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Rising surface temperatures lead to more frequent and longer burrow retreats in males of the fiddler crab, *Minuca pugnax*

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ABSTRACT

The fiddler crab *Minuca pugnax* occupies thermally unstable mudflat habitats along the eastern United States coastline, where it uses behavioral thermoregulation, including burrow retreats, to manage body temperature (T_b). We explored the relationship between frequency of burrow use and environmental conditions, including burrow and surface temperatures, relative tidal height, and time of day, by twenty male *M. pugnax* in breeding areas around Flax Pond, New York, USA. We found a highly significant positive correlation between burrow use and surface temperature, with a clear shift to longer times underground above 32 °C degrees. We also experimentally heated live crabs in the laboratory and allowed them to retreat into cooled artificial burrows while continuously measuring T_b. Laboratory data on cooling times were compared to field observations of burrow retreat durations. The median burrow duration in the field of 2.74 min was enough time for our laboratory crabs to capture over 70% of the cooling potential of artificial burrows 10 or 15 °C below T_b. Because crab bodies in burrows experience exponential declines in T_b due to Newton's law of cooling, there are diminishing returns to remaining in a burrow, and many crabs probably leave before coming to equilibrium. For *M. pugnax*, burrow retreats reduce time spent feeding and courting, activities that only occur on the surface. Current concerns about the impacts of climate change on animals include whether compensatory mechanisms, like more frequent and longer burrow retreats, will come at the cost of other behaviors necessary for survival and reproduction.

1. Introduction

Most organisms function optimally within a restricted range of body temperatures partly due to the presence of thermally adapted proteins (Fields and Somero 1997; Hochachka and Somero 2002). However, for ectotherms, which lack the internal mechanisms to regulate their body temperatures, maintaining this optimal range often requires costly physiological and behavioral responses to changing external conditions. Stenothermal taxa minimize these costs by living in stable thermal environments, such as the interiors of caves (e.g., Adis et al., 1997; Bernabò et al., 2011; Šustr et al., 2005) or polar or tropical habitats (Ghalambor et al., 2006; Janzen 1967; Logan and Buckley 2015). However, this has led to the loss of traits, such as the heat shock response (Tomanek 2010), making these taxa exceptionally vulnerable to the rising temperatures of the Anthropocene. In contrast, eurythermal taxa inhabit less thermally stable environments, including a wide range of aquatic and terrestrial habitats in temperate regions. For them, physiological and behavioral compensatory mechanisms are frequently deployed to avoid cellular damage and death (Dominguez-Guerrero et al., 2019, Logan and Buckley, 2015). Concerns about the impacts of climate change include whether these compensatory mechanisms will suffice to counter rapid changes in temperature (Kearney et al., 2009; Somero 2010) and if thermoregulatory behaviors, in particular, will come at the cost of other behaviors necessary for survival and reproduction (Adolph and Porter 1993; Huey et al., 2010), or even, paradoxically, slow the evolution of greater thermal tolerance (the Bogert effect; Bogert 1949; Huey et al., 2003).

As highly mobile intertidal ectotherms that occupy thermally complex environments, fiddler crabs (Phylum Arthropoda, Order Decapoda, Family Ocypodidae) are an ideal group for investigating thermoregulatory behaviors and their potential costs. While most of the 106 named fiddler crab species are tropical (Rosenberg 2001), some are found at higher latitudes, including *Minuca pugnax*, a species that occupies marsh mudflats from northern Florida to New Hampshire, USA (Barnwell and Thurman 1984; Johnson 2014). In its subtropical and temperate habitats, *M. pugnax* occupies a heterogenous thermal landscape in space and time, experiencing significant shifts in temperature as it moves from surface to burrow or is alternately exposed and submerged during semi-diurnal tidal exchanges. In the northern part of its range, *M. pugnax* also experiences large temperature extremes over the course of the year, remaining underground in a state of quiescence during the coldest half and then experiencing surface temperatures that can surpass its CT_{max} of

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40 °C (Teal 1958) during the warmer months when it is active. These dangerously hot conditions are met with thermoregulatory responses, the most effective of which is the burrow retreat (Smith and Miller 1973).

