Journal of Experimental Marine Biology and Ecology 581 (2024) 152060

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Reduced predator avoidance behavior and higher exposure to thermal stress for prey during heat wave events

Wissam A. Jawad [*], Ana L. Salgado, Morgan W. Kelly

Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA

ARTICLE INFO

Keywords:
Behavioral thermoregulation
Anthropogenic climate change
Heat waves
Predation
Microhabitat

ABSTRACT

Heat wave events threaten natural communities by causing mass mortalities and altering species interactions. Some organisms can use behavioral thermoregulation to avoid extreme temperatures, which may buffer them against rising incidents of heat events. While behavioral thermoregulation is effective at avoiding stressful temperatures, less is known about how it can alter other adaptive behaviors like predator avoidance. In this study, we used laboratory and outdoor mesocosm experiments to understand how behavioral thermoregulation is impacted by the presence of local predators during heat wave events, by exposing intertidal marsh periwinkles (*Littoraria irrorata*) to simulated heat waves and cues from blue crabs (*Callinectes sapidus*). We measured snail climbing height and body temperatures to disentangle snail decisions to thermoregulate or avoid predators under increasing heat stress. Our results indicate that antipredator behavior can be severely reduced in heat wave simulations, in temperatures well below the snail's upper thermal limits. Snails chose lower climbing heights that allowed them to avoid stressful temperatures but brought them within reach of subtidal predators. Thus, while heat waves may not directly kill snails because they can behaviorally thermoregulate, reduction in antipredator response can increase their encounters with subtidal predators. Additionally, when snails maintained anti-predator climbing behavior in lower intensity heat wave simulations, snails occupied hotter microclimates and had higher body temperatures, indicating predator avoidance increases the temperatures snails experience. Local predator presence can increase the exposure of prey species to temperature stress during heat events, and these events can decrease the size and number of tolerable microhabitats for mobile ectotherms.

1. Introduction

Heat waves – extreme temperatures above the historical baseline for several days or more – are among the major climatic events that are increasing in frequency and intensity due to anthropogenic climate change (Meehl and Tebaldi, 2004; Oliver et al., 2018). Considerable work has now demonstrated the large-scale negative effects of heat waves on natural communities, with cases of mass mortalities of coastal species and complete reshaping of biologically rich ecosystems (Leggat et al., 2019; Smale et al., 2019; Wernberg et al., 2013; Smale et al., 2017). Broad changes in community compositions are often the result of shifts in species interactions that can lead to the proliferation of species that benefit from the new conditions, or the increased mortality of species that are harmed by them (Kroeker and Sanford, 2022; Sanford, 1999). Although changes in species abundance may be attributed to the extreme temperatures experienced during heat waves, the effects of heat waves can be moderated in thermally heterogeneous habitats that include thermal refuges. As a result, the effects of heat waves on species persistence are difficult to predict from coarse-grain air or sea temperature measurements alone (Jost and Helmuth, 2007; Helmuth et al., 2010; Chapperon and Seuront, 2011). The effects of heat waves may thus depend in part on a species' capacity to regulate their body temperatures by occupying thermal refuges within these habitats.

Behavioral thermoregulation can be an effective way to maintain optimal body temperatures and to avoid stressful ones within thermally heterogeneous habitats. For mobile ectotherms living in these environments, extreme temperatures can be avoided by moving into shade or near water (Chapperon and Seuront, 2011; Sunday et al., 2014). Thus, behavior can buffer against selection for increased thermal tolerance, a phenomenon termed the Bogert effect (Bogert, 1949; Muñoz et al., 2014; Muñoz, 2022). If Bogert effects have limited past evolution of physiological thermal tolerance, mobile ectotherms will have to rely more strongly on behaviors to regulate their body temperatures as heat events become more severe. Indeed thermoregulatory behaviors have been

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[*] Corresponding author.
E-mail address: aetonarinari@gmail.com (W.A. Jawad).

https://doi.org/10.1016/j.jembe.2024.152060
Received 19 November 2023; Received in revised form 13 September 2024; Accepted 1 October 2024

recognized as a potential mitigating response against rising temperature stress (Huey and Tewksbury, 2009; Fey et al., 2019), positing that animals will need to spend more time behaviorally thermoregulating in future conditions to decrease exposure to heat stress. However, behavioral thermoregulation can be ecologically constrained - choosing more suitable microhabitats to thermoregulate can increase exposure to other threats like local predators (Vaudo and Heithaus, 2013; Carr and Lima, 2012; Milling et al., 2017). As extreme heat events increase, the cost of occupying suboptimal temperatures to avoid predators can increase compared to current conditions. To better predict the effectiveness of thermoregulation as a buffering mechanism to climate change and the heat stress species can experience during heat events, it's essential to incorporate ecological interactions like antipredator behavior.

Littorinid snails make an ideal group for testing the roles of predator avoidance and behavioral thermoregulation in shaping the outcomes of the heat stress snails experience during heat wave events. Littorinids are common herbivores found in intertidal systems worldwide, where they often occupy thermally extreme microhabitats high in the intertidal, and their physiological and behavioral responses to heat stress have been well documented (Chapperon and Seuront, 2011; Iacarella and Helmuth, 2011; Marshall et al., 2013). Littorinid snails employ a suite of behaviors to minimize heat stress, including foot retraction and changes in shell postering to reduce body temperatures by 3–5 °C (Chapperon and Seuront, 2011; Iacarella and Helmuth, 2012; Iacarella and Helmuth, 2011). Snails will also climb to exploit more suitable microclimates within their habitats, which can result in the greatest reduction in body temperatures, by up to 11 °C (Chapperon and Seuront, 2011; Marshall et al., 2013). Because of these adaptations to thermally extreme habitats, as well having exceptionally high upper thermal limits (>50 °C) (Marshall et al., 2015), *Littorinid* snails are considered to be less vulnerable to habitat warming compared to other ectotherm taxa (Marshall et al., 2015). However, a major gap remains in understanding how adaptive behaviors like predator avoidance and thermoregulation can be impacted by heat events. To address these questions, we focus on a common intertidal periwinkle (*Littoraria irrorata*) and its primary predator, the blue crab (*Callinectes sapidus*) (Silliman and Bertness, 2002).

