



## Body temperature and desiccation constrain the activity of *Littoraria irrorata* within the *Spartina alterniflora* canopy

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### ABSTRACT

Behavioral patterns of motile ectotherms are often constrained by their microclimate conditions. For intertidal ectotherms, thermal and desiccation stresses are primary limiting factors. In this study, we developed and tested a steady-state heat budget model to calculate the duration of time that the salt marsh snail, *Littoraria irrorata* (Say), would maintain active behaviors (crawling or attached on stalks of marsh grass *Spartina alterniflora*) before switching to an inactive state (retracted and glued with a mucus holdfast on the stalks) due to desiccation. The snails' water loss tolerance limit was found to be  $43.6 \pm 16.0$  mg in a laboratory experiment using 5 temperature treatments (25–45 °C in 5 °C increments) with a vapor density (VD) deficit of  $\sim 15$  g/m<sup>3</sup> (saturated VD-air VD). We found that snails attached to *S. alterniflora* at lower heights in the canopy had higher body temperatures during daytime hours but lower water loss rates. Furthermore, we found that calculated activity times generally matched daily and seasonal patterns of life history behaviors reported in the literature. If tidal emersion began at night ( $\sim 20:00$ – $4:00$  h), calculated activity times were much higher than if emersion began in the daytime. The total monthly activity times for 2005–2010 were the highest in May, the lowest in July, and increased from July to September. Therefore, *L. irrorata*'s behaviors appear to be constrained by microclimate conditions within the *S. alterniflora* canopy as predicted by the heat budget model. The extent to which the snails' life history traits are controlled by environmental conditions will have important implications for their population dynamics as climate change progresses, and heat budget models can help to predict future changes in behavioral responses.

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### 1. Introduction

An ectotherm's behavioral responses are constrained by the mechanistic relationship between its physiological condition and its ability to exhibit activity within its microclimate (Grant and Porter, 1992). Many researchers have suggested connections between the behavior of ectotherms and the conditions of their environments (Bingham, 1972a; Gallagher and Reid, 1974; Kemp et al., 1990; McMahon, 1990). However, studies that mechanistically relate the physiological condition of organisms to their capacity to perform different behaviors have largely focused on terrestrial ectotherms such as reptiles (Bartlett and Gates, 1967; Christian et al., 1984; Grant, 1990; Grant and Dunham, 1990; Grant and Porter, 1992; Adolph and Porter, 1993). These studies have shown that the activity times of lizards generally correspond to the duration of time that they are able maintain an optimal body temperature (Christian et al., 1984) or the prevalence of microclimates within their home range that produce an optimal

body temperature (Grant, 1990). Furthermore, differences in life history traits such as reproduction, feeding behavior, and growth rates have been found to correspond to the variability in environmental conditions between habitats (Grant and Dunham, 1990). As has been exemplified with lizards, many of the indirect relationships that have previously been found between environmental conditions and the behaviors of ectotherms can be better elucidated by the mechanistic determination of environmental constraints on organisms.

Marine intertidal systems have long served as model ecosystems for examining the relationship between environmental stress and patterns of species distributions at local and geographic scales (eg. Barnes, 1958; Southward, 1958; Foster, 1971; Wolcott, 1973; Wetthey, 1983). For instance, a number of studies have focused on correlations between body temperatures and microhabitat selection for intertidal gastropods (Wolcott, 1973; Gómez-Cornejo, 1993; Williams and Morrill, 1995; Muñoz et al., 2005, 2008; Williams et al., 2005; Chapperon and Seuront, 2011; Judge et al., 2011). Gastropods have been found to reduce body temperatures through avoidance behaviors such as orienting their shell to minimize surface area exposed to the sun in the summer (Muñoz et al., 2005), by taking refuge on east facing rocks or in

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shaded crevices in the rocky intertidal (Williams and Morritt, 1995), or by hiding under tree roots in mangroves (Chapperon and Seuront, 2011). These and other studies have shown that there can be large differences in body temperatures depending on behavioral avoidance (Gómez-Cornejo, 1993; Williams and Morritt, 1995; Muñoz et al., 2005, 2008; Williams et al., 2005; Chapperon and Seuront, 2011; Judge et al., 2011; Miller and Denny, 2011), though it is acknowledged that microhabitat selection can also be influenced by biotic factors (Williams and Morritt, 1995; Muñoz et al., 2005, 2008; Chapperon and Seuront, 2011).

Heat budget modeling approaches have been used to mechanistically relate the body temperatures of ectothermic invertebrates (eg. Helmuth, 1998; Wethey, 2002; Denny and Harley, 2006; Szathmary et al., 2009) and algae (Bell, 1995) to environmental parameters. Miller and Denny (2011) have used a heat budget model to compare how shell morphology (color and smoothness) and behavior (foot retraction and lifting the shell off the substratum) affect body temperatures of five rocky intertidal *Littorina* species. Their model revealed body temperature differences of 1.5–2.3 °C between behaviors at the hottest times of day (Miller and Denny, 2011). However, such approaches have not been applied in salt marsh ecosystems, and seldom have they been extended to examine quantitatively the effects of an organism's microclimate on its behavior. Here we develop and test a heat budget model for the salt marsh snail *Littoraria irrorata* (Say), and use the model to examine the relationship between environment and behavioral responses as a function of desiccation stress.