M. pugnax crabs feed and court each other on exposed sediment during low tides in areas where burrow density can exceed 100/m^2 (pers obs). During the reproductive season, males display themselves near burrows that they maintain and guard, waving and sometimes drumming with the one giant claw that has evolved to be both an ornament to attract females (Pope 2000) and a weapon to repel rival males (Pratt and McLain 2006). All fiddler crabs periodically retreat to burrows, where they mate and incubate embryos (Christy 1982a), hide (Jennions et al., 2003), rehydrate (Levinton et al., 2015), and warm or cool, depending on temperature differences between burrow and surface (Hews et al., 2021; Watson et al., 2018). Burrow retreats are not the only response to a dangerously hot surface–fiddler crabs also thermoregulate by moving to shade (Munguia et al., 2017; Smith and Miller 1973), wetting themselves at the water's edge (Christy, 1982a; Crane 1975), using the large claw as a thermal sink (for males; Darnell and Munguia 2011; Windsor et al., 2005), changing their orientation relative to the sun (Smith and Miller 1973), or altering the distribution of pigments in their carapaces (Barnwell 1968; Wilkens and Fingerman 1965). Compared to these other strategies, a burrow retreat is generally the most effective, as burrows can be more than 20 °C cooler than the surface (Hews et al., 2021; this publication). However, this effectiveness comes at a cost because burrow retreats disallow feeding and courtship, activities that only occur on the surface. These costs become apparent in the decision-making of males that have been found to risk overheating to court females and stay on the surface longer when burrows are in the shade (Allen and Levinton 2014; Darnell et al., 2019). As temperatures rise with climate change, burrow retreats may become more frequent and longer. Hence, rising temperatures will impact crab bodies not only directly but also indirectly by triggering costly burrow retreats that result in feeding and reproductive losses due to time spent underground.

In this study, we used video recordings to document the frequency and duration of burrow retreat behaviors for male *M. pugnax* in breeding areas in Flax Pond, New York, USA. These males were on elevated, exposed areas in the marsh and were actively courting females during the week of the first neap tide in June when courtship was particularly intense. Burrow retreat behaviors for females were not included because there were too few of them occupying burrows in these open areas where individual crabs could be viewed continually in the video recordings. While measuring surface and burrow depth temperatures, we recorded the surface activity of male *M. pugnax* to investigate the relationship between burrow use and environmental conditions, including burrow and surface temperatures, relative tidal height, and time of day. We tested the hypothesis that rising environmental temperatures would lead crabs to shift from being surface active to spending more time underground. We also experimentally heated live crabs in the laboratory and allowed them to retreat into cooled artificial burrows while continuously measuring their body temperatures (T_b). Laboratory data on cooling times were compared to field observations of burrow retreat durations to explore how the diminishing returns of remaining underground to cool might influence the decision to return to the surface.

