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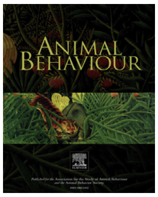

Balancing risk and reward: mating opportunity influences thermal refuge use in fiddler crabs

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Behavioural thermoregulation can ameliorate thermal stress but is costly. For species that court in a thermally stressful microhabitat, sexual selection via endurance rivalry favours individuals that are able and willing to endure harsh conditions in the courtship habitat, as retreats to a thermal refuge will reduce mating opportunities. The relative costs and benefits of refuge use versus continued courtship in the face of thermal risk, which vary across abiotic and biotic contexts, determine the optimal behavioural strategy. We examined the social and abiotic factors driving behavioural decisions related to thermoregulatory retreat in the fiddler crab *Austruca mjoebergi*. Male fiddler crabs perform a courtship display on the thermally stressful intertidal sediment surface. Time on the surface, and thus time available for display, was limited by high temperatures; as temperature increased, surface time decreased. Yet when presented with a stimulus female, males were more likely to perform the courtship display, displayed at a higher rate and increased time spent on the surface. These results demonstrate that behavioural decisions related to thermal retreat depend both on the abiotic conditions that influence the degree of thermal stress and on the social conditions that influence the reproductive prospects of the individual.

Behavioural thermoregulation by ectotherms to ameliorate thermal stress is a crucial factor in understanding responses to climate extremes (Chown et al., 2010; Kearney, Shine, & Porter, 2009). Behaviour can reduce the range of thermal extremes experienced by individuals, which can move to moist and shady microhabitats or retreat into burrows to avoid heat stress (Huey et al., 2012; Kearney et al., 2009; Porter, Mitchell, Beckman, & DeWitt, 1973). Yet behavioural responses to thermal stress can lead to a profound but underemphasized trade-off, as thermoregulatory behaviours are costly (Angilletta, 2009; Huey & Slatkin, 1976). Most obvious are energetic costs, as energy expended during thermoregulation cannot be used for growth or reproduction and can cause deficits in these components of fitness (Brewster, Sikes, & Gifford, 2013; Zhao, Ding, & Zhang, 2014). Both energetic costs and mortality risk associated with thermoregulatory behaviours are relatively easily quantified and have been the subject of much research (Brewster et al., 2013; Huey & Slatkin, 1976; Sears & Angilletta, 2015; Vickers, Manicom, & Schwarzkopf, 2011; Webb & Whiting, 2005; Zhao et al., 2014). Less studied are opportunity costs encumbered by behavioural responses to thermal stress. Fitness may be reduced as an individual shifts habitat use to ameliorate stress, because this shift limits time for other vital functions (e.g. reproduction) that must be performed in the stressful microhabitat (Gvoždík, 2002; Shine, Harlow, Elphick, Olsson, & Mason, 2000).

In many species, sexual selection via endurance rivalry favours extended tenure in the courtship habitat, which is frequently associated with an increase in the number of mating opportunities (Banks & Thompson, 1985; Darnell, Fowler, & Munguia, 2013; Salvador, Díaz, Veiga, Bloor, & Brown, 2008). When courtship occurs in a thermally stressful environment, tenure in the courtship area may be limited by thermal and/or desiccation stress (Campagna & Leboeuf, 1988; Darnell et al., 2013). Selection thus favours individuals that are able and willing to endure harsh conditions in pursuit of mating opportunities, as retreat to a thermal refuge will result in reduced mating opportunities. The relative costs and benefits of refuge use versus continued courtship in the face of adverse thermal conditions, and thus the optimal behavioural strategy, depend not only on the abiotic conditions that influence the degree of stress, but also on the reproductive prospects of the individual (e.g. the 'asset protection principle' often applied to antipredator behaviour; Clark, 1994). Given the strongly asymmetric nature of many thermal performance curves (Martin & Huey, 2008), the consequences of exceeding optimum body

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temperatures are high, so continued courtship under harsh thermal conditions represents a type of risk-taking behaviour. Fitness advantages may be gained if individuals alter risk-taking strategies (i.e. to continue courtship in the face of thermal risk or retreat to a thermal refuge) based on the relative costs and benefits of their behavioural options across social and environmental contexts.