The behavioral and physiological responses of the salt marsh snail, *L. irrorata*, to the environmental conditions of temperature (Bingham, 1972a; Shirley et al., 1978; McBride et al., 1989; Vaughn and Fisher, 1992), humidity (Bingham, 1972a; Shirley et al., 1978; Gómez-Cornejo, 1993) and tidal conditions (Vaughn and Fisher, 1992) have been previously studied, though it is not well understood how the snail's behaviors are dictated by its environment (but see Gómez-Cornejo, 1993). For instance, Bingham (1972a) found that *L. irrorata* moved down stalks of *Spartina alterniflora* when introduced to temperatures of 36 °C and higher, while McBride et al. (1989) found that the snails either moved up the stalks or were inactive when introduced to the same temperatures. High temperatures have also been found to instigate mating behavior (specifically 35 °C air temperature), though the behavior was only inducible during the summer months of May–July (Bingham, 1972b). Additionally, littorinids are known to behaviorally thermoregulate and avoid desiccation by retracting their mantle into the shell and secreting mucus to lift their shell off the substratum (Vermeij, 1971; Bingham, 1972c; McMahan, 1990; McMahan and Britton, 1991). However, the amount of time that snails may be constrained by this behavioral avoidance, and whether this may limit other behaviors such as feeding and reproduction, has not been elucidated. Relating mechanistic determinations of the snails' physiological conditions to their behavioral activity may improve the current understanding of how *L. irrorata* responds to its environment.

Peak reproductive activity (Baxter, 1983) and energy assimilation and use (Odum and Smalley, 1959; Shirley et al., 1978; Cammen et al., 1980; Kemp et al., 1990) of *L. irrorata* all roughly coincide during summer months. *L. irrorata* feeds on dead *S. alterniflora*, marsh sediment, and live *S. alterniflora*, in descending order of prevalence (Alexander, 1979; Silliman and Zieman, 2001). The total amount of nitrogen that the snail assimilates from *S. alterniflora* has been found to increase from May to September, with the peak in August and September (0.156 g N/m<sup>2</sup>), and decrease with the onset of winter months (Kemp et al., 1990). This observed increase in nitrogen assimilation did not coincide with shell growth, and is likely to have been used for the development of

gametes (Kemp et al., 1990), as mating occurs from May to September (Bingham, 1972b). *L. irrorata* lays planktonic eggs the high tide following copulation (Bingham, 1972b). The energy flow and content of *L. irrorata* is also highest in summer (energy flow ~0.95 Kcal/m<sup>2</sup>/day, Odum and Smalley, 1959; Cammen et al., 1980) and autumn months (ave. energy content ~12.1 Kcal/m<sup>2</sup>, Cammen et al., 1980). Similarly, respiration rates of *L. irrorata* have been found to increase from May to July and begin declining in August and September. Respiration rates were the highest in June (day: 822.2 ± 37.4, night: 1039.2 ± 75.8 µl O<sub>2</sub>/g dry wt/h) and July (day: 893.7 ± 63.3, night: 968.7 ± 70.2 µl O<sub>2</sub>/g dry wt/h) when the average monthly air temperature was 27 °C and 26 °C, respectively, and snails were held at 30 °C air temperature (Shirley et al., 1978).

While *L. irrorata*'s energetic and reproductive traits indicate it is most active in summer months (Shirley et al., 1978; Cammen et al., 1980; Baxter, 1983; Kemp et al., 1990), this time period may also lead to high thermal and desiccation stresses. The occurrence of active behaviors during potentially physiologically stressful conditions could lead to trade-offs between maintaining activity and avoiding stress that dictate the snail's activity times. The goal of this study was to mechanistically determine how microclimatic conditions within the *S. alterniflora* canopy affect *L. irrorata*'s physiological condition in relation to thermal and desiccation stresses, and how this may constrain its activity times. Specifically, we aimed to improve the current understanding of how *L. irrorata*'s behaviors are influenced by environmental conditions by developing a heat and mass budget model, and using it to calculate the body temperature, desiccation rate, and duration of activity of *L. irrorata* for different heights in the canopy, times of day, and summer months.

## 2. Methods

### 2.1. Microclimate conditions in the high marsh

Observations of microclimate conditions were recorded at a high marsh site 1.4 m above Mean Lower Low Water (MLLW) in the North-Inlet Winyah Bay National Estuarine Research Reserve (NERR) in Georgetown, South Carolina (33.335°N, 79.195°W). Microclimate parameters of solar radiation, relative humidity (RH), air temperature, *S. alterniflora* temperature, and soil temperature were measured from July 3rd–8th and on September 6th, 2010 during daytime low tides. Solar radiation was measured with a Licor pyranometer (Li-200 LI-COR Biosciences, Lincoln, NE), and RH was recorded with a HOBO logger (Onset Computer Corporation, Pocasset, MA), at heights of 10, 20, and 40 cm from the ground and within the *S. alterniflora* canopy (~30 cm high). Air temperature measurements were also made at 1 min intervals at the same stalk heights with type T thermocouples shaded by Styrofoam bowls with fans to circulate airflow. The thermocouples were connected to a Campbell data logger contained in a cooler near the site (Campbell Scientific Inc., Logan, UT). *S. alterniflora* and soil temperatures were measured with a type K thermocouple connected to an Omega (Omega Engineering, Inc., Stamford, CT) hand-held data logger at heights of 0, 5, 10, and 20 cm from the ground. These lower heights were chosen based on the observation that *L. irrorata* was most often found below 20 cm on the stalk. We also measured wind speed with a handheld Omega airflow meter at 10, 20, and 30 cm from the ground on 5 separate occasions. We recorded snail body temperatures and biomimic snail temperatures within a meter of the microclimate measurements to test the heat budget model predictions. The biomimics were made by filling empty snail shells of a similar width with silicone and inserting a thermocouple wire through a drilled hole in the shell (Yamane and Gilman, 2009).

