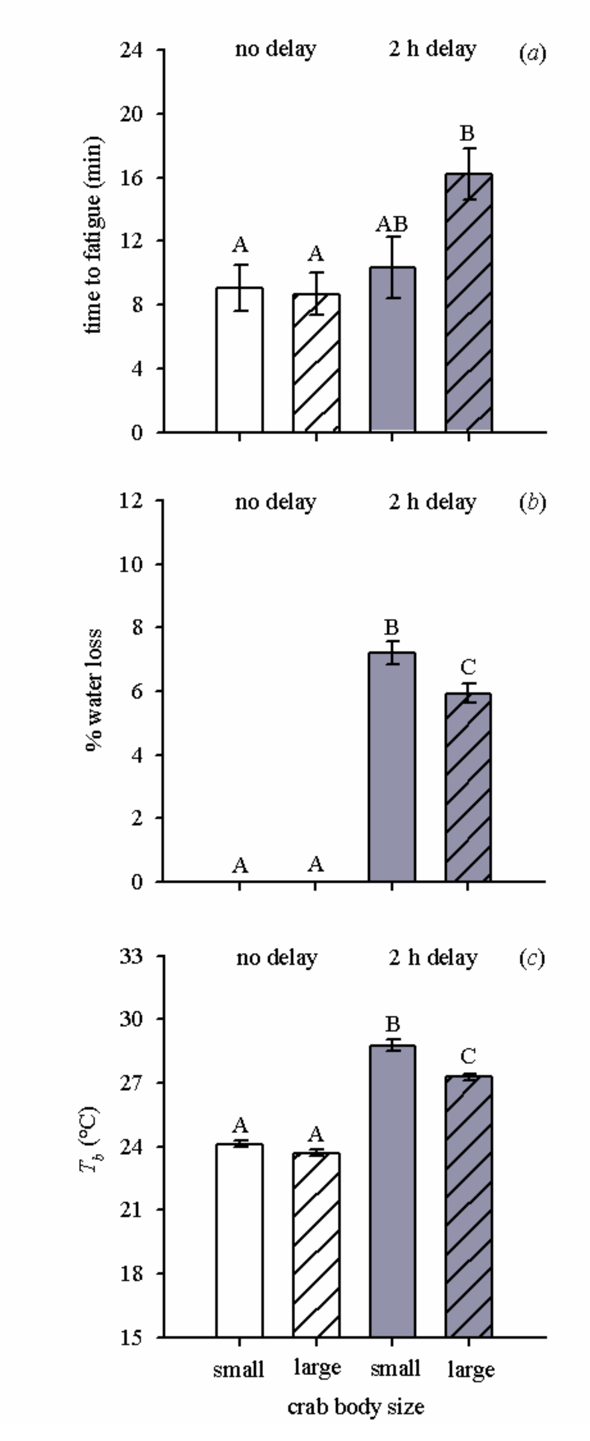

Figure 1. Mean ± s.e.: (*a*) endurance capacity; (*b*) percent water loss; and (*c*) body temperature of male *Uca pugilator* as a function of body size and aerial exposure. Data were collected either immediately following removal of the crabs from seawater, or after a 2 h delay [small crabs (*open bars*); large crabs (*hatched bars*); no delay (*white bars*); and 2 h delay (*gray bars*)]. Different letters indicate significant differences among treatments at the $\alpha = 0.05$ level with Tukey's HSD test.

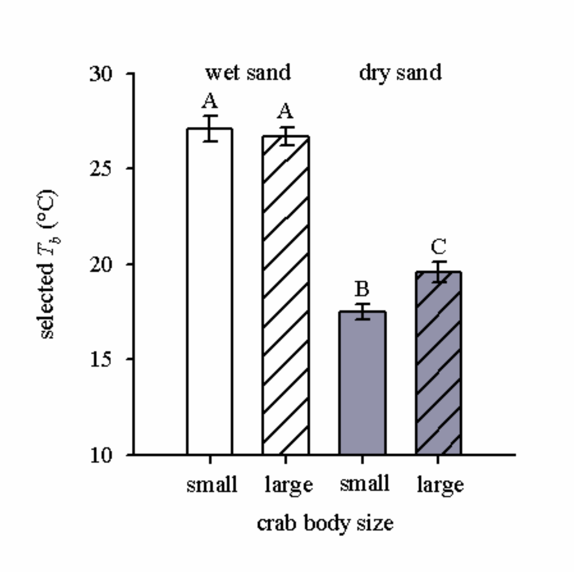

Figure 2. Mean ± s.e. body temperature (T_b) selected by male *Uca pugilator* in a laboratory thermal gradient as a function of body size and sediment hydric state (wet or dry) [small crabs (*open bars*); large crabs (*hatched bars*); wet sand (*white bars*); and dry sand (*gray bars*)]. Different letters indicate significant differences among treatments at the $\alpha = 0.05$ level with Tukey's HSD test.