Littoraria irrorata is an abundant grazer found in salt marshes dominated by *Sporobolus alterniflorus* (Loisel.) P.M. Peterson & Saarela (= *Spartina alterniflora* Loisel.) from the northern Gulf of Mexico and Southeastern United States, a range entirely shared with blue crabs. Snails in these marshes experience substantial fine-scale thermal heterogeneity within the marsh grass, with body temperatures that can differ by over 10 °C across <15 cm, indicating the potential benefit of behavioral thermoregulation (Fig. 1). Previous work suggests that periwinkle microhabitat selection is strongly influenced by a mixture of avoiding heat and desiccation stress, as well as subtidal crab predators (Dix and Hamilton, 1993; Warren, 1985; Iacarella and Helmuth, 2012; Iacarella and Helmuth, 2011). Blue crabs are subtidal predators which stay submerged while hunting, avoiding the extreme high and variable air temperatures that snails experience. During high tides, blue crabs move into the marsh to feed on periwinkles, which can perceive both air and water borne crab cues (Dix and Hamilton, 1993). Periwinkles avoid predation by moving up the grasses and outside of crab reach (<10 cm above the water) when crab cues are present (Warren, 1985). Marsh periwinkles are especially vulnerable to crab predation by shell crushing because they have a large and exposed aperture, no sculpturing on the shell surface, and a thin operculum, making avoidance behaviors the primary defense for this species compared to snails with better defended shells (Vermeij, 1973).

Although snails are safe from blue crab predators when perched 10 cm or above on grasses, they are exposed to greater temperature stress by receiving more direct solar radiation and being further from the cooler water below (Fig. 1). Littorinids can occupy these safer microhabitats above the tide line because of their high physiological capacity to deal with heat stress i.e. high upper thermal limits (69). However as heat waves become more frequent and severe, snails could experience changes in predator avoidance behavior that could alter their vulnerability to predators and exposure to heat stress. In this study, we test the hypothesis that heat waves reduce snails' behavioral capacity to occupy microhabitats above the reach of crab predators. Additionally, we hypothesize that if predator avoidance behaviors are maintained during heat waves, snails will experience higher body temperatures in the presence of predators due to restricted behavioral thermoregulation. We use a combination of laboratory and outdoor experiments to simulate heat wave events in chambers that replicate the thermal gradients and microhabitats available for marsh periwinkles, and measure snails climbing heights and body temperatures to untangle the role of predator avoidance and behavioral thermoregulation in determining the heat stress snails can experience during heat wave events.

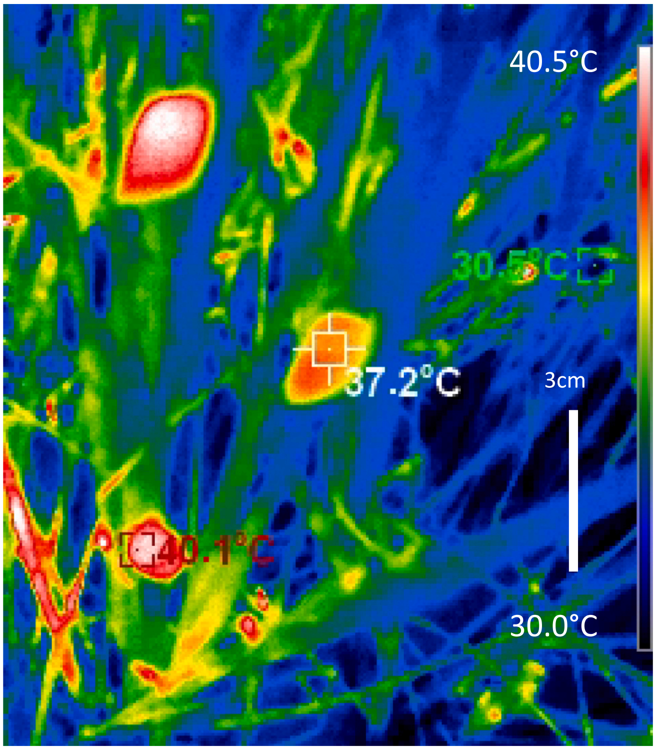

Fig. 1. Thermal image of *Littoraria irrorata* body temperatures in a *Sporobolus alterniflorus* marsh. A large range of temperatures is found within a 0.5 m section of marsh, from 30.5 °C near the water (green square) to a L. *irrorata* with a body temperature of 40.1 °C on a *S. alterniflorus* blade (red square). Red to white indicate the highest temperatures in the image, whereas green to dark blue are the coolest temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. General experimental design

Littoraria irrorata snails used in this study were collected from a *Sporobolus alterniflorus* dominated marsh at the Louisiana Universities Marine Consortium (LUMCON) in Cocodrie, Louisiana, USA (29.255428, −90.662145). Based on Worldclim climate data for the years 1970–2000, which has a spatial resolution of ~1 km^2, historical average and maximum temperatures from June–August for the region are 26.6 °C and 30.1 °C, respectively (Fick and Hijmans, 2017). To obtain more local temperatures from our study site, we downloaded the average and maximum temperatures for June–August from a local weather station, which are 29.5 °C and 34 °C, respectively (Table S8). However, temperatures within the *Sporobolus* habitat are often much higher and more variable than the weather station temperatures. Thus, we placed seven iButton temperature loggers (DS1921G, accuracy ±1 °C, Maxim Integrated Products, USA) within the grasses near *L. irrorata* during June and July of 2021 to account for these differences and inform the temperatures used for the heat wave simulations. The iButtons were placed within PVC tubes with predrilled 1 cm holes to allow air to flow over the iButtons to prevent inaccurate readings from resting on hot surface. The highest recorded temperatures were 45.5 °C, and one datalogger registered 7 days with temperatures equal to or above 40 °C (Table S9).

All the collected snails were of the adult size class with shell length between 18 and 22 mm, which is the most common sized snail in this region (Rietl et al., 2018). Snails were randomly collected from *Sporobolus* blades across a 20-m transect in the marsh during high tide. Although tides are diurnal, the marsh is highly wind driven, which often resulted in 10+ days of flooded marshes, or only brief periods of low tide during which mud was exposed for a few hours each day. Blue crabs are highly abundant at this site, where snails are almost always found high on the grasses during high tides, and crabs were observed in the marsh during all of our collection days. Although the height needed to avoid crabs depends on the size of the crab, snails are completely out of the range of any crabs if snails are over 10 cm above the waterline (WAJ personal observation, (Barton, 2011a).

Chambers used for all of the experiments were 19-l PVC buckets, with 4 × 2 cm diameter holes drilled at equal distances, 10 cm above the bottom. All chambers contained roughly two cm of mud collected from the marsh, and the tops were wrapped with food-grade plastic wrap (Uline Wrapper, USA), with a 12 cm diameter hole cut in the middle to allow for humidity and heat retention, heat emission from heat lamps when present, and prevent snail escapes. For simulating heat waves, we used 75-watt lamps (Fluker Clamp Lamp, USA) with 60-watt ceramic heat emitters (Zoo Med Repticare Infrared, USA) which we placed on top of metal screening that sat over the plastic wrap. Air temperatures were recorded using iButtons (DS1921G, accuracy ±1 °C iButtonLink Technology, USA) placed at different heights in the chambers.