The biomimic provided an operative temperature (Bakken, 1992) that was comparable to a live snail attached to a stalk. Twelve live snail temperatures were measured every 2 h during low tide with an Omega infrared sensor (OS36-3) held close to the shell. A preliminary lab experiment showed that snail body temperatures measured with thermocouples inserted through the shell were on average only  $1.0 \pm 1.2$  °C ( $\pm$ SD) different from the temperatures measured with the infrared sensor ( $n=3$  snails, 19 observations). The height of the snails on the stalks of *S. alterniflora* was also recorded, along with observations of active (attached to the stalk or crawling) or inactive behavior (retracted and glued to the stalk with a mucus holdfast). In addition, four biomimic snails were attached to a *S. alterniflora* stalk with a zip-tie at heights of 0 (on the soil), 5, 10, and 20 cm, with thermocouples connected to the Campbell data logger. The live snails were rarely found above 10 cm on the stalk during our time in the field, so this allowed us to obtain body temperatures at higher heights in the canopy.

## 2.2. Heat budget model

We used microclimate data recorded at a local weather station to derive microclimate conditions throughout the *S. alterniflora* canopy using a series of regressions. Solar radiation (converted from photosynthetically active radiation), air temperature, and RH data were obtained from the North-Inlet Winyah Bay National Estuarine Research Reserve (NERR) meteorological station (<http://cdmo.baruch.sc.edu>)  $\sim 1.5$  km away from the site. Linear regressions were used to calculate air, *S. alterniflora* and soil temperatures, and a 2nd-order polynomial regression was used to calculate RH. Regressions were chosen based on the best fit (highest  $r^2$ ). Solar radiation was calculated using an equation for light extinction in canopies (Morris, 1989) and a nonlinear regression to calculate the light extinction coefficient. Monthly canopy biomass measurements used in the equation were obtained from data collected for the North Inlet *Spartina* database (<http://links.baruch.sc.edu/Data/NISpartina/index.html>; Morris and Haskin, 1990). Verified tidal heights were obtained from the National Oceanic and Atmospheric Administration's North-Inlet station (Station 8662245, [www.tidesandcurrents.noaa.gov](http://www.tidesandcurrents.noaa.gov)), and were supplemented with tidal predictions (Clambank Creek station, <http://tbone.biol.sc.edu/tide>) when data were missing.

Mainstream wind speed ( $U_{inf}$ ) was compared to wind speed measured within the *S. alterniflora* canopy ( $U$ ) to determine the relationship between wind speed from a meteorological station and within the canopy. We obtained wind speed data at heights of 30, 40, and 50 m from a Santee Cooper wind tower measuring wind from North and South directions that was  $\sim 50$  m away from the site. The North-Inlet NERR meteorological station provided wind speed data 4.6 m from the ground, which was used for all model simulations. The North-Inlet station is located in a treeless expanse of the marsh, so there is no obstruction to the wind sensor. We ran a regression on wind speed measured across 4 day within the canopy (0.05, 0.1, 0.2, and 0.3 m from the ground), directly above the canopy (0.63, 0.96, and 1.3 m from the ground), and in mainstream flow (4.5, 30, 40, and 50 m from the ground), with the log of height as the independent variable. Wind speed at every height was normalized to the wind speed at the top of the canopy ( $U/U_h$ ; 0.3 m), and height was normalized to the height of the top of the canopy ( $z/z_h$ ; Huq et al., 2007). We calculated the 75% confidence intervals from this regression for heights of 5, 10, 15, and 20 cm in order to predict how much body temperatures and water loss rates would change due to variability in normalized wind speed. We then ran a regression to calculate wind speed within the canopy with  $z/z_h$  and  $U_{inf}$  at 4.5 m as the independent variables.

The equations used to calculate energy fluxes for the heat budget model are prevalent in the literature (Gates, 1980; Campbell and Norman, 1998; Helmuth, 1998; Denny and Harley, 2006) and Miller (2008) has modeled body temperatures for several rocky intertidal snails. The heat budget model used in this study is presented in the Supplementary Material, but in general the equations for energy flow ( $Q$ ) into and out of an ectothermic organism are

$$Q_{\text{stored}} = Q_{\text{short}} \pm Q_{\text{long}} \pm Q_{\text{conv}} \pm Q_{\text{cond}} - Q_{\text{evap}}$$

where  $Q_{\text{stored}}$  is the change in stored heat,  $Q_{\text{short}}$  is the energy from short-wave solar radiation,  $Q_{\text{long}}$  is the energy gained and lost through long wave radiation,  $Q_{\text{conv}}$  is the heat flux via convection,  $Q_{\text{cond}}$  is the heat flux via conduction, and  $Q_{\text{evap}}$  is the heat lost through evaporative cooling (see Supplementary Materials S1 for specific equations). For the steady-state equation used here, the organism is assumed to be at thermal equilibrium at each fixed interval of 15 min, so  $Q_{\text{stored}}$  is set to zero (Denny and Harley, 2006). The calculated body temperature of the organism and the temperatures of its surrounding environment determine the direction of energy flow.