Here, we examined the social and abiotic factors driving behavioural decisions related to thermal risk-taking versus retreat in the fiddler crab *Austruca* (= *Uca*) *mjoebergi*. Fiddler crabs are ideal model organisms for examining trade-offs, costs and constraints associated with thermal stress and mating opportunities. In many species, males defend territories in open, unvegetated areas of the high intertidal zone where they perform a waving display with their greatly enlarged claw to attract and court potential mates (Crane, 1975). Yet the high intertidal sediment surface is thermally stressful (Allen & Levinton, 2014; Darnell et al., 2013; Munguia, Backwell, & Darnell, 2017); operative environmental temperatures regularly exceed optimum and lethal temperatures (Allen & Levinton, 2014; Darnell, Nicholson, & Munguia, 2015) and males must periodically retreat to a burrow to avoid overheating and rehydrate (Darnell et al., 2013; Levinton, Lord, & Higeshide, 2015; Smith & Miller, 1973). The burrow is an effective thermal refuge (Munguia et al., 2017; Smith & Miller, 1973), yet a retreat to the burrow represents an opportunity cost as it imposes a cessation of courtship display behaviour. There thus exists a clear trade-off between refuge use and mating opportunity for male fiddler crabs. Females are not subject to the same constraints or trade-offs when mate searching since each female only spends a few minutes searching for a mate each month (Christy, 1983; Reaney & Backwell, 2007) and females are able to rapidly sample multiple males before choosing a mate (Reading & Backwell, 2007; Reaney & Backwell, 2007).

We conducted a field experiment to address three hypotheses concerning behavioural decisions made by male fiddler crabs when faced with a trade-off between thermal stress and the opportunity to attract females: (1) although the courtship display occurs regardless of female presence, display behaviour increases in frequency and intensity in the presence of a female; (2) thermal stress limits the duration of surface activity in courting male fiddler crabs, yet males take greater thermal risks by remaining on the surface longer when the probability of attracting a mate is high; and (3) these behavioural decisions also take into account female quality such that males are willing to take greater thermal risks when larger, and thus potentially more fecund, females are nearby.

METHODS

Study Species and Site

The fiddler crab *Austruca mjoebergi* lives on intertidal mudflats of the tropical Indo-Pacific, where males defend territories (~10 cm diameter) centred on a burrow (Reaney & Backwell, 2007). During the mating period (6–8 days of neap tides each semilunar cycle), sexually receptive females wander through the population searching for a mate. Males perform a waving display (using the greatly enlarged major claw) on the surface near their burrows to attract searching females. Mating occurs in the male's burrow, and the male guards the female until oviposition (1–2 days after mating). While the male leaves the burrow after oviposition, the female remains in the burrow for the ~20-day incubation period until emerging to release larvae (Reaney & Backwell, 2007).

This study was conducted in December 2019 at East Point Reserve, Darwin, Northern Territory, Australia (12°24.53′S, 130°49.85′E). The study site covered an area of approximately 200 × 50 m and consisted of a matrix of open, unshaded mudflat interspersed with areas shaded by mangroves. All experiments took place on the open, unshaded mudflat between 0830 and 1330 hours during the neap tide mating period, when the mudflat is exposed throughout the tidal cycle and mating activity peaks.

To quantify the thermal environment, multiple sensors were deployed in a single representative location on the open, unshaded mudflat and logged data every minute throughout the 5-day experimental period using a HOBO USB Micro Station Data Logger (H21-USB, Onset Computer Corp., Bourne, MA, U.S.A.). Air temperature and relative humidity were measured at a height of 193 cm (S-THB-M002, Onset Computer Corp.), and wind speed and solar irradiance were measured at 200 cm (wind speed: S-WSB-M003, irradiance: S-LIB-M003, Onset Computer Corp.). Air temperature was additionally measured 6 cm above the sediment surface (S-TMB-M002, Onset Computer Corp.), and sediment temperature was measured ~2 mm below the surface (S-TMB-M006, Onset Computer Corp.). Air temperature sensors were shaded to ensure accurate air temperature measurements.