2.2. Laboratory experiment

180 snails were collected in December 2021, brought to Louisiana State University (Baton Rouge, USA), separated and acclimated into four chambers with marsh mud to laboratory temperatures at 30 °C for 48 h (outdoor daytime temperatures were 27 °C during collection time), before being added to the experimental chambers. The laboratory received natural daylight and was supplemented by fluorescent lights on a 12 h day/12 h night cycle. Fifteen snails chosen randomly were placed into twelve chambers, with six chambers placed in a non-crab pool and the other six placed in the crab pool (pool size = 2.50 m length x 1.15 m width x 3 m high). The pools contained approximately 150 l of synthetic sea water (Instant Ocean, USA) mixed to the marsh salinity of 10 ppt, and the salinity was maintained with daily top offs for the duration of the experiment. Water was circulated using a 303 l per hour water pump (Uniclife UL80 Submersible Water Pump, USA), which allowed water to circulate around the pool and into the holes in the bottom of the chambers. Water level remained constant in chambers at 8 cm above the mud. The crab pool contained a single blue crab for crab cue (125 mm carapace width) that was fed with approximately three live periwinkle snails a day (not used in the experiment) for the duration of the experiment. Half of the chambers in each crab treatment were randomly assigned heat wave and non-heat wave treatments. Air and water temperatures in the ambient chambers were maintained at room temperatures (30 ± 0.5 °C). In the heat wave chambers, water temperatures remained at 30 ± 0.5 °C, while air temperatures increased from 30 ± 0.5 °C in the water to ~42 ± 0.5 °C at the tops of the chambers, creating a top-down thermal gradient similar to that of the marsh. Snails were added to the chambers and acclimated to the experimental setup for 24 h before conducting the first survey. Climbing height was assessed by measuring the height of snails within each chamber. Three surveys were conducted each day for five consecutive days at 9:00, 12:30, and 14:30. Snail heights did not vary across the survey times, so data were combined for statistical analysis.

2.3. Outdoor experiment

160 snails were collected in June 2022 and held in the same conditions previously described, before being brought to an outdoor greenhouse space at Innovation Park drive in Baton Rouge, USA where they were acclimated to outdoor conditions for 48 h. A similar set up was used as the laboratory experiment, but with some modifications. Eight plastic pools (114 cm diameter x 20 cm height) were filled with approximately 150 l of synthetic sea water at approximately 10 ppt. All the pools had a 303 l per hour water pump for circulation and were covered with a UV top (Vigoro Matrix Grid, USA) to keep water temperature cool and predators protected from direct sun. An adult blue crab (125 mm carapace width) was added to four pools; crabs were fed three live periwinkles a day for the duration of the experiment (Fig. S1). Note that crab cue was standardized as closely as possible between the laboratory and outdoor experiment by using a single, similarly sized crab in an equal volume of water for both experimental setups. Although variations in water and air temperatures between the experiments can alter the release and movement of chemical cues, we found that L. *irrorata* was extremely sensitive to crab cue, displaying similar antipredator responses across a range of cue concentrations in preliminary experiments that were lower (1 cup of water from crab aquarium per pool) and higher (several crabs per pool) than those ultimately used in these experiments. A single crab of 125 mm carapace width per 150 l of water was determined to be sufficient to saturate the water and air within the covered pools across the tested temperatures. Four circles were cut into the UV top to hold chambers that were designed the same as in the laboratory experiment, with the addition of six *Sporobolus* stems placed equidistant along the sides of the inside of the chambers. Stems were added in this experiment because we wanted to test the possibility that, in addition to height choice, snails could also be using the undersides of grass blades to thermoregulate. Ten snails chosen randomly were added to two chambers in each pool (the other two chambers were being used for a separate experiment), and one chamber per pool had a heat lamp; the first survey began 24 h later. Three surveys were conducted for five consecutive days, at 7:30, 14:00, and 19:30. These survey times were selected to incorporate three distinct temperature gradients noted in the field, and replicated in our ambient chambers: at 7:30, the water and air temperature were cool and similar (water and air temperature = ~28 ± 0.5 °C). At 14:00, air temperature was highest (>40 ± 0.5 °C; water temperature = ~38 ± 0.5 °C), and at 19:30, air temperature dropped to near morning temperatures (~31 ± 0.5 °C), but now water temperature was slightly warmer than air temperatures (~36 ± 0.5 °C), creating a reverse gradient. Within our heat wave chambers, the air temperatures rose from ~30 ± 1 °C in the morning (water temperature = 29 ± 0.5 °C) to an air temperature of ~47 ± 0.5 °C in the afternoon (water temperature = ~40 ± 0.5 °C), before returning to ~32 °C in the evening (water temperature = ~38 ± 0.5 °C). Snail height (cm) and temperature (°C) was measured for each survey. Due to storms, we could not survey snails for two of the five evening surveys.

To better understand the role of behavioral thermoregulation in reducing snail mortality during heat events, we conducted a complimentary tethering experiment during the outdoor study on the same day of the outdoor experiments. We immobilized snails within a separate set of heat wave and non-heat wave chambers by gluing their shells to 2 cm segments of fishing line to restrict behavioral thermoregulation (4 heat wave and 4 non-heat wave chambers with 10 tethered and 10 non-tethered snails per chamber). We excluded mud from these chambers because free moving snails could have access to more food in the mud than tethered snails during this experiment. Snail mortality between tethered and untethered snails was monitored each day for 5 consecutive days in the chambers.

2.4. Snail body temperature measurements

Snail temperatures were measured using a HT-19 Thermal Camera (Hti Instruments, China) pointed at the shells of the snails. From lab trials, we found that snail internal body temperatures, measured by drilling the shell and inserting a thermometer probe into the snails' soft body, matched external shell temperatures within one minute of changes in external air and water temperatures, thus external shell temperatures represent an accurate temperature for internal temperatures. Thermal cameras measure the infrared radiation reflected from the objects they are measuring, so we calibrated the camera's emissivity reading according to the cameras instructions to match the surface reflectivity of the shells of L. *irrorata* to 95, which is a level commonly used for measuring the body temperatures of other intertidal molluscs (Lathlean and Seuront, 2014).

2.5. Statistical analysis

Statistical analyses were performed using R software version 4.3.1 (R Core Team, 2021) and all plots were created using *ggplot2* (Hadley, 2016). For each dataset, we performed data exploration following (Zuur et al., 2010) to avoid violations of model assumptions and over-dispersion. We compared the cumulative density distribution of the snail's climbing height within the chambers in the laboratory experiment using permutation tests. We first filtered the data using only the observations with no crab cue, as the data plotted showed differences only in the distribution of this treatment (Fig. 2A and C). We then calculated the absolute differences in the count number of individuals below or equal to a threshold (10, 15, 20, 25, 30, and 35 cm) between the heat wave and non-heat wave treatments. We set 10,000 permutations per threshold and calculated the *P*-value for each permutation.