We measured snail shell areas specific to each heat flux by taking pictures of 10 *L. irrorata* and calculating average areas using ImageJ (<http://rsbweb.nih.gov/ij/>; see Supplementary Materials Table 1 for parameter values). The area of conduction included the shell area, which was measured by pressing retracted snails onto an inkpad and leaving their mark on paper (Miller, 2008), and the tissue area of the foot, which was analyzed separately in ImageJ. The mass transfer coefficient was measured by placing a wet sponge inside of an empty shell with the same area protruding as the tissue exposed on an "attached" snail. We then placed the snail in a wind tunnel mid-stream and used a Kurz anemometer (441 M Kurz Instruments, Inc., Monterey, CA) to measure wind speed at the same distance from the sides of the wind tunnel. RH and air temperature were recorded inside the wind tunnel with a Vaisala HMT333 instrument (Vaisala, Helsinki, Finland). The shell with sponge was measured before and after 20 min under wind speeds of 0.03, 0.8, 1.5, and 3 m/s, replicated three times each. A linear regression was used to calculate the mass transfer coefficient based on wind speed. Heat transfer coefficients were obtained from Nusselt (Nu)–Reynolds (Re) regressions for a brass model of *L. irrorata* with a shell area of 492 mm<sup>2</sup> (Gómez-Cornejo, 1993).

The heat budget model was compared to body temperatures of 10 snails attached to stalks and 12 biomimics to test for accuracy. When predicting biomimic temperatures, evaporative cooling is not a component of the heat budget model equations, while it is for live snails. We selected replicates from a distribution of heights in the canopy and days of measurements (5 day total). The snails and biomimics used for comparison represented 8 replicates at 4–6 cm, 5 at 8–10 cm, 5 at 20 cm, and 5 at 30 cm from the ground. We then ran the model to simulate changes in body temperatures and water loss rates of attached snails at heights of 5, 10, 15, and 20 cm on July 3rd, 2010 from 6:00–18:00 h with 15 min intervals.

## 2.3. Duration of activity

We calculated how long the snails were likely to remain active before switching to the glued behavior to avoid further water loss. A preliminary experiment was run to test behavior and weight loss responses at different temperatures. Temperature levels were set at 25–45 °C in 5° increments (25, 30, 35, 40, 45 °C) using ceramic heat emitters ranging from 60–250 W. The temperature values were based on the temperatures of a biomimic snail placed inside of each container. Humidity levels were set at a conservative vapor density (VD) deficit (saturated VD–air VD) of  $\sim 15$  g/m<sup>3</sup>,

while VD deficits in the high marsh can reach  $\sim 30 \text{ g/m}^3$  (J. Iacarella personal observation). We measured humidity with HIH 4010 humidity sensors (Honeywell International Inc., Morristown, NJ) attached to the tops of each container and controlled it with water vaporizers or silica gel, depending on the desired air VD. Twenty *L. irrorata*, collected from the high marsh site the previous day, were blotted dry and weighed before being placed into the containers. After 1.5, 3, 6, and 9 h, the behavior of five designated snails was noted and they were removed from the containers to be reweighed. Behaviors were classified as “attached”, foot stuck to surface, “gaping”, mantle retracted with an opening between the operculum and the shell aperture (McMahon and Britton, 1991), “retracted”, operculum sealed, and “glued”, retracted with mucus excreted to attach the shell to the surface (Vermeij, 1971). These experiments were repeated three times. When we observed the mode of behavior from the three replicates combined had switched from “attached” to “retracted” or “glued” between successive measurement intervals in a treatment, we assumed the behavioral change was due to water loss avoidance. It is unlikely that the change in behavior was due to thermal stress avoidance because there were only two cases of mortality due to high body temperatures and both were indicated by the “gaping” behavior. We then calculated the snails’ water loss tolerance as the amount of water the snails had lost at the interval when they were observed to be “attached” and directly before the interval when they switched to “retracted” or “glued”.

We used this water loss tolerance and predictions of water loss rates on July 3rd to determine the duration of activity the snails would exhibit given their height in the canopy. We compared the predicted duration of activity to behavioral observations made on that day to verify the accuracy of the model and experimental calculations. We also modeled how the duration of activity would change if the tide had started at 0:00, 4:00, 8:00, 12:00, 16:00, or 20:00 h instead of the observed time at 6:00 h, or if the snails were positioned at 5, 10, 15, or 20 cm in the canopy. We made these calculations using meteorological data (with 15 min intervals) on a monthly basis (the 3rd of each month) for May–September, 2009–2010. We used the 3rd of each month so that we could compare our model predictions to our observations in the field on July 3rd, 2010 while also obtaining a spread in climatic conditions. The effect of tidal emersion time and height

in the canopy on activity time was tested with a two-way analysis of variance (ANOVA) and Bonferroni post-hoc tests. We also analyzed how frequently tidal emersion began at the same 4 h intervals with a one-way ANOVA, using tidal data for the site from May 1st–September 30th, 2003–2010.