2. Materials and methods

2.1. Field-based observations of burrow retreats and environmental temperatures

The burrow retreats of displaying *Minuca pugnax* males were observed in the marsh by the Flax Pond Marine Laboratory in Old Field, New York, USA (40.9633274,-73.1439265) on an open area of exposed sediment in a location otherwise dominated by *Spartina alterniflora* and *Iva frutescens*. During the study period, which began on a neap tide in June 2022, the area was not inundated during the daily tidal cycle. Video data were collected with a GoPro Hero5 camera mounted on a tripod with a boom arm that extended horizontally over the study area. Eleven recordings (1–3 per day) lasting between 54 and 130 min were made between June 7–12, 2022. Crabs were recorded throughout the tidal cycle during daylight hours between 08:45 and 15:40, although the durations varied between sampling days. From these recordings, 23 focal crabs (4–6 per day) were selected and scored for burrow retreat behaviors. Focal crabs, which were chosen based on a quick scan of the videos before any scoring took place, were individual burrow owners deemed likely to stay in view (e.g., not obscured by vegetation or near the edge of the field of view). We assumed that burrow owners seen in different video segments for the same day were the same crab and that different crabs were filmed each day as the camera was moved to different locations in the same general area. The assumption of consistent burrow occupancy was supported by the fact that we never saw a focal crab give up a burrow and leave the area during 870 total minutes of video segments. Two Tidbit temperature loggers (Onset model UTBI-001) were placed within 0.5 m of the area where crabs were video recorded each day. One was at the bottom of an artificial burrow made of an open-ended PVC tube with a diameter of 5 cm (Brodie et al., 2017), hammered to a depth of 25 cm, and the other was on the surface of the substratum adjacent to the artificial burrow. Artificial burrows were used to obtain temperatures at a consistent depth, which would have been too difficult with crab-constructed burrows, which vary in pitch and morphology. Temperature measurements were collected at 1-min intervals continuously throughout the day. For each video segment, focal crab scoring began 10 min into the recording to allow for a return to normal behavior following disturbances caused by a camera setup or a battery change. Using an instantaneous sampling approach (Altmann 1974), we scored whether each focal crab was in or out of its burrow at 1-min intervals following the acclimation period. Additionally, we recorded the durations of burrow retreats for each focal animal. A burrow retreat was scored if the entire crab disappeared from view, with the time of the retreat beginning when half of the crab's body was inside the burrow and ending when half of its body had emerged. This approach was used because crabs exiting their burrows sometimes paused at the entrance, with the distal parts of some walking legs still inside. Waiting for the entire body to emerge would have artificially increased our estimate of the burrow duration.

Three types of burrow retreats were observed during this study: retreats following a chase by a con- or heterospecific male (another fiddler species, *Leptuca pugilator*), retreats related to courtship where the focal crab entered its burrow and a female followed, and retreats that were not initiated by chases or potential mates. We only included the latter type in the analysis ($n = 229$) because they were more likely related to thermoregulation. Although courtship and aggression-related retreats ($n = 13$) might have turned into thermoregulation-related retreats, they were usually short, often less than 30 s, and appeared to be relatively shallow (none of the females we observed entering a focal male's burrow remained there long enough for mating to have occurred). We did not observe any retreats associated with burrow construction or potential predators.

2.2. Statistical analysis for field-based observations

To explore how environmental conditions and time of day impacted the frequency of burrow retreats, we fit our data to a binomial logistic linear mixed model using the glmmTMB package in R, where burrow occupancy (in versus out) was the binary response variable. Sampling day and individual crab were coded as random effects, while surface temperature, burrow temperature, time of day, and relative tidal height (scaled between 0 and 10) were fixed effects. Tidal height was estimated using the NOAA tide station water level data from Port Jefferson (station 8514560), with a lag time of 1.5 h added (Flax Pond Marine Laboratory curator Stephen Abrams, pers. comm.). Relative tidal height was included as a variable even though the site remained exposed throughout the study because fiddler crabs show lunar periodicity for reproductive behaviors (Christy, 1982b; Morgan and Christy 1995). Hence, the timing of high and low tides might affect burrow-related behaviors. In the original data set, each crab was recorded as either in or out of its burrow for each minute of sampling, resulting in 3727 total observations. However, including all data points led to a highly unstable model with an autocorrelation coefficient of 1.0, probably because crabs in burrows at one observation point were likely to still be there at the next one, as were crabs on the surface. To address the high serial correlation, binary data were combined into 20-min increments for each crab's time series, where the response variable became the number of times the crab was in the burrow for each increment. Time of day, tidal height, surface temperature, and burrow temperature were then averaged for each of these increments. This change resulted in a stable model with 196 observations and an autocorrelation of 0.75. The autoregression process (AR1) was applied to observations within crabs. Random intercepts were used to model the correlation among observations incurred by the hierarchical nature of the data, i.e., crabs were sampled within sampling day, and observations were clustered within crabs. Finally, we normalized all variables with the scale() function in R to avoid numerical instability when looking for interaction effects.