We investigated whether snails' climbing height changed under different conditions. In the laboratory experiment, we categorized the snail's climbing height into two groups: 1 for snails 17 cm or higher (considering a predation risk threshold of 10 cm above the water, with water at 7 cm high), and 0 for those below. Using this classification as a response variable, we applied a generalized linear mixed model (GLMM) with a binomial distribution, heat wave (yes/no) and crab cue (yes/no) as independent variables, adding the interaction between treatments, and including chamber number as a random effect using the *glmmTMB* package (Brooks et al., 2017). For the outdoor experiment, with more replicates per chamber, we analyzed the proportion of snails at predation risk across treatments. We assessed the proportion of snails at 17 cm or lower, and we fitted a GLMM with a beta-binomial distribution and *logit* link with the proportion of snails as the response variable, using heat wave,crab cue, survey time, and their interaction as independent variables, and the random effect of chamber number. We conducted two separate multiple comparisons to determine where the difference between treatments are in both the laboratory and the outdoor experiment, using Tukey's all-pair comparisons from the *glht* function in the *multcomp* package (Hothorn et al., 2008).

For the body temperature data in the laboratory experiment, we fitted a linear mixed model (LMM) with individual snail temperature as a response variable, heat wave, crab cue treatment and their interaction as explanatory variables using the *lmer* function in the *lm4* package (Bates et al., 2015). We log transformed temperature values for a normal distribution and accounted for multiple observations by including a random effect of the chamber. Additionally, we performed multiple comparisons using pairwise comparisons among all possible group combinations with the *glht* function (Hothorn et al., 2008). For the outdoor experiment, we fitted another LMM using body temperature but adding survey time (i.e.: morning, afternoon and evening) as a response variable and the three way interaction with heat wave and crab cue. And pairwise comparisons were performed as above. Finally, we determined if differences in mortality between tethered and untethered snails were significant in heat wave and non-heat wave chambers using Fisher's exact test.

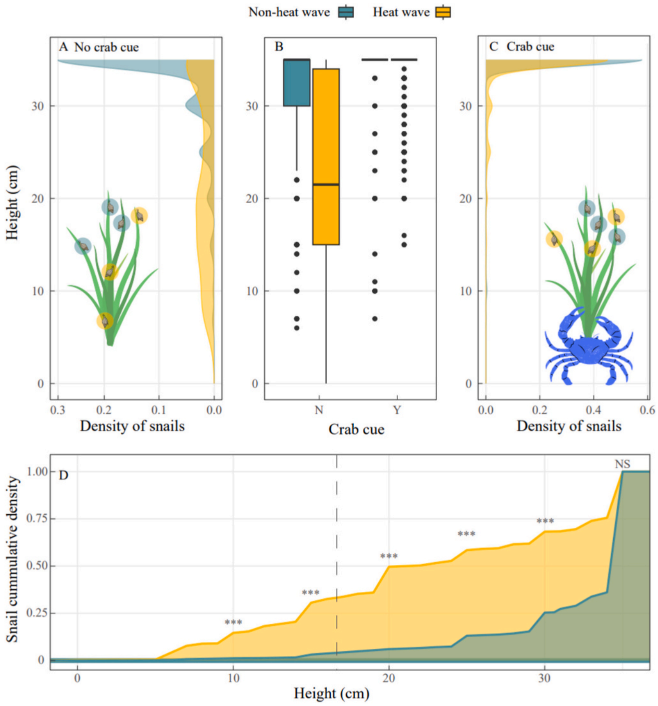

Fig. 2. Effects of heat waves on L. *irrorata* climbing heights (cm) in the laboratory experiment. The side panels show the snail densities at each height. Panel A is in the absence of crab cue, and panel C is in the presence of crab cue, comparing heat wave (light blue) and non-heat wave (yellow) treatments. Panel B represents snail height in the chambers according to the crab cue (no = N, yes = Y) and the heat wave treatments. Boxplots represent the median, 25th and 75th percentiles. Whiskers are values within 1.5× interquartile, black dots are outliers. Panel D displays the cumulative height density of L. *irrorata* in the absence of crab cue. Grey dotted line represents the height at which snails are safe from crab predators if above (17 cm). Permutation tests for detecting significant differences in snail cumulative density were performed at five cm increments ($P < 0.001$) and are represented with ***, and non-significance is represented with NS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Effects of heat waves on snail climbing height and vulnerability to predation

In the laboratory experiment, the climbing height distribution of snails in the chambers without crab cues was lower in heat wave treatments compared to non-heat wave (Fig. 2A and B, Table S1) and the number of snails occupying all heights at or below 30 cm was greater in heat wave treatment (Permutation tests: $P < 0.\ 001$; Fig. 2D; Table S2). When the crab cue was present, snails in both heat wave treatments moved to the highest points of the chambers (Fig. 2B and C; Table S1). The frequency of snails above 10 cm of water, the height at which snails are not at risk of predation, decreased by the heat wave treatment, but increased by the crab cue or when the heat wave and the crab cue treatments are together (Table 1, Fig. 3). In the absence of a crab cue, the heat wave treatment had a higher frequency of snails below 10 cm (200 out of 614 total) compared to non-heat wave treatment (21 out of 662; Fig. 3; Table S3). In the presence of a crab cue, we detected no difference in the frequency of vulnerable snails (below 10 cm) in heat wave (3 out of 654) and non-heat wave treatments (7 out of 711; Fig. 3), supported

Table 1
Results of the generalized linear mixed model analyzing snail climbing heights in the laboratory and the proportion of snails at risk in the outdoor experiments. Chi-square (χ^2) values are reported with significant *P-values* indicated in bold.

Laboratory experiment

Explanatory variable	Estimate	χ^2	*df*	*P-value*
Heat wave	−2.70	74.53	1	**<0.001**
Crab cue	1.19	45.60	1	**<0.001**
Heat wave:Crab cue	3.47	20.88	1	**<0.001**

Outdoor experiment

Explanatory variable	Estimate	χ^2	*df*	*P-value*
Heat wave	1.45	37.33	1	**<0.01**
Crab cue	−2.26	73.63	1	**<0.01**
Survey time	4.02	118.38	2	**<0.01**
Heat wave:Crab cue	0.19	0.80	1	0.371
Heat wave:Survey time	−1.86	4.19	2	0.123
Crab cue:Survey time	1.23	8.79	2	**0.012**
Heat wave:Crab cue:Survey time	1.05	1.22	2	0.542

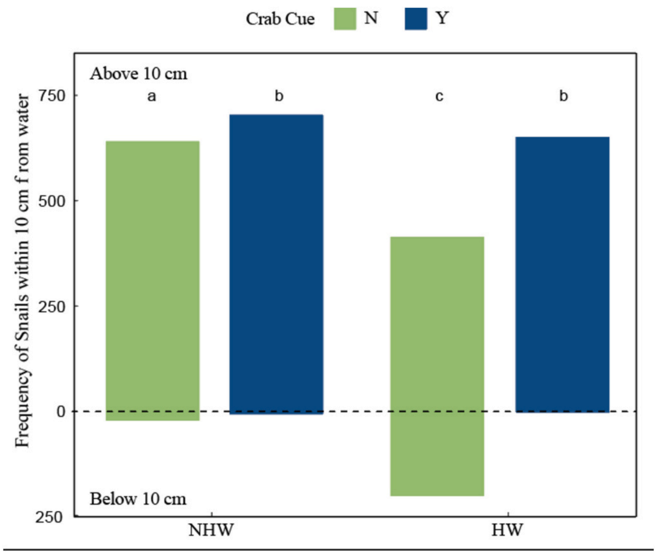

Fig. 3. Effects of heat waves and crab cues on the snail climbing heights of L. *irrorata*. The dashed line at zero delineates the height climbed above and below 17 cm. Green bars represent scenarios without crab cues (N), while blue bars depict scenarios with crab cues (Y). NHW denotes non-heat wave conditions, and HW represents heat wave conditions. Significant differences are indicated by different letters, as determined by post-hoc Tukey's all-pair comparison tests (refer to Supplemental Table S3 for details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by the post hoc analysis (Table S3).