We then calculated the total amount of time snails at 5 cm in the canopy could be active before retracting to avoid water loss for each month from May–September, 2005–2010. A multivariate analysis of variance (MANOVA) and Bonferroni post-hoc tests were used to analyze the effect of summer months on the activity time of the snails, the number of times the site was submerged, and average air temperature at 5 cm. Furthermore, we ran a linear regression with monthly activity time as the dependent variable to determine how much variability was due to monthly values of average air temperature, number of submerging tides, and average solar radiation.

### 3. Results

By using regressions to calculate microclimate parameters within the *S. alterniflora* canopy (Supplementary Materials Table S2), and then using these data as inputs to a heat budget model, we were able to predict body temperatures of *L. irrorata* and biomimics attached to stalks with an average accuracy of  $1.97 \pm 1.21 \text{ }^\circ\text{C}$  ( $\pm$  SD, absolute difference between body temperature measurements and model predictions,  $n=22$ ). The average difference between biomimic and predicted body temperatures was  $1.53 \pm 0.85 \text{ }^\circ\text{C}$  ( $n=12$ ), and between live snail and predicted body temperatures was  $2.51 \pm 1.40 \text{ }^\circ\text{C}$  ( $n=10$ ). The minimum measured body temperature of the live snails we compared to the model was  $27 \text{ }^\circ\text{C}$ , and the maximum temperature was  $37 \text{ }^\circ\text{C}$ .

On July 3rd, 2010, the tide receded at 6:00 h and did not submerge the high marsh site for the rest of the day. The emersion period lasted until 17:30 h on July 7th, and during this time, none of the snails observed climbed above 5 cm height on the stalks ( $n=12$ ). Similarly to field measurements, predicted body temperatures were hotter lower in the *S. alterniflora* canopy during the day (Fig. 1 and Supplementary Figure S1). The maximum and minimum body temperatures predicted for July 3rd were  $29.9 \text{ }^\circ\text{C}$  and  $17.8 \text{ }^\circ\text{C}$ , both for snails at 10 cm. At 6:00 h, body temperatures at 5 and 10 cm were predicted to be an average of

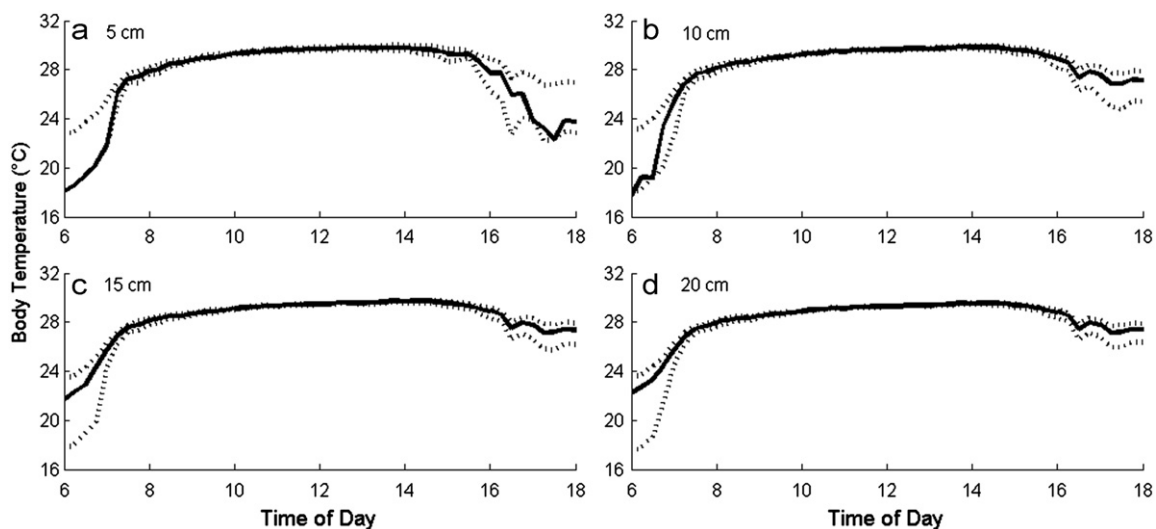


Fig. 1. Predicted body temperatures (solid lines) and 75% confidence intervals (dotted lines) produced by a steady-state heat budget model for conditions on July 3rd, 2010 in a high marsh site (1.4 m above Mean Lower Low Water) in Georgetown, SC. Body temperatures were modeled for *Littoraria irrorata* in the attached position on stalks of *Spartina alterniflora*. Confidence intervals represent variation in wind speed.