Experimental Design

To initiate the experiment, an adult male crab (hereafter the ‘focal male’) that was actively waving was identified, driven into their burrow (by approaching the burrow), and haphazardly assigned to one of two treatments: female present or female absent. The burrow was then temporarily capped to prevent the male from emerging. To prevent interference by other males, all burrows within 50 cm of the focal burrow were temporarily sealed. For males assigned to the female-present treatment, a clear plastic cup (base diameter = 29 mm, height = 41 mm) containing a female *A. mjoebergi* (mean ± SE carapace width = 9.72 ± 0.21 mm) and 3–5 mm of water was placed 10 cm from the burrow entrance (distance from centre of the burrow to centre of the cup). For males assigned to the female-absent treatment, a clear plastic cup containing only 3–5 mm of water was placed 10 cm from the burrow entrance. The focal burrow was then uncapped and observed from >2 m away. When the focal male emerged from the burrow, the time spent on the surface before the next retreat to the burrow (hereafter referred to as ‘surface duration’) and the number of waving displays performed during that period (Fig. 1) were recorded. Over the 5-day experimental period, a total of 31 observations were made for the female-present treatment and 30 observations were made for the female-absent treatment. Two observations were excluded from analyses – one male that was scared into the burrow by a predator, and a second where the female died during

Figure 1. Male *Austruca mjoebergi* displaying to a stimulus female.

observation – leaving a sample size of 29 in the female-present treatment and 30 in the female-absent treatment.

Data Analyses

To assess whether males increased courtship behaviour in the presence of a female, we used Fisher's exact test to compare the proportion of crabs that waved at least once during their time on the surface between the two treatments. We then calculated waving rate (waves/s) for each focal male that did wave and used a Mann–Whitney *U* test to compare waving rate between the two treatments.

All temperature measurements were strongly correlated with each other ($r > 0.901$), and all were also strongly correlated with solar irradiance ($r > 0.829$). Sediment surface temperature was chosen as a representative temperature metric for use in analyses as sediment surface temperatures represent the temperature measurement closest to the location of crab activity. To examine the effect of temperature and female presence on the duration of surface activity, surface duration was first log-transformed to meet assumptions of normality. A linear model was fit using log-transformed surface duration as the response variable and including treatment (female present or female absent), sediment surface temperature and a treatment × temperature interaction as predictor variables. Sediment temperatures used in the analysis represent the average sediment temperature over the time when the focal male was on the surface. For crabs with surface durations <1 min where there was not a temperature measurement during the observation period, the nearest sediment temperature measurement to the end time of the observation (i.e. when the crab retreated to the burrow) was used.

To test for an effect of female size on the duration of surface activity, we fitted a linear model using log-transformed surface duration as the response variable and included female carapace width, sediment surface temperature and a female carapace width × temperature interaction as predictor variables. Only data from the female-present treatment were included.

Ethical Note

ASAB/ABS Guidelines for the use of animals in research were followed. The methods used in this study are based on previous experiments and designed to minimize mortality and stress. All female crabs were collected by hand and (with the exception of the female that died during experimentation) released alive at the collection site following experimentation. Prior to use, females were held in the shade in individual plastic containers containing ~1 cm of water to minimize thermal and desiccation stress. This research was conducted under a research permit from the Darwin City Council (permit 4144940).

RESULTS

Throughout the full 5-day period of measurement, air temperatures recorded at 193 cm above the mudflat surface ranged from 25.57 to 35.21 °C and air temperatures recorded at 6 cm above the mudflat surface ranged from 25.67 to 39.63 °C. Sediment surface temperatures ranged from 27.58 to 57.02 °C. Full microclimate data are shown in Fig. 2.

Although males in both treatments performed the waving display, males increased display behaviour in the presence of a female. The proportion of males waving in the female-present treatment was significantly greater than the proportion of males waving in the female-absent treatment (female present: 0.97, female absent: 0.63; Fisher's exact test: $N_{\text{F-present}} = 29$, $N_{\text{F-absent}} = 30$, $P = 0.002$). Furthermore, excluding males that did not wave, the