To determine if duration of burrow retreats increased with increasing surface temperatures, we calculated median time underground and median surface temperature experienced for each focal crab and performed a Spearman correlation analysis. Also, upon discovering a behavioral shift around 30–32 °C, above which focal crabs were more likely to be underground, we performed a post hoc analysis, comparing the median burrow retreat durations above and below this temperature with a Wilcoxon Rank Sum Test. These analyses were performed in R with the ggpubr package. Finally, crab body sizes were measured from video images with ImageJ by comparing crab carapace width to a 2 cm ruler that was placed on the substratum within the crab habitat.

2.3. Laboratory-based cooling experiments

Around 20 *Minuca pugnax* males were collected from Wareham, Massachusetts, USA (41.7587424, −70.7148547) on five different days between June 3 and July 5, 2021, for the burrow cooling experiment and two additional investigations not described here. Crabs were brought to a laboratory at Mount Holyoke College (South Hadley, Massachusetts), where approximately ten individuals each were kept in covered plastic containers (27 × 20 × 13 cm) partly filled with mud and water from the collection site, in addition to other natural items like rocks, shells, and seagrass. Because crabs were observed to deposit feed on the exposed mud inside their containers, we did not supplement their food. Crabs were selected at random for each treatment of the burrow cooling experiment and used within a week of collection.

For all treatments in the burrow cooling experiment, we heated individual crabs to a body temperature (T_b) of around 35 °C by placing them on damp fine white marine sand (Clifford W. Estes Company, NJ) in a glass container warmed by a hot plate, while simultaneously heating them from above with a 250-W heat lamp bulb. While 35 °C is warmer than they prefer (Hews et al., 2021), we commonly find crabs in the field with this T_b, and crabs warmed to this temperature in the laboratory did not appear to be impaired. Once a T_b of around 35 °C was recorded (see below), crabs were allowed to enter an artificial burrow cooled to 30, 25, or 20 °C (n = 10 for each temperature). Burrow temperatures of around 20–25 °C are within the range that we have seen for deeper burrows (25–30 cm) in the field, and 30 °C could be experienced near the top of a burrow, closer to the surface. The burrow was constructed using a 15 mL plastic centrifuge tube with a 1.5 cm diameter (Falcon) to create a hole in damp fine marine sand that filled a beverage cooler (YJ Home). T_b was measured continuously (two measurements per 0.01s) using a flexible Type T microprobe connected to a Thermes USB Temperature Acquisition system (Physitemp Instruments, NJ). The microprobe was inserted through a hole in the crab's carapace into the branchial chamber and reversibly affixed to the carapace with a 50:50 pine rosin (Velesco) and beeswax (Stakich Inc., MI) mixture melted by a dental wax carving tool (SJK Lab, model J0801). Crabs were heated to the target temperature immediately following the probe insertion and then allowed to enter the burrow. Once crabs cooled to the target temperature, they were retrieved from the burrow, and the microprobe was removed. Crabs survived this procedure, and most were released at the collection site.

Cooling curves for each temperature showing average T_b and 95% confidence intervals were constructed with the seaborn package version 0.12.1 in Python 3. Crab body sizes were determined by measuring carapace width with a digital caliper.