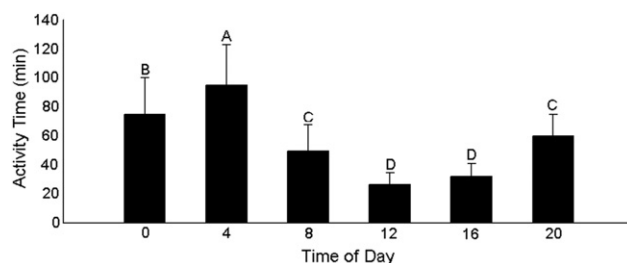
4 °C cooler than body temperatures at 15 and 20 cm. Body temperatures at each height became more similar during midday, and the lower heights became hotter than higher heights. For instance, at 12:00 h, snails at 5 cm were predicted to be 0.4 °C hotter than snails at 20 cm. From 14:00 h to 17:00 h, body temperatures at 5 cm were predicted to drop by 6.0 °C whereas at the other heights, temperatures dropped by an average of 1.9 °C. Confidence intervals (25% and 75%), showing changes in predicted body temperatures due to variation in normalized wind speed, deviated from the base case predicted body temperatures the most in the morning (~6:00–8:00 h) and evening (~16:00–18:00 h; Fig. 1). The maximum body temperatures predicted with the wind speed regression and lower and upper confidence intervals were 29.8, 29.7, and 30.0 °C, respectively. The minimum predicted body temperatures were 18.0, 18.0, and 22.6 °C, respectively. Differences in predicted body temperatures between upper and lower confidence intervals were the highest at 5 cm ( $1.49 \pm 1.65$  °C) and the lowest at 20 cm ( $0.89 \pm 1.48$  °C).

Water loss rates showed a more consistent trend between heights, with the highest predicted water loss rates occurring higher in the canopy (Fig. 2 and Supplementary Figure S2). Water loss was negative, i.e. water was gained, until 7:15 h at 5 cm, whereas water loss was always positive at 20 cm. The maximum predicted water loss rate was 1.2 mg/min at 20 cm, which was 33% higher than the maximum loss at 5 cm. The highest water loss rates occurred from ~10:00–16:00 h and were relatively constant, with the highest standard deviation of 0.06 mg/min at 5 cm. Confidence intervals (25% and 75%) showing changes in predicted water loss rates due to variation in normalized wind speed deviated from the base case water loss rates more at higher heights in the canopy (Fig. 2). The average difference ( $\pm$  SD) in water loss rates between upper and lower confidence intervals was  $0.2 \pm 0.1$  mg/min at 5 cm,  $0.3 \pm 0.0$  mg/min at 10 cm,  $0.4 \pm 0.1$  mg/min at 15 cm, and  $0.4 \pm 0.2$  mg/min at 20 cm.

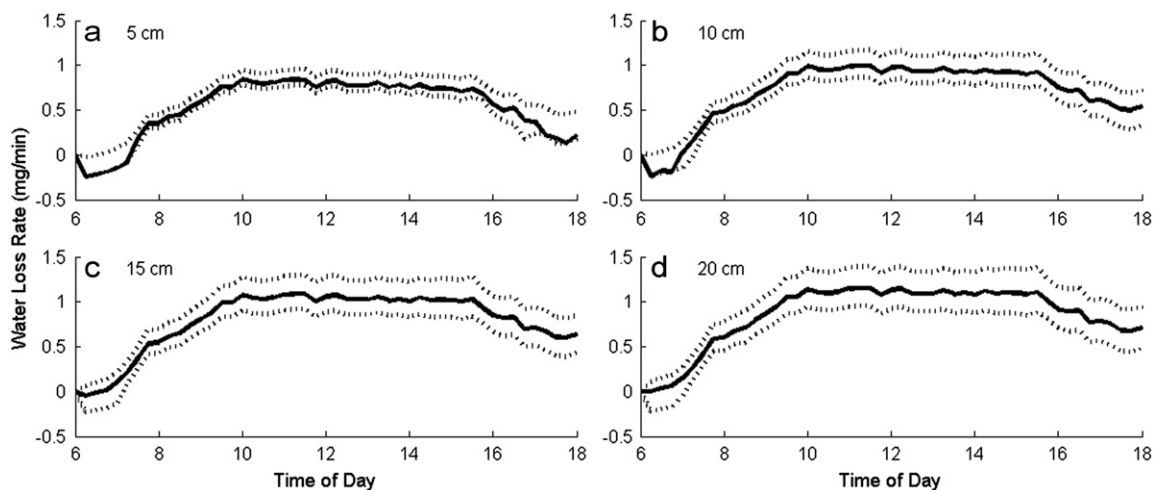
In the laboratory experiments used to determine the duration of time snails could remain active (“attached” or “crawling”) before retracting into the mantle to avoid water loss, we found a switch in the mode of active to inactive behaviors in the 40 °C and 45 °C treatments after 1.5 h. The average amount of water the snails had lost after 1.5 h of exposure in these treatments was  $43.6 \pm 16.0$  mg ( $n=30$ ). In the other temperature treatments, the snails remained inactive throughout the 9 h exposure, so these were not used in water loss tolerance calculations. Using water loss rates from the model, we predicted that with the tide

receding at 6:00 h on July 3rd, 2010, snails at 5 cm would remain active for 195 min, or until 9:30 h. We observed in the field that 10 out of 11 snails were active at ~5 cm on the stalks from 6:00–8:00 h. At 10:00 h, only 5 out of 11 snails were still active, and the other 6 were glued to the stalks. From 12:00 h on July 3rd to 17:30 on July 7th, when the tide reached the site again, 301 out of 312 behavioral observations ( $n=12$ ) were of inactive snails. As we calculated the water loss tolerance at the time interval before observing the switch from active to inactive behaviors in the lab experiment, the model was able to predict the point at which the snails began transitioning to avoid water loss in the field.