In the outdoor experiment, snails in the heat wave treatments occupied lower mean climbing heights in both crab cue and no crab cue treatments compared to non-heat wave treatments (Table S4). The greatest difference in climbing heights between heat wave and non-heat wave treatments occurred in the morning, when air temperature was coolest (five-day mean: non-heat wave = 29.9 ± 1.1 °C, heat wave = 35.7 ± 3.6 °C). In non-heat wave treatments, mean climbing heights were lower in the absence of a cue (16.1 cm) compared to with a cue (28.3 cm; Table S4). In the heat wave treatments, mean climbing heights in the absence and presence of a cue dropped to 10.1 cm and 19.3 cm, respectively (Table S4). In the afternoon, mean climbing heights in the non-heat wave treatments were lower in no cue (4.6 cm) compared to with cue (8.2 cm; Table S4). In the heat wave treatments, the climbing height means dropped to 3.6 cm and 5.4 cm, respectively (Table S4). The considerable drop in heights in both treatments compared to the morning was likely due to the much higher air temperatures (five-day mean in non-heat wave chambers = 42.0 ± 2.1 °C, heat wave = 46.2 ± 3.9 °C) that snails experienced during the middle of the day in both heat wave and non-heat wave treatments. In the evening, air temperatures dropped (three-day mean in non-heat wave chambers = 31.1 ± 2.2 °C, heat wave = 35.2 ± 2.1 °C). Mean climbing heights in the non-heat wave treatment were 9.3 cm in the absence of crab cue, and 21.2 cm with crab cue (Table S4). In the heat wave treatment, climbing heights were 10.1 cm in the absence of crab cue and 15.4 cm with crab cue, respectively (Table S4). The small difference in climbing height between snails in heat waves vs non-heat waves can be explained by the fact that water temperatures (three-day mean of pools = 35 ± 1.4 °C) in the evening were warmer than air temperatures in non-heat wave treatments and equal to those heat wave treatments, creating a reverse temperature gradient in non-heat wave conditions. This is common in the marshes, when the water maintains the higher temperatures from the afternoon while air temperature decreases into the evening.

Heat waves and survey time increased the proportion of snails vulnerable to crab predation while the crab cue reduced it as snails climbed higher (Table 1, Fig. 4). The interaction between heat wave and crab cue, and heat wave and survey time did not influence the proportion of snails vulnerable to crab predation. While the interaction between crab cue and survey time, and the three way interaction increased this proportion (Table 1). Regardless of crab cue, the proportion of vulnerable snails in non-heat wave treatments was lower than in heat wave treatments except for the afternoon (Table S5). In the morning, the presence of crab cue in the non-heat wave reduces the proportion of snails at risk of predation compared to the other treatments, and in the heat wave treatment the presence of crab increased the proportion of snails at risk by 44 % compared to the no crab cue treatment (Table 2, Fig. 4A; Table S5). In the afternoon, heat wave and crab cue decreased the proportion of vulnerable snails to crab predation (Fig. 4B), but there were no differences in their means (Table S5). In the presence of crab cue, 93 % of snails were within crab range in non-heat wave treatments and increased to 99 % in heat wave treatments (Table 2). In the absence of crab cue, 100 % of snails were within crab range in non-heat wave treatment, and 99.5 % in heat wave treatments (Table 2, Fig. 4B). In the presence of crab cue in the evening, 38 % of snails in non-heat wave treatments were within the predation risk range and increased to 70 % in heat wave treatments (Table 2, Fig. 4C, Table S5).

3.2. *Effects of heat waves and predator cue on snail body temperature*

Heat wave, crab cue, and their interaction increased snail body temperatures in the laboratory (Table 3). For snails in the heat wave treatments, those with a crab cue had higher body temperatures than those without; Table 2, Fig. 5, Table S6). This suggests that the restriction of snail movements in the presence of predators directly increases snail body temperatures. We did not detect a difference in body temperature in the non-heat wave treatments in either crab cue or no crab cue treatments (Table 2, Fig. 5, Table S6), because temperatures in the control chambers were held at constant room temperature (five-day mean = 30 ± 0.1 °C), and thus did not provide a temperature gradient for the snails.

In the outdoor experiment, we found that heat wave, crab cue and survey time increased snail body temperatures, however the interaction between heat wave and crab cue was not significant (Table 3, Fig. 6). Furthermore, the interaction between survey time with heat wave or crab cue reduces body temperature, while the three way interaction (heat wave, crab cue and survey time) increases it (Table 3, Fig. 6). In the morning, snails had higher body temperatures with crab cue compared to no crab cue treatments, but snails in the heat wave were experiencing higher body temperatures compared to the non-heat wave (Table 2, Fig. 6A, Table S7). In the afternoon,snails in both crab cue and