3. Results

3.1. Field-based observations of burrow retreats and environmental temperatures

The 23 focal crabs had an average carapace width of 1.68 cm (1.2–2.1 cm). We found that surface temperature was a highly significant predictor of burrow occupancy, with higher temperatures leading to a greater likelihood of crabs being in a burrow than on the surface. In contrast, none of the other predictors or interactions were significant (Table 1). During the five-day observation period, surface temperatures ranged from 20.0 to 43.1 °C, with an average of 31 °C (SD = 6.3), while artificial burrow temperatures ranged from 19.5 to 23.9 °C, with an average of 21.2 °C (SD = 0.6). The difference between burrow and surface temperatures ranged from 0.29 °C to −21.9 °C, with an average of −9.9 °C (SD = 5.9).

Duration of burrow retreats ranged from 0.13 to 32.02 min (Fig. 1), with a median of 2.74 min (n = 22). Surface temperatures significantly impacted the median duration of burrow retreats, with higher median surface temperatures experienced by crabs leading to more extended periods underground ($r_s = 0.53$, p = 0.011, n = 22). Most burrow retreats were less than 5 min across the range of temperatures measured (Fig. 1); however, there was a threshold around 30–32 °C, above which the median retreat was significantly longer (W = 92, p = 0.015; Fig. 2).

3.2. Laboratory-based cooling experiments

Crabs in the three temperature groups had an average carapace width of 1.35–1.36 cm, and there were no significant body size differences across treatment groups ($F_{2,27} = 0.012$, p = 0.99). We found that crabs cooled from an average of 35.14 to 30 °C captured most of the burrow's cooling potential in a short duration of time; half of these crabs had reached the temperature of the burrow after 2.52 min, and all had by 3.38 min. By 2.74 min, the median time spent in burrows by our focal crabs in the field, the four out of ten crabs from this group that were still cooling had a T_b of 30.6 (0.08 SD), which meant that they had captured around 88% of the cooling potential of the burrow (the other six had captured 100% of the cooling potential). Crabs that cooled from an average of 35.3 to 25 °C took 6.72 min for half to achieve the burrow temperature and 21.6 min for all to do so. By 2.74 min, crabs from this group had a T_b of 27.56 (1.28 SD), which meant that they had captured

Table 1
Binomial logistic linear mixed model of predictors of burrow occupancy.

	Estimate	S.E.	Z	p
Intercept	−6.477	8.416	−0.770	0.442
Tide	−0.117	0.188	−0.624	0.533
Surface temperature	0.202	0.044	4.592	4.39e-06***
Burrow temperature	0.091	0.290	0.316	0.75
Time of day	−0.126	0.246	−0.512	0.609

*Only main effects were retained in the model as all interactions were insignificant.