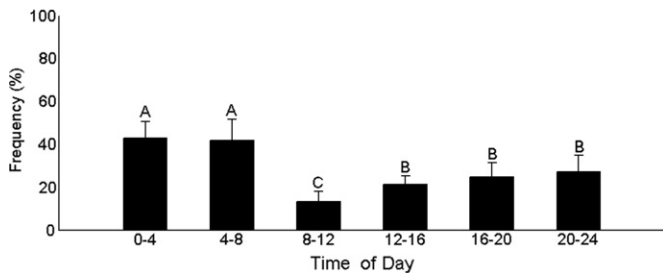
The two factors of tidal emersion time and height in the canopy did not have an interactive effect on activity time ( $F_{15,240}=0.198$ ,  $p=1.0$ ), allowing the use of post-hoc tests to determine differences between factor levels. Activity time was affected by the time the tide went out ( $F_{5,240}=95.659$ ,  $p < 0.001$ ) but not by height in the canopy ( $F_{3,240}=1.753$ ,  $p=0.157$ ). Activity time was the highest if the tide went out at 4:00 h ( $96 \pm 24$  min), and the second-highest if the tide went out at 0:00 h ( $77 \pm 26$  min, Fig. 3,  $p < 0.01$ ). Activity time was the lowest if the tide went out at 12:00 h or 16:00 h ( $p < 0.01$ ), with average times of  $25 \pm 9$  min and  $31 \pm 8$  min, respectively. Between May and September, the frequency of tidal emersion at the site differed depending on the time of day (Fig. 4,  $F_{5,48}=64.43$ ,  $p < 0.001$ ). Tidal emersion periods most often began from 0:00–8:00 h ( $48.4 \pm 5.3\%$  from 0:00–4:00 h and  $46.4 \pm 3.9\%$  from 4:00–8:00 h,  $p < 0.05$ ). The least frequent time for tidal emersion was



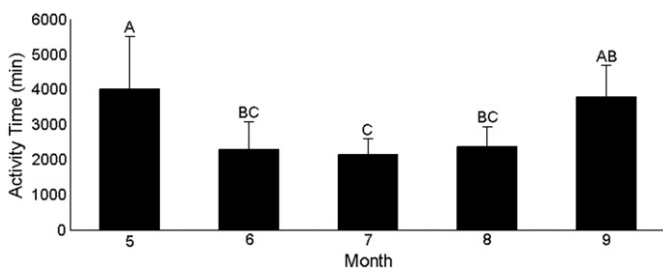
**Fig. 3.** Predictions for the amount of time that *Littoraria irrorata* maintains the attached, or active, behavior as a function of the time of day that low tide begins (0:00, 4:00, 8:00, 12:00, 16:00, 20:00 h). Simulations are for conditions on the 3rd of May–September, 2009–2010 in a high marsh site (1.4 m above Mean Lower Low Water) in Georgetown, SC. Data are averages  $\pm$  1SD, and letters indicate significant differences in activity times.



**Fig. 2.** Water loss rates calculated for *Littoraria irrorata* from an evaporative cooling equation based on body temperatures predicted using a heat budget model. Predictions are for conditions on July 3rd, 2010 in a high marsh site (1.4 m above Mean Lower Low Water) in Georgetown, SC. Confidence intervals represent variation in wind speed.



**Fig. 4.** Frequency of tidal emersion periods beginning from 0:00–4:00, 4:00–8:00, 8:00–12:00, 12:00–16:00, 16:00–20:00, and 20:00–24:00 h at a high marsh site (1.4 m above Mean Lower Low Water) in Georgetown, SC. Data are from May 1st–September 30th, 2003–2010. Data are averages +1SD, and letters indicate significant differences in frequencies.



**Fig. 5.** Total activity time for *Littoraria irrorata* attached to stalks of *Spartina alterniflora* at 5 cm from May–September. Data are from 2005–2010 for a high marsh site (1.4 m above Mean Lower Low Water) in Georgetown, SC. Data are averages +1SD, and letters indicate significant differences in activity times.

8:00–12:00 h at  $14.0 \pm 4.8\%$  ( $p < 0.05$ ). From noon to midnight, emersion frequencies were not significantly different ( $p > 0.05$ ) and ranged from  $23.9 \pm 6.2\%$  to  $29.4 \pm 4.4\%$ , respectively.