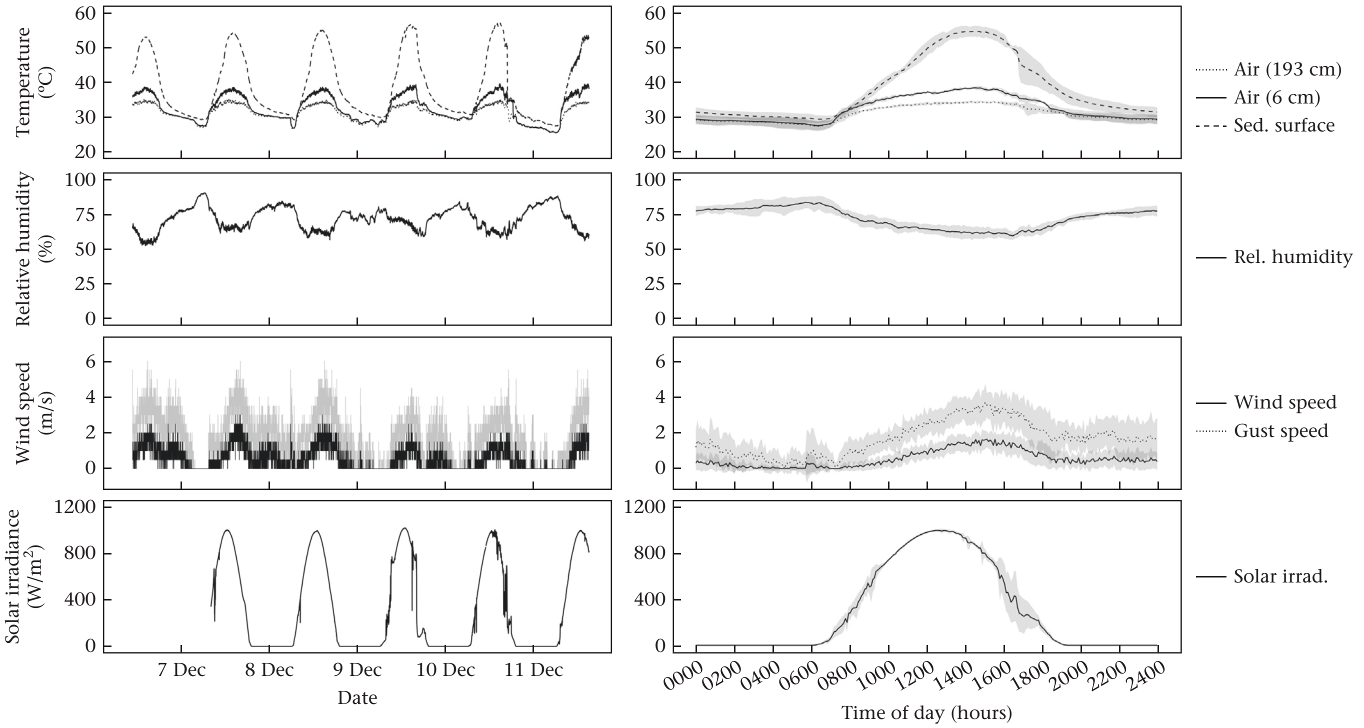

Figure 2. Temperature, humidity, wind and solar irradiance data from the microclimate monitoring station deployed at the study site. Panels on the left contain raw data measured every 1 min over the full 5-day experimental period, while panels on the right represent means (±1 SD, indicated by shading) after averaging into 5 min bins across all days. Note that the pyranometer for measuring solar irradiance was not deployed until late morning on 7 December 2019.

Table 1
Results of linear model testing effects of treatment (female present or female absent) and sediment temperature on male surface duration

Source	SS	*df*	*F*	*P*
Treatment	5.186	1	35.151	<0.0001
Sediment temperature	1.358	1	9.204	0.004
Treatment × temperature	0.0001	1	0.001	0.981
Residuals	8.114	55		

Table 2
Results of linear model testing effects of female carapace width and sediment temperature on male surface duration, using only data from the female-present treatment

Source	SS	*df*	*F*	*P*
Female carapace width	0.063	1	0.455	0.506
Sediment temperature	0.707	1	5.141	0.032
Female carapace width × temperature	0.084	1	0.614	0.441
Residuals	3.438	25		

waving rate was significantly higher when a female was present than when a female was absent (mean ± SE: female present: 0.147 ± 0.014 waves/s, female absent: 0.078 ± 0.016 waves/s; Mann–Whitney *U* test: $W = 134$, $N_{\text{F-present}} = 28$, $N_{\text{F-absent}} = 19$, $P = 0.004$).