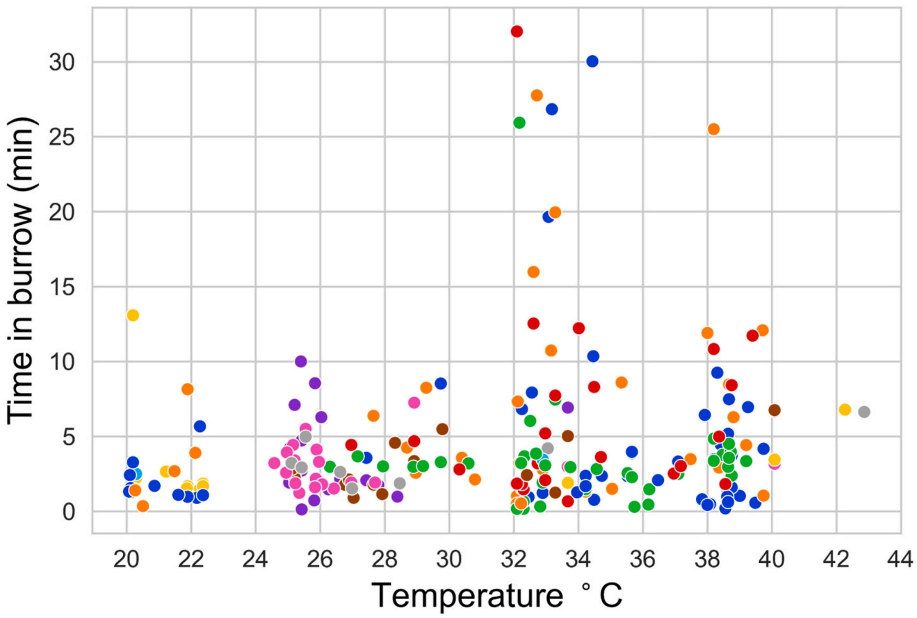

Fig. 1. Time spent in burrows across the range of surface temperatures measured in the study. The surface temperature for each data point was measured at the retreat's start. Colors denote each of the 22 focal crabs (out of 23) that spent time underground. While some burrow retreats were longer than 15 min at surface temperatures higher than 32 °C, most were shorter than 5 min regardless of temperature. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

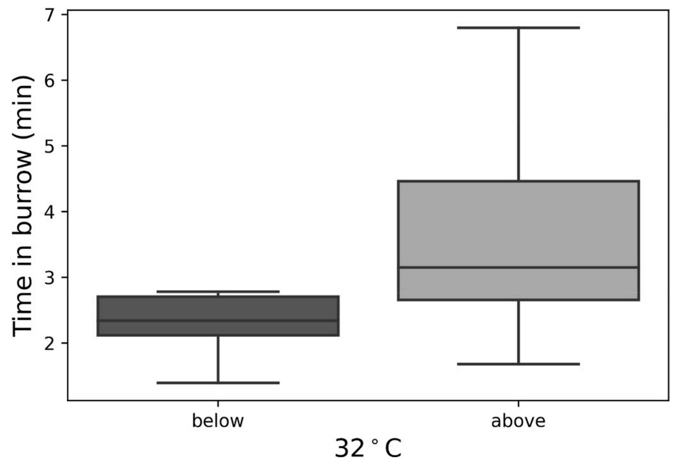

Fig. 2. Median time spent in burrows by focal crabs at surface temperatures below (N = 8) and above (N = 14) 32 °C. Focal crabs spent significantly more time underground at the higher temperatures, p = 0.02.

around 75% of the cooling potential of the burrow. Crabs cooled from an average of 34.3 to 20 °C took 14.17 min for half to reach the target temperature, and one was still cooling after 27.33 min when its measurements were ended (it had achieved a body temperature of 21.94 °C). By 2.74 min, crabs in this group had reached an average T_b of 24.34 (1.5 SD) °C, or around 70% of the cooling potential of the burrow.

4. Discussion

We explored the relationship between burrow occupancy and environmental conditions by testing whether the frequency of burrow retreats was significantly correlated with surface temperature, burrow temperature, time of day, and relative tidal height. We found that surface temperature was the strongest predictor of whether or not crabs were in burrows, with higher temperatures leading to a higher likelihood of crabs being in a burrow and longer burrow stays. Daytime surface temperatures in June at Flax Pond, New York fluctuated by more than 20 °C during our study period, including periods that exceeded *Minuca pugnax's* CT_{max} of 40 °C. However, burrows offered an escape to a cool, stable thermal environment, mitigating the risk of overheating. At 25 cm, the depth of our artificial burrows, temperatures averaged 21 °C and never rose above 24 °C. The strategy of retreating to a burrow to thermoregulate is common to many taxonomically diverse ectotherms that live in thermally variable environments, such as Namibian spiders *Ariadna Audouin* (Mulder et al., 2019), bull snakes *Pituophis catenifer sayi* (Johnson et al., 2022), tuataras *Sphenodon punctatus* (Corkery et al., 2018), and robber flies *Machimus occidentalis* and *Machimus formosus* (O'Neill and Kemp, 1992).