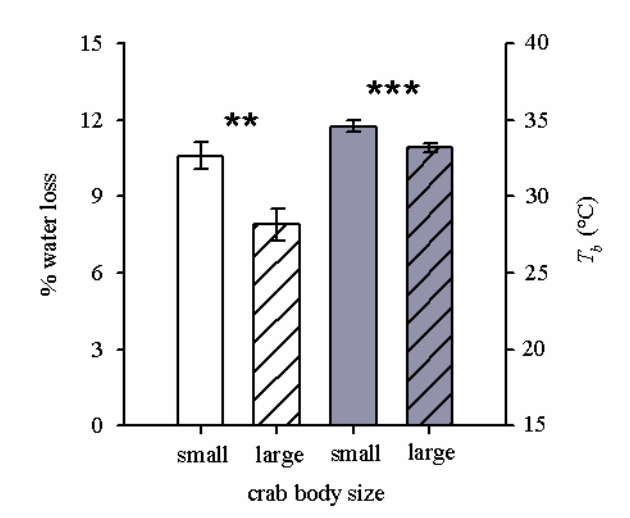

Figure 3. Mean ± s.e. percent water loss and body temperature (T_b) of male *Uca pugilator* under field conditions as a function of body size [small crabs (*open bars*); large crabs (*hatched bars*); % water loss (*white bars*); and T_b (*gray bars*)]. Asterisks indicate a significant difference between treatments at the $\alpha = 0.01$ (**) or 0.001 (***) level.

Chapter 5: Conclusion

In this dissertation, I used a model organism, the sand fiddler crab, *Uca pugilator*, to shed light on one of the central themes in evolutionary biology – costs and constraints associated with sexual selection. In particular, I focused on ecological costs to males arising from the strong preference by females for mating in breeding burrows located in open sand flats high on the shore. The spatial structure of temperature and desiccation stress and food availability across salt marsh microhabitats drives a trade-off between participation in reproductive activity and energy acquisition for male fiddler crabs. Male tenure in the breeding area is both physiologically costly and condition-dependent, suggesting that the very factors that make the breeding area so physiologically challenging may serve to filter out weaker competitors. As a consequence, female preference for mating in the high intertidal zone may allow them to obtain mates of higher than average quality relative to those in other parts of the marsh. My work therefore provides a possible mechanistic explanation for the maintenance of the sand fiddler crab mating system.

Of course, as with any research, there seem to be more questions that were generated than answered during the course of this study. Several of the outstanding problems are particularly obvious: First, what drives female choice in this system? It remains unclear whether female *U. pugilator* prefer larger males or those with relatively larger claws directly, or are instead choosing mates indirectly based on the location and quality of the breeding burrow they control. Given the strong positive correlation between the two variables, the end results are functionally equivalent – females mate with higher quality males. Nevertheless, elucidating the mechanistic basis of female mate choice is critical if we are to develop a complete understanding of the evolution and maintenance of sexually selected mating systems.

Second, what is the benefit to females of mating in high intertidal breeding burrows? Although Christy (1978, 1982, 1983) convincingly demonstrated the importance of sediment water content and associated burrow stability to female crabs, there may be additional factors contributing to the observed strong female preference for burrows in this location. For example, the underground thermal environment in different salt marsh microhabitats may be quite variable. The effects of temperature on ectotherm physiology and development are well documented (reviewed in Huey 1982; Cossins & Bowler 1987; Hochachka & Somero 2002) and it might be very interesting to compare the physiological consequences to females of brooding eggs in burrows exhibiting different thermal conditions (e.g., see Huey et al. 1989; Huey 1991).