The duration of time spent on the surface was limited by high temperature, with a significant negative relationship between sediment surface temperature and surface duration (Table 1, Fig. 3). Surface duration was significantly greater when there was a female present than when females were absent (Table 1, Fig. 3). On average, males in the female-present treatment spent 288 ± 54.1 s (median = 225 s) on the surface between retreats to the burrow, while males in the female-absent treatment spent 69.9 ± 10.3 s (median = 57 s) on the surface between retreats to the burrow. There was no significant treatment × temperature interaction.

Surface duration of males in the female-present treatment was not related to the size of the stimulus female (Table 2). As in the analysis described above, surface duration was negatively related to sediment temperature (Table 2), but there was no significant female size × temperature interaction.

DISCUSSION

For species that court in a thermally stressful microhabitat, sexual selection via endurance rivalry favours individuals that are able to endure harsh conditions and outlast competitors in the courtship habitat (Campagna & Leboeuf, 1988; Darnell et al., 2013). Endurance rivalry can be a useful framework for examining the linkages between sexual and natural selection, both synergistic and conflicting, that drive animal behaviour. In many species of tropical and subtropical fiddler crabs, there exists a clear and direct trade-off between thermal refuge use and mating opportunity. Males perform a waving display to attract potential mates on the sediment surface, where they experience thermal and desiccation stress (Chou et al., 2019; Darnell et al., 2015; Darnell, Backwell, Stockbridge, Dyson, & Munguia, 2019; Munguia et al., 2017). A retreat to the burrow is effective for lowering body temperature, but requires a cessation of courtship. Examining the abiotic and social cues driving behavioural decisions associated with burrow retreat can provide insight into how ectotherms manage conflicting behavioural demands imposed by sexual and natural selection.

Tropical animals with diurnal activity can be subject to extreme heat stress. For ectotherms, behavioural thermoregulation can buffer against thermal extremes but can also be costly, as thermoregulatory behaviours can increase energy expenditure and mortality risk and impose opportunity costs (Angilletta, 2009; Huey & Slatkin, 1976). Male fiddler crabs displaying in the high intertidal zone experience thermally stressful conditions throughout the breeding season (Allen & Levinton, 2014; Chou et al., 2019; Darnell et al., 2015; Munguia et al., 2017). We observed sediment temperatures exceeding 57 °C and air