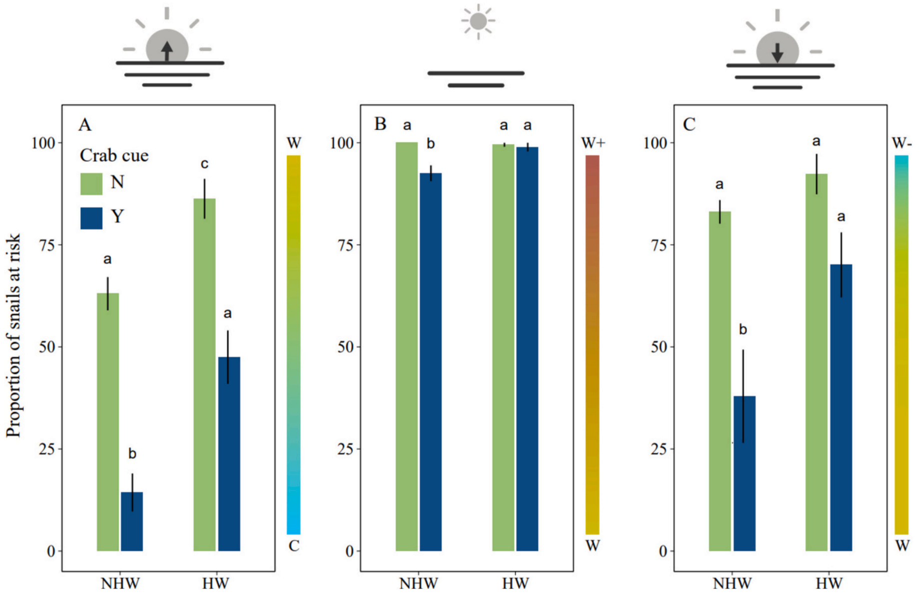

Fig. 4. Effects of heat waves on the mean proportion of L. *irrorata* vulnerable to crab predation in the outdoor experiment. No crab cue (N) are the green boxes, and crab cue (Y) are the blue boxes. Non-heat wave is represented by NHW and heat wave by HW. The vertical black lines represent standard errors. Different letters indicate significant differences based on post-hoc Tukey's all pair comparisons test (Supplemental Table S7). Icons on the tops of the panels represent survey time: Panel A is 7:00, Panel B is 12:00; and Panel C is at 19:00. Colored bars at the right of each panel depict the temperature gradient from the bottoms of the chambers to the tops in the chambers during each survey time. Blue is cool (C), blue to green is warmer (W-), yellow is warm (W), and red is hot (W+). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Mean, standard error (SE) and sample size (n) of the proportion of snails at risk and snail body temperatures in the outdoor experiment. Heatwave is represented by HW, non-heat wave by NHW, crab cue by Y and no crab cue by N.

		Proportion of snails at risk			Snail body temperature (°C)		
Heat wave	Crab cue	Mean	SE	n	Mean	SE	n
Morning							
NHW	N	63.03	4.07	4	31.16	0.15	185
NHW	Y	14.34	4.66	4	33.54	0.17	189
HW	N	86.28	4.88	4	32.59	0.17	169
HW	Y	47.49	6.54	4	35.22	0.21	184
Afternoon							
NHW	N	100	0	4	41.99	0.12	193
NHW	Y	92.53	1.94	4	41.38	0.22	189
HW	N	99.51	0.49	4	42.55	0.14	195
HW	Y	98.94	1.06	4	42.37	0.17	192
Evening							
NHW	N	83.07	2.89	4	34.12	0.21	104
NHW	Y	37.93	11.42	4	31.8	0.2	113
HW	N	92.33	4.94	4	35.95	0.19	105
HW	Y	70.08	7.96	4	35.5	0.21	106

Table 3
Outcome of the linear mixed model assessing snail's body temperature in the laboratory and outdoor experiments. Chi-square (χ^2) values are reported and with significant *P-values* highlighted in bold.

Laboratory experiment				
Explanatory variable	Estimate	*χ2*	*df*	*P-value*
Heat wave	0.13	806.674	1	**< 0.01**
Crab cue	0.01	21.564	1	**< 0.01**
Heat wave:Crab cue	0.03	6.821	1	**0.009**

Outdoor experiment				
Explanatory variable	Estimate	χ2	df	P-value
Heat wave	0.05	54.74	1	**<0.01**
Crab cue	0.08	6.56	1	**0.01**
Survey time	0.38	6235.45	2	**<0.01**
Heat wave:crab cue	0.003	2.55	1	0.11
Heat wave:Survey time	−0.02	72.71	2	**<0.01**
Crab cue: tSurvey time	−0.23	291.35	2	**<0.01**
Heat wave:crab cue:time survey	0.06	14.18	2	**<0.01**

non-crab cue had similar high temperatures (Table 2, Fig. 6B). Interestingly, the difference between heat wave vs non-heat wave temperatures was also smaller compared to other survey times (Table 2, Fig. 6). In the evening, Heat wave treatments had similar temperatures in crab cue compared to no crab cue (Table 2, Fig. 6C, Table S7). Interestingly, in non-heat wave treatments, body temperatures were lower in the crab cue treatment compared to no crab cue (Table 2, Fig. 6C, Table S7). This could be explained by the fact that water temperatures at this time were warmer (three-day mean = 34.5 ± 1.5 °C) than air temperatures (three-day mean = 31.1 ± 2.2 °C), and it is likely that the higher heights that snails occupied in the presence of crab cue also kept them cooler in non-heat wave conditions.

3.3. *The effects of restricting thermoregulatory behaviors on snail survival*

We predicted that L. *irrorata*'s ability to behaviorally thermoregulate plays a crucial role in preventing mortality during heat waves. The results of our tethering experiment support this prediction, where we found snails without tethers in both heat wave and non-heat wave chambers had 100 % survival after 5 days, while only 5 of the 40 snails tethered in heat wave chambers survived (Fisher's exact test: $P < 0.01$).

4. Discussion

Behavioral selection of preferred microhabitats is widespread in animals. Global climate change is decreasing the number and size of suitable microclimates for many animals and leading to increased mortality for vulnerable populations (Harley, 2011; Salgado et al.,

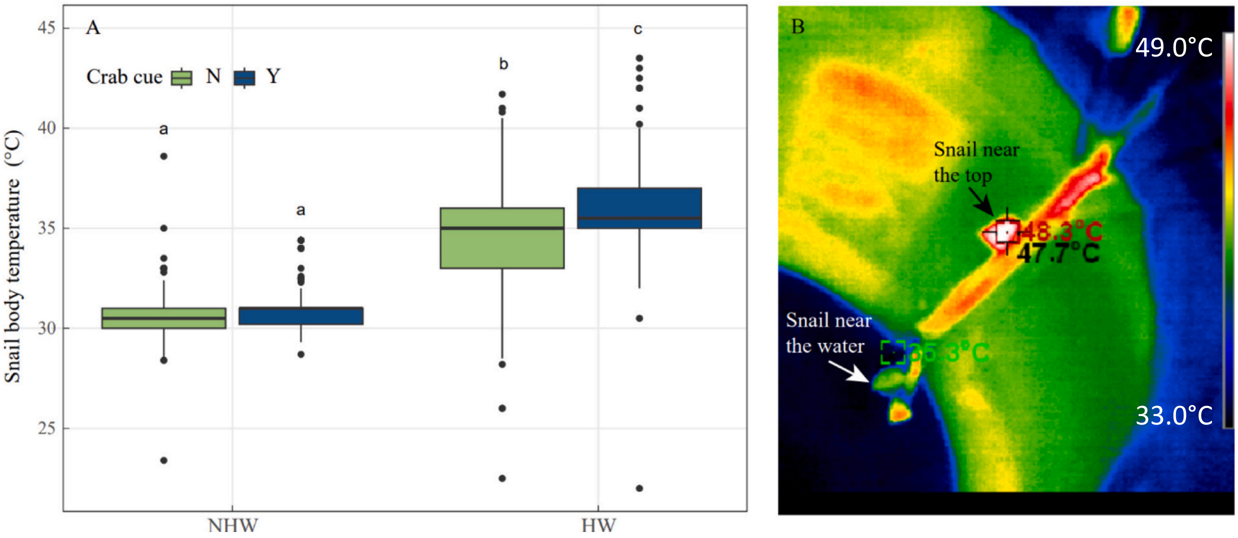

Fig. 5. Effects of heat waves and crab cue on L. *irrorata* body temperatures in the laboratory experiment (Panel A). No crab cue (N) is the green boxes, crab cue (Y) is the blue. Non-heat wave is represented by NHW, heat wave by HW. Box plots represent the median, 25th and 75th percentiles. Whiskers are values within 1.5× interquartile, black dots are outliers. Panel B image showing the temperature gradient in the chambers, and between snails found at the top (red square = 48.3°) vs the bottom (green square = 35.3 °C). Red to white is the hottest, whereas green to dark blue is coolest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