None of the other variables measured were significant predictors of burrow use frequency. There was no evidence of a daily tidal rhythm, although tidal clocks organize other important behaviors in fiddler crabs, such as spawning times (Christy 1982b; Morgan and Christy 1995) and larval swimming behaviors (Tankersley and Forward 1994). If our site had been inundated at high tide, many males would have likely retreated to their burrows; however, the area remained uncovered during the study, and males actively courted females throughout the day. We also did not find evidence of a diurnal rhythm in burrow use. However, this might have been due to the restricted periods during which we collected video footage, typically starting in the morning and ending mid-afternoon. The thermal gradient between burrow and surface typically reverses from late evening until early morning (Watson et al., 2018, pers. obs.), during which the burrow is warmer than the surface, which might alter crab burrow retreat behaviors. Also, it has been demonstrated that male fiddler crabs in a related species, *Austruca mjoebergi*, will increase time on the surface and take greater thermal risks while actively courting females (Darnell et al., 2020). Our data collection occurred during full daylight when males were courting. Had we continued our observations into the evening when low light levels would have led to courtship behaviors tapering off, then we might have seen different burrow-related behaviors. Hence, our findings pertain to the conditions of an exposed habitat with full daylight when males are courting and during times of day when burrows are cooler than the surface.

On exposed sites occupied by *M. pugnax* in our study, we observed a clear behavioral shift at surface temperatures above 31–32 °C, where frequencies of focal crabs in burrows often surpassed 0.5. It is apparent to any casual observer that there are fewer crabs on the surface of mud and sand flats when temperatures increase, and this phenomenon has been quantified for other fiddler species (e.g., Munguia et al., 2017; Darnell et al., 2013). The unexpected result for *M. pugnax* was that this shift appeared to happen at a threshold temperature rather than gradually. We have previously noted another threshold temperature for *M. pugnax* (Hews et al., 2021) when we found that this species begins to thermoregulate to cool itself at a T_b of 24 °C (denoted as the T_{reg} temperature) on Sapelo Island, Georgia, USA. Unfortunately, we did not have enough surface temperature readings in this investigation in the low 20s when T_b would have been correspondingly low to discern whether there might also be an increase in burrow use around T_{reg}. However, both the T_{reg} and burrow use investigations show that this species has multiple thermoregulatory thresholds between their CT_{min} and CT_{max}. Temperatures above 32 °C, while well below the CT_{max} of 40 °C, have a dampening effect on courtship and feeding, and hence, on fitness.

Once *M. pugnax* entered a burrow, we found that durations underground varied from 7.8 s to 32.0 min, with a median of 2.7 min. Jennions et al. (2003) found that the burrow retreats of males of *Austruca perplexa* typically lasted less than 4 min, with most being under 2.5 min (based on Jennions et al., 2003, Fig. 2). We found a significant positive correlation between burrow use and surface temperatures, with a clear shift to longer times underground above 32 °C. However, most burrow retreats at all temperatures were less than 5 min.

Our laboratory investigation into the effectiveness of burrow retreats for cooling crab bodies addressed the implications of these relatively short burrow stays. In the laboratory investigation, we experimentally cooled crab bodies from a starting T_b of 35 °C to either 30, 25, or 20 °C, which was 5, 10, and 15 °C lower than the starting T_b. This compared well to the temperature differences between burrow and surface in our field study, which varied from 0.29 to −21.9 °C, with an average of −9.9 °C. The median burrow stay of 2.7 min by the field-based crabs was enough time for crabs in the laboratory experiment to capture at least 70% of the cooling capacity of artificial burrows that were 10 or 15° cooler than T_b (Fig. 3). However, it is worth noting that the crabs that we video recorded in the field were larger (average = 1.67 cm) than those in the laboratory cooling experiment (average = 1.35 cm). Since larger crabs cool more slowly than smaller ones due to their lower surface area to volume ratio, they would have harvested even less of the cooling potential of their burrows in 2.7 min. Regardless of size, crabs entering cooler burrows follow Newton's law of cooling, whereby their heat loss to the burrow is proportional to the difference in temperature between their body and the burrow. This results in an exponential decay of T_b, where most heat transfer occurs quickly, and there is a diminishing return on remaining in the burrow to cool down. The brevity of their burrow stays suggests that field-based crabs often emerge before reaching an equilibrium temperature.