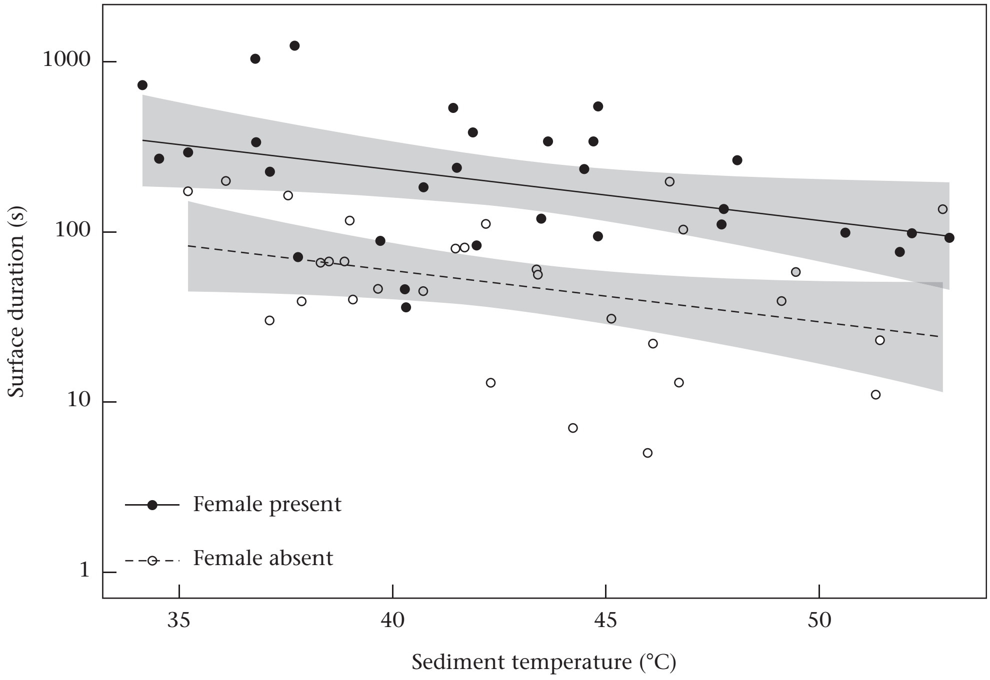

Figure 3. Relation between sediment temperature and surface duration of male fiddler crabs in the presence and absence of a female. Lines represent predicted relationships from the linear model, shaded areas represent 95% confidence intervals. Note the logarithmic scale of the *Y* axis.

temperatures (measured 6 cm above the sediment surface) exceeding 39 °C (Fig. 2). Although not quantified here, Munguia et al. (2017) documented *A. mjoebergi* body temperatures exceeding 38 °C on the unshaded mudflat surface, approaching the critical thermal maximum (CT_{max}) for the species (40.2 ± 0.42 °C, Munguia et al., 2017). These high temperatures necessitate thermoregulatory retreats to the burrow and limit the time available for courtship (Fig. 3). We observed that surface duration decreased by over 60% (female-present treatment: from 324.9 s to 116.2 s; female-absent treatment: from 83.6 s to 29.4 s) as sediment temperatures increased from 35 °C to 50 °C. This decrease in surface time represents a direct opportunity cost of thermoregulatory behaviour, as time spent in the burrow represents time that is not spent performing the courtship display, and thus potential lost mating opportunities.

As the cost of thermoregulation increases, the optimal level of thermoregulation is expected to decrease (Huey & Slatkin, 1976). For example, Withers and Campbell (1985) observed that lizards shifted from near-perfect thermoregulation to near-perfect thermoconformation as the energetic cost of thermoregulation increased. While the energetic cost of a retreat to a burrow is likely low for fiddler crabs, the opportunity cost is high. We observed that male fiddler crabs remained on the surface longer (despite stressful thermal conditions) if a female was present (Fig. 3). This observation is consistent with the expected costs and benefits associated with the thermoregulation–courtship trade-off. When there are no females nearby and the probability of mating is low, the opportunity cost of thermoregulation (i.e. burrow retreat) is relatively low. In contrast, when there is a female nearby and the probability of mating is high, the opportunity cost of thermoregulation is much higher, driving the male to accept potentially stressful body temperatures in pursuit of mating opportunities.

The behavioural decision to continue courtship despite harsh environmental conditions or to retreat to the burrow can also be viewed in the context of risk management. Thermal performance curves are generally asymmetric (Huey & Stevenson, 1979; Martin & Huey, 2008), including those of fiddler crabs (Darnell et al., 2015), with a sharp decrease in performance once the optimal temperature (T_{opt}) is exceeded. Increased time on the surface thus represents increased thermal risk as it increases the likelihood that T_{opt} or even CT_{max} will be exceeded. Our observation that male fiddler crabs were willing to take a greater thermal risk by remaining on the surface longer if a female was present (Fig. 3) is analogous to the observation that many organisms, when confronted by a predator, are willing to take greater risks if the probability of mating is high. Such results have been previously observed in fiddler crabs (e.g. Gruber, Kahn, & Backwell, 2019; Reaney, 2007) as well as other taxa including hermit crabs (Hazlett & Rittschof, 2000), lizards (Cooper, 1999; Martín, López, & Cooper, 2003) and birds (e.g. Habig, Chiyo, & Lahti, 2017; Kålås, Fiske, & Saether, 1995). Extending this analogy leads to the hypothesis that other aspects of the social environment, such as the density of displaying males (e.g. competitors) may also influence behavioural decisions related to burrow retreat by modulating the strength of the thermoregulation–courtship trade-off, although this hypothesis was not tested here. Male lesser waxmoths *Achroia grisella*, for example, are willing to take greater risk by continuing courtship signalling behaviour when within a simulated lek compared to when in isolation (Brunel-Pons, Alem, & Greenfield, 2011; Edomwande & Barbosa, 2020) and also vary risk-taking behaviour based on the attractiveness of competitor males (Edomwande & Barbosa, 2020).