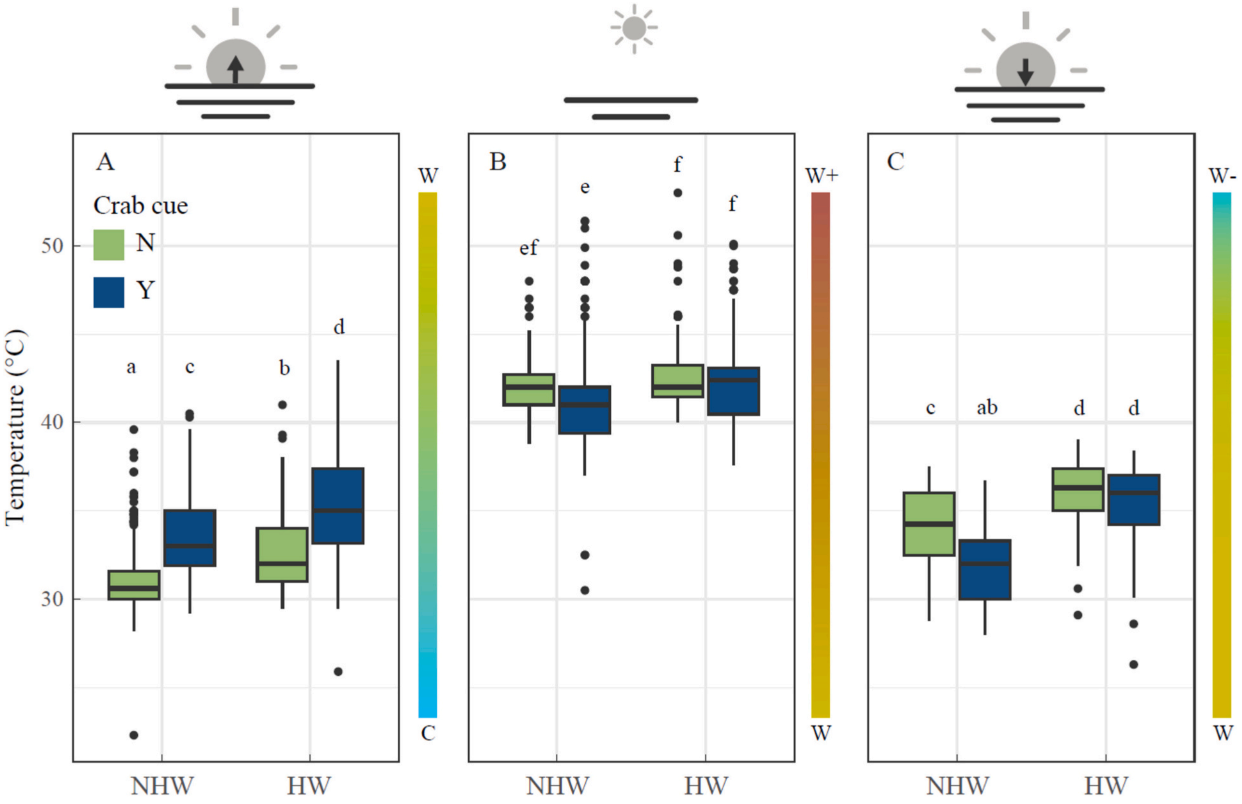

Fig. 6. Effects of heat wave and crab cue on *L. irrorata* body temperatures in the outdoor experiment. No crab cue (N) is the green, and crab cue (Y) is the blue boxes. Heat wave is represented by HW, non-heat wave by NHW. Panel A, B, and C represent the morning (7:00), afternoon (12:00), and evening surveys (19:00), respectively. Box plots represent the median, 25th and 75th percentiles. Whiskers are values within 1.5× interquartile, black dots are outliers. Letters on top of the box plots represent the significant differences based on post-hoc Tukey's all pair comparisons test (Table S7). Colored bars at the right of each panel depict the temperature gradient from the bottoms of the buckets to the tops in the chambers during each survey time. Blue is cool (C), blue to green is warmer (W-), yellow is warm (W), and red is hot (W+). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2020). Our results are consistent with previous studies on sessile intertidal (Harley, 2011) and terrestrial arthropod systems (Barton, 2011b) showing that increasing heat stress can reduce predator free space by reducing thermally suitable microhabitats. Intertidal snails live in thermally challenging environments and are known to be effective at using behaviors to avoid stressful temperatures (Chapperon and

Seuront, 2011; Hayford et al., 2018). Snails in our experiments effectively chose the cooler parts of the heat wave chambers and maintained temperatures well below their upper thermal limits of 51 ± 1 °C (Table 2, Fig. 5), while snails that were tethered and could not behaviorally thermoregulate experienced high mortality.

In the outdoor experiment, our results suggest that as temperatures increase, predator avoidance behavior was reduced and snails stayed closer to the water and within the feeding range of blue crabs. Together, this suggests that although heat wave events are not directly lethal for periwinkles because temperatures remained well below their upper thermal limits of 51 ± 2 °C, reduction in predator avoidance behavior occurred at lower temperatures, closer to 45 °C (Table 2, Fig. 4). At lower temperatures, antipredator response was a strong factor influencing snail climbing heights, and we found that the restriction of snail movements when a crab cue is present can directly increase the temperatures that snails experience. These findings demonstrate that non-consumptive interactions can have important influences on the physiological stress imposed by heat waves, and that it is essential to include species interactions to understand the temperatures and risks that organisms can experience as global climate change stressors increase (Pitt, 1999; Matassa and Trussell, 2015; Miller et al., 2014).