Finally, what are the implications of the apparent discrepancy between male and female tenure in the breeding area? Males are sequentially polygynous and can accumulate multiple females in a single burrow (Christy 1978; Pratt & McLain 2002). Nevertheless, while males spend an average of five to six consecutive days guarding a burrow and courting females in the breeding area (Christy 1978; this study), mated females brood their eggs for an average of 12-14 days (Christy 1978; 1982). These observations suggest that at any point in time, at least some of the females in a given burrow will be carrying eggs fertilized by a male other than the current resident. There are currently no data on the patterns of paternity found within and among burrows, or even on the behavioral responses of male crabs to finding mated females in residence when they take control of an existing breeding burrow.

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Appendix 1: Fiddler crab locomotor performance as a function of body temperature

Introduction

The importance of temperature to ectotherm physiology and ecology has been extremely well documented over the past century (reviewed in Huey 1982; Cossins & Bowler 1987; Hochachka & Somero 2002). Body temperature can significantly influence an individual's locomotor ability, feeding success, development and growth rate and social interactions (Kingsolver 1979; Huey 1982; Weinstein 1998; Lagerspetz & Vainio 2006). Not surprisingly, temperature is a strong driver of fiddler crab activity at all latitudes; fiddler crabs in temperate marshes are conspicuously inactive during the winter months when they stay deep in burrows (Crane 1975; Montague 1980). As temperature increases in spring, so does the number of fiddler crabs active on the marsh surface at low tide. By mid-summer, reproductively active males are spending much of their time exposed in high intertidal sand flats, guarding specialized breeding burrows from other males and waving to attract receptive females (Christy 1982, 1983; Pratt & McLain 2002). Temperature and desiccation stress increase with increasing shore height across the salt marsh intertidal zone, suggesting that the timing and location of *U. pugilator* mating activity may be thermally challenging for male crabs (Chapter 2). Nevertheless, there are currently few data on the body temperatures (T_b's) of active fiddler crabs in the field and or on the relationship between body temperature and physiological performance other than respiration (but see Weinstein 1998; this dissertation).

I investigated how locomotor performance (endurance capacity and sprint speed) varies as a function of T_b for male fiddler crabs.

Methods

I collected surface-active male *U. pugilator* from Flax Pond, a *Spartina alterniflora* salt marsh located on the northern shore of Long Island, New York, USA (40º 58' N, 73º 08' W), in the summers of 2004. Prior to experimentation, crabs were held in the laboratory at 20 ºC in large aquaria with re-circulating seawater and fed TetraMarine fish flakes (Tetra, Blacksburg, VA) *ad libidum*. I used adult crabs similar in size to those displaying in the breeding areas of the marsh (mean carapace width ± s.d. = 19.88 ± 0.91 mm; n = 370; measured to the nearest 0.01 mm with digital calipers).

(a) *Locomotor performance: endurance capacity*

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 m min^{-1} (0.24 km h^{-1}) at one of eight possible body temperatures (5, 10, 15, 20, 25, 30, 35 and 40 °C; n = 20 crabs per T_b). This velocity represents the mid-range of treadmill speeds used by Full & Herreid (1984) (0.06 – 0.40 km h^{-1}). The treadmill was located in an environmental chamber set to produce the appropriate T_b for crabs in each trial. To minimize disturbance to experimental animals, I measured T_b's for a separate set of crabs in each treatment group that were otherwise handled identically to those described above (n = 5 for each T_b).

Body temperatures were measured with a digital thermometer and hypodermic thermocouple probe (accuracy of ± 0.1 °C). Prior to being run to fatigue, crabs were given a 20-min acclimation period on the treadmill. Following the protocol of Full & Herreid (1984), I defined fatigue as the time when a crab did not maintain pace with the treadmill, dragged its abdomen and did not respond to prodding.

(b) *Locomotor performance: maximum sprint speed*

I determined the relationship between sprint speed and T_b for male *U. pugilator* by running individuals in a straight raceway at 5, 10, 15, 20, 25, 30, 35 and 40 °C (n = 25 crabs per T_b). The wooden raceway measured 1.80 m long x 0.20 m wide x 0.24 m high, had a running surface of packed sand and was located in the environmental chamber described above. I released individual crabs at one end of the track and chased them to the other end. 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.