Activity patterns of intertidal and terrestrial ectotherms can be limited by desiccation stress in addition to thermal stress (Iacarella & Helmuth, 2012; Kearney, Munns, Moore, Malishev, & Bull, 2018) and it can be difficult to disentangle effects of thermal and desiccation stress in field experiments. In addition to serving as a thermal refuge, the fiddler crab burrow also serves as a site of rehydration. Fiddler crabs cannot absorb water vapour from the air (Yoder, Reinsel, Welch, Clifford, & Rellinger, 2005), instead relying on water extraction from moist sand via capillary action or feeding in moist sediment (Hadley, 1994; Wolcott, 1984). During the neap tide mating period, the high-intertidal sediment surface remains exposed throughout the tidal cycle and becomes progressively drier through the 6–8-day mating period (M. Z. Darnell, personal observation). The burrow thus serves as the primary site of rehydration. Darnell et al. (2019) examined desiccation rates of *A. mjoebergi* during the nonmating period (i.e. spring tide, when the habitat is exposed at low tide and submerged at high tide) and observed a desiccation rate of 0.125 ± 0.015% body mass/min while on the unshaded sediment surface. Desiccation likely occurs more rapidly during the mating period, although this has not yet been quantified. In the subtropical/temperate fiddler crab species *Leptuca pugilator* and *Minuca pugnax*, males displaying on the sediment surface did not show evidence of desiccation stress (Levinton et al., 2015), although *A. mjoebergi* experiences harsher abiotic conditions than either *L. pugilator* or *M. pugnax*. It is thus possible that the male crabs observed here were responding to desiccation stress in addition to thermal stress. Further work is needed to clarify the relative roles of thermal and desiccation stress in driving behavioural decisions related to burrow retreat.

Surface duration was not related to female size, despite the fact that larger females are more fecund (Greenspan, 1980; Murai, Goshima, & Henmi, 1987; Reading & Backwell, 2007) and male *A. mjoebergi* preferentially court larger females (Greenspan, 1980; Murai et al., 1987; Reading & Backwell, 2007). Similar to our results, Reading and Backwell (2007) previously observed that the duration of a male's courtship bout (time from first wave to last wave) was not related to female size. Male mate choice (i.e. choosiness) is expected when female quality varies, male mating investment is high, the cost of mate searching is low and mate encounter rate (i.e. the likelihood of attracting an alternative female) is high (Kokko & Johnstone, 2002). In many fiddler crabs, including *A. mjoebergi*, males do not search out females but instead perform the courtship waving display to attract searching females, and this display is quite costly, both energetically (Matsumasa & Murai, 2005) and in terms of thermal risk. Additionally, the operational sex ratio is often highly male biased, resulting in very limited mating opportunities for males (i.e. low mate encounter rate). In the same population of *A. mjoebergi* studied here, Reading and Backwell (2007) observed ~45 displaying males for each mate-searching female. Male mate choosiness is thus tempered in *A. mjoeberi*, reflected by the lack of a relationship between surface duration and female size.

Animals are constantly confronted with behavioural trade-offs, as many behaviours are incompatible and time spent performing one behaviour represents time that cannot be spent on another. Animals are expected to choose between incompatible behaviours based on the costs and benefits of each behaviour in order to optimize fitness outcomes. In male fiddler crabs, thermoregulatory behaviour is in direct conflict with courtship/display behaviour. We demonstrate here that, in *A. mjoebergi*, behavioural decisions related to thermoregulatory burrow retreat are influenced by abiotic (i.e. thermal and/or desiccation stress) and social (i.e. availability of potential mates) context; when the immediate likelihood of attracting a mate was high, the benefit of continued courtship outweighed the cost of above-optimal body temperatures. These results demonstrate that behavioural decisions related to thermal retreat depend both on the abiotic conditions that influence the degree of thermal stress and on the social conditions that influence the reproductive prospects of the individual, and highlight the complex interactions between sexual and natural selection that drive behavioural decisions by ectotherms in harsh environments.

Data Accessibility

Data and analysis code are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.wm37pvmjb).

Declaration of Competing Interest

None.

Acknowledgments

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