The use of controlled laboratory and outdoor experiments allowed us to compare the antipredator responses of snails under varying levels of temperature stress. The results of our experiments, as well as observations from the field, suggest that a local crab cue is one of the strongest factors influencing snail climbing behavior when temperature stress is minimal. In the laboratory experiment, antipredator response was fully expressed, where snails in the crab cue treatments remained at the highest points of the chambers (35 cm) in both heat wave and non-heat wave treatments. In contrast, in the outdoor experiment, antipredator response was dampened in all the survey times in heat wave treatments, and almost completely absent in the afternoon surveys when temperatures were highest. Although the outdoor temperatures were hotter in the afternoon, which could explain the drastic decrease in snail climbing heights in both the absence and presence of a crab cue, the morning and evening air temperatures were comparable to the laboratory experiment. Lower heights in the outdoor chambers in the crab cue treatment could be related to the fact that snails in the outdoor experiment experienced more variability in daily temperature in both heat wave (~Δ 15 °C daily) and non-heat wave treatments (~ Δ 10 °C) compared to the lab (<Δ 1 °C). Growing evidence suggests that temperature variability can be an increasing threat due to global change (Thompson et al., 2013) and can be particularly stressful for ectotherms (Terblanche et al., 2010). It is likely that snails in outdoor treatments were under greater physiological stress relative to those in the laboratory, and thus required greater movements downward to regulate body temperatures. The outdoor experiment likely better reflected the conditions snails can experience in the marsh. This has important implications for interpreting species responses under laboratory conditions, which can overestimate the temperatures that species can withstand when natural temperature variability is excluded from the experimental design.

Our study did not directly test how desiccation stress influences thermoregulatory behaviors. Although snail body temperature and desiccation are positively correlated, the rate of desiccation is also dependent on the distance to a water source, as well as shell postering and retracting behaviors (Iacarella and Helmuth, 2012; Iacarella and Helmuth, 2011). Previous work with L. *irrorata* has demonstrated that during low tides when marsh mud is exposed and hottest, snails that are closer to the mud during the day can have higher body temperatures but lower desiccation rates than those that are higher in the grasses (Iacarella and Helmuth, 2012). When the marsh is flooded, our data demonstrates that the temperature gradient is reversed, and snail body temperatures and presumably desiccation stress is lowest nearer the flooded mud. It is likely that snails remain near the water during times of high heat stress for avoiding heat and desiccation stress, both of which are higher towards the tops of grasses when the marsh is flooded.

Additionally, it would be important to test if there is local adaptation in periwinkle responses to heat stress and blue crab presence, and if less heat adapted populations function differently than more northern, cooler adapted populations, as demonstrated in other predator-prey systems (DeBlock et al., 2012; Rosenblatt et al., 2019). Previous work with other *Littoraria* species from the east coast of China has demonstrated strong inter- and intra-population variation in thermal sensitivity (Dong et al., 2017), indicating that adaptive differentiation in responses to heat stress can be present in this system. Similarly, previous work with L. *irrorata* from the Atlantic coast of North America has demonstrated that antipredator behaviors can vary significantly within and between populations (Salerno and Kamel, 2023; Carroll et al., 2018), where some snails can be bolder than others in the presence of blue crabs. Together, these studies suggest that adaptive differentiation for anti-predator and thermoregulatory behaviors are likely present along the wide range of L. *irrorata*.

One important consideration is the role of the grass architecture in influencing behavioral thermoregulation. Previous work has demonstrated that organisms can use the microrefugia of leaf blades to avoid heat stress (Pincebourde and Arthur Woods, 2012) making it possible that snails could have maintained lower body temperatures even in the presence of predators by moving to different sides of the grasses rather than changing their heights on the grasses altogether. While we did not test this prediction thoroughly, we incorporated grass blades into our outdoor experiment to provide an alternative to moving up and down the grass. The results do not support grass blade microrefugia as an alternative to making adjustment in climbing height. Snail body temperatures were higher when predators were present and similar to the laboratory results, only maintained lower temperatures by making changes in their height selection rather than exploiting microrefugia within the grass blades themselves.

Our findings have important implications for determining the negative effects of increasing temperatures on species persistence. Measures of critical thermal maximum (CT_{max}) and upper lethal limits (UTL) are often the measures used to determine if species will persist or perish in future conditions (Deutsch et al., 2008). In our study, we found that snails are effective at using behaviors to avoid temperatures that approach their CT_{max} (47 °C ± 2). However, our findings suggest that increased mortality could still occur due to increased exposure to predators. Behavioral thermoregulation is considered a possible defense against increasing temperatures, as we have demonstrated. But it may only preserve species if those behaviors do not also result in greater vulnerability to other risks, like local predators. Even though heat events as tested here are short in duration, short-term shifts in temperature can lead to dramatic shifts in a species' abundance due to shifts in the strength of species interactions (Sanford, 1999). Periwinkles are important grazers of detritus, algae, and fungus in marsh communities (Silliman and Newell, 2003). Reductions in their numbers can lead to shifts in community structure, which could favor proliferation of algae and biofilms which flourish in other ecosystems when natural grazers have been removed (Power et al., 1988; Lv et al., 2022). Because of the essential role that periwinkles play as the most abundant consumers of detritus and *Sporobolus* grass in the marsh, and the potential shift in microhabitat use that can occur during heat waves, this community module (Gilman et al., 2010) can be a potential ecological leverage point, defined by Sanford (1999) as key species interactions that are sensitive to abiotic change and whose alteration leads to large-scale shifts in community structure (Kroeker and Sanford, 2022; Sanford, 1999). However, more field experiments are required to directly evaluate the variation in predation rates that could occur during these events, and how decreased periwinkle abundance due to increased predation can alter the salt marsh community.

In summary, our results indicate that heat waves can decrease the predator free space for marsh periwinkles by forcing them closer to the water and into the range of subtidal predators. Although behavioral thermoregulation aids snails in avoiding stressful temperatures, it resulted in reduced predator avoidance behavior, suggesting a trade-off between heat stress and vulnerability to predators. When antipredator behavior was expressed, snails experienced higher body temperatures compared to when snails chose to thermoregulate, indicating the important and often overlooked role of local species influence on an organism's experience of a global climate change stressor. Heat waves are predicted to have devastating effects on natural communities by exposing organisms to extreme high temperatures. Our results demonstrate that local predator presence can alter an organism's exposure to high temperature stress during heat wave events, and that these events can lead to shifts in microhabitat use that pose new risks to mobile prey.

CRediT authorship contribution statement

Wissam A. Jawad: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana L. Salgado:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Morgan W. Kelly:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing interests.

Data availability

Data will be available in Github upon acceptance.

Acknowledgement

We are grateful to Ria Salway, Mark Yeats, Maram Khalaf, and Margaret Thomas for their help setting up the experiments. Jerome LaPeyre and Jim Cronin for allowing us to use lab and outdoor space, and Brian Roberts for supporting our work at LUMCON. For Michael Hellberg, Kyle Harms, Brian Roberts, Rujuta Vaidya and Abdul Ada for their intellectual input for the ideas considered in these experiments and revisions for the manuscript. We thank to the anonymous reviewers for their comments to improve this paper. MWK was supported by NSF IOS 2154283 and Sea Grant NA18OAR4170098 and ALS was supported by NSF DBE 2216631.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2024.152060.

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