(c) *Upper critical body temperature*

The critical thermal maximum and minimum are the T_b's at which locomotor performance is impaired to the point that an organism is effectively unable to move (Lowe & Vance 1955; Lagerspetz & Vainio 2006). I raised the T_b's of (n = 10) male fiddler crabs from 20 to 48 °C at a rate of 1 °C per minute with a temperature-controlled water bath. This rate of heating is similar to what crabs experience in the field on warm sunny days (Smith & Miller 1973; author's 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 recorded 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 were removed. Body temperatures were measured with a digital thermometer and hypodermic thermocouple probe. I calculated the upper critical T_b for male fiddler crabs as the mean of the T_b's at which individuals were unable to right themselves (Lagerspetz & Vainio 2006).

Results

Male endurance capacity was maximized at T_b's of 30 °C, while sprint speed was maximized at 35 °C (Figure 1*a, b*). In both cases, locomotor performance initially improved with increasing T_b, was maximized at some presumably 'optimal' intermediate T_b and declined precipitously at T_b's above this range. The performance maxima coincided remarkably well with the temperatures selected by fiddler crabs in a laboratory thermal gradient (Figure 1*a*, *b*; see Chapter 2 for details on the thermal gradient experiment). The upper critical T_b for male fiddler crabs was 43.1 °C.

Discussion

The observed patterns of fiddler crab locomotor performance as a function of T_b are typical of many ectothermic organisms (e.g., references in Huey 1982; Lutterschmidt & Hutchison 1997; Weinstein 1998). Combined with the results of the thermal gradient experiment described in Chapter 2, these data suggest that in the absence of competing costs and constraints, fiddler crabs can and do select T_b's that optimize their locomotor performance (see also Weinstein 1998). Of course, selection by crabs of lower T_b's under dehydrating conditions (Chapters 2, 4) highlights that locomotor performance is not the only trait individuals might optimize. Presumably, the lower T_b's selected in this situation represent a compromise between locomotor performance and water conservation that optimizes their overall ecological performance (Huey & Stevenson 1979). Like many terrestrial ectotherms (Huey 1982; Cossins & Bowler 1987), fiddler crabs are clearly responsive to local environmental conditions and their physiological state.

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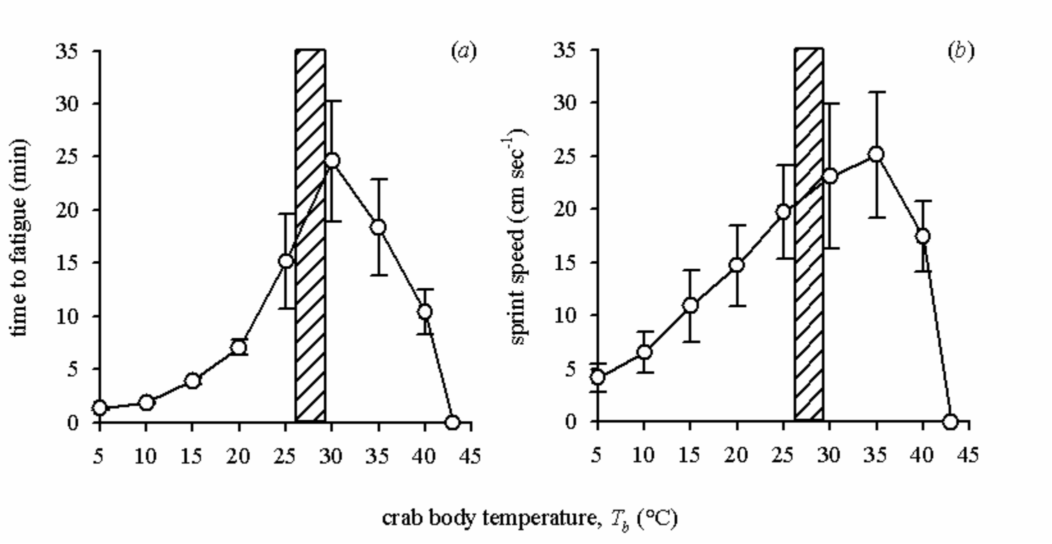

Figure 1. Locomotor performance of male *Uca pugilator* as a function of body temperature (T_b): (*a*) endurance capacity; and (*b*) sprint speed. The hatched bars represent the range of body temperatures selected by male fiddler crabs in a laboratory thermal gradient (T_{set}; see Chapter 2 for details).