Finally, many crabs in our videos were noticeably wet when they emerged from their burrows. In addition to providing a place to dump heat, burrows often extend below the water table and offer the chance to rehydrate and wet the external surface to take advantage of evaporative cooling (Edney 1960; Thurman 1998). Levinton et al. (2015) found that male *M. pugnax* displaying in open, hot environments were not water-stressed due to their access to burrows.

In this study, we addressed how surface temperatures influence burrow retreats in *M. pugnax*, but questions remain about what crabs actually do in their burrows. For example, it would be interesting to know if a particular T_b triggers a return to the surface and, if so, how that T_b relates to preferred and optimal body temperatures. There are also unanswered questions about how crabs use thermal gradients within burrows to regulate body temperatures. Do they move to the coolest depths to enhance cooling rates or remain closer to the top, where it is easier to expel intruders and sense surface temperatures? Finally, does the gradient influence their likelihood of leaving a burrow—e.g., are they checking temperatures at the top of the burrow? Temperature loggers that are small enough to be worn by crabs in their burrows will someday allow us to address questions like these.

Conclusion: Crabs use burrows to escape potentially stressful or even lethal thermal conditions on the surface and are more likely to be underground as surface temperatures increase. While burrow stays lengthened with rising surface temperatures, overall, they tended to be short—long enough to bring T_b down but not to reach thermal equilibrium. This reveals a balance between the need to cool and the need to be on the surface. Thermoregulatory behaviors that have evolved in thermally hostile environments may initially blunt the harm done by the rising temperatures associated with climate change. However, this balance will likely be disrupted as rising temperatures lead to higher metabolic demands , reduced feeding windows to address those demands, and fewer courtship opportunities.

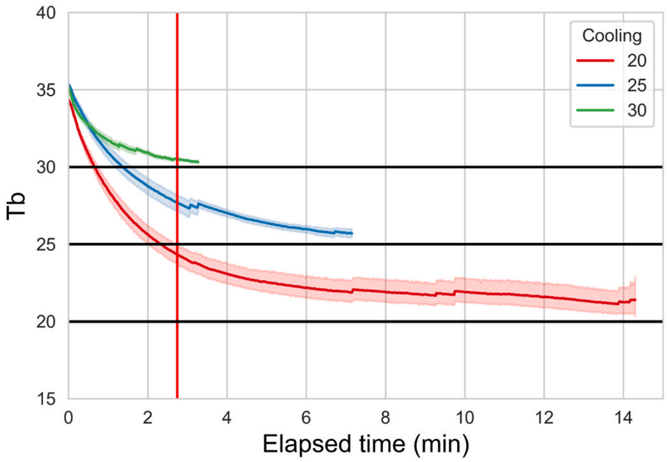

Fig. 3. Cooling curves with 95% confidence intervals for crabs heated to 35 °C in the laboratory and then allowed to cool in artificial burrows that were 30, 25, or 20 °C (N = 10 for each target temperature). Curves are truncated at the elapsed time when half of the crabs had reached the target temperature. Horizontal black lines indicate the burrow temperatures for each curve, and the vertical red line denotes the median time spent in burrows by 22 focal crabs from the field study (2.74 min). Because their body temperatures decline exponentially while cooling, crabs can capture all or most of the cooling potential of burrows in under 5 min. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Contributor roles

Renae Brodie: Conceptualization, Methodology, Analysis, Writing-Original draft preparation. **Myrha-Lissa Chery:** Software, Investigation, Validation, Data curation. **Umme Habiba:** Software, Investigation, Validation, Data curation. **Adishri Pradhan:** Software, Investigation, Validation, Data curation.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

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