Activity times at 5 cm ( $F_{4,30}=5.792$ ), average air temperatures at 5 cm ( $F_{4,30}=44.687$ ), and number of submerging tides ( $F_{4,30}=6.498$ ) varied between summer months ( $p \leq 0.002$ ). May ( $4010 \pm 1498$  min) had the highest activity times, while September ( $3783 \pm 898$  min) had similar activity times to all months but was higher than July (Fig. 5,  $p < 0.05$ ). Activity times for June ( $2285 \pm 791$  min), July ( $2140 \pm 461$  min), and August ( $2378 \pm 551$ ) were not significantly different ( $p > 0.05$ ). Average air temperatures at 5 cm were the lowest in May ( $28.6 \pm 0.9$  °C), followed by September ( $31.0 \pm 0.7$  °C, Supplementary Materials Fig. 3). July ( $32.9 \pm 0.5$  °C) and August ( $33.2 \pm 0.5$  °C) had higher air temperatures than all summer months ( $p < 0.05$ ), except for June ( $32.1 \pm 0.7$  °C,  $p > 0.05$ ). The number of times the site was submerged from May–September was the highest in September ( $49 \pm 4$ ,  $p < 0.05$ , Supplementary Materials Fig. 4). May ( $35 \pm 6$ ), June ( $33 \pm 9$ ), and July ( $33 \pm 5$ ) had the least number of submerging tides, while August was similar to all months ( $39 \pm 8$ ,  $p > 0.05$ ). The linear regression indicated that 85% ( $r^2$ ) of the variation in activity time was explained by average air temperatures at 5 cm, number of submerging tides each month, and average solar radiation at 5 cm (activity time =  $-5.3 \times$  solar radiation  $-505.8 \times$  air temperature  $+12.2 \times$  # of submerging tides  $+2021$ ;  $F_{3,29}=49.205$ ,  $p < 0.001$ ).

#### 4. Discussion

As has been demonstrated with lizards (Grant, 1990; Grant and Dunham, 1990; Grant and Porter, 1992), the activity times of *L. irrorata* can help to explain the patterns found in its life history phenotypes. By mechanistically determining the body temperature and desiccation rates of *L. irrorata* in the high marsh, we were able to make predictions for its activity times that corresponded

with what we observed in the field and with patterns of breeding (Baxter, 1983) and energy uptake (Odum and Smalley, 1959; Cammen et al., 1980; Kemp et al., 1990) reported in the literature. Furthermore, the model revealed how microclimate variation in the *S. alterniflora* canopy and time of tidal emersion affected the snails physiologically and behaviorally. This study confirms that the use of mechanistic thermal and desiccation models provides a quantitative understanding of ectotherms' behaviors that can help to explain patterns and observations made in the field.

The model predictions that midday body temperatures were higher and desiccation rates lower closer to the ground were consistent with field measurements of body temperatures and locations of the snails. During the emersion period from July 3rd–7th, 2010, *L. irrorata* was always found at 5 cm or lower on the stalks of *S. alterniflora* where its body temperature was hotter than it would have been at higher heights, but where it was also losing less water. Though a few reached potentially lethal temperatures ( $44\text{--}46$  °C; Bingham, 1972c; Gómez-Cornejo, 1993) on July 7th, the observation that the snails remained at low heights in the canopy indicates that avoiding desiccation during the emersion period may be more important than avoiding high body temperatures. Furthermore, though the snails' high body temperatures created a higher vapor density (VD) deficit at lower heights, which increases desiccation, the model showed that the higher mass transfer coefficients at higher heights due to increased wind speed led to the highest levels of desiccation. While Bingham (1972a) and McBride et al. (1989) were able to artificially stimulate *L. irrorata* to move up or down on stalks of *S. alterniflora* by introducing a heat source, they did not take desiccation into account and therefore may not have obtained a complete picture of what determines the snail's position in the canopy.

The model predictions were found to be the most sensitive to variation in wind speed when convection played a larger role in dictating body temperatures. For instance, in the morning hours of July 3rd, air temperatures were several degrees higher than body temperatures. The 25% confidence intervals for wind speed variation had no wind input at all heights in the canopy until 6:30 h, whereas the 75% confidence intervals had wind input at all heights. Hence, convection into the snails was much higher in the morning for 75% confidence interval predictions. Similarly to *L. irrorata*, Denny and Harley (2006) noted that limpet body temperatures were very sensitive to wind speeds close to 0 m/s. Our model did not capture air flow due to free convection, which may have led to an underestimation of body temperatures for the lower confidence intervals and at low heights in the canopy, particularly in morning and evening hours when wind speeds were very low (Denny and Harley, 2006). Helmuth et al. (2011) recently showed that convection was sufficient to counteract fairly large increases in air temperature, pointing to the importance of this heat exchange mechanism for intertidal ectotherms. Since wind speed controlled evaporative cooling and water loss rates in our model, the difference between confidence intervals for water loss rates was consistent throughout the day.

The model did not predict differences in activity times when *L. irrorata* is attached at different heights in the canopy. However, this is likely due to the large amount of variation in water loss between months and times of day. The model predicted a trend of decreasing activity times with height in the canopy, particularly at 0:00, 4:00, and 20:00 h. Though these trends are not significant, they are consistent with field observations. Gómez-Cornejo (1993) observed over 14,000 snails at a site within of 250 m of ours and found that the snails were most frequently attached on stalks at 1–3 cm, where they were also most often in an active state. Furthermore, he found that snails were glued more often than active at heights above 3 cm. The calculated activity times

and water loss rates help explain these observations by showing that activity times may be more limited higher in the canopy due to desiccation avoidance.

The duration of time that *L. irrorata* could be active was much higher if the tide went out at night (particularly at 4:00 h). *L. irrorata* has been found to have higher respiration rates (Shirley et al., 1978), higher occurrences of activity (Gómez-Cornejo, 1993), and higher feeding rates at night (Graca et al., 2000). The predictions that snails are much more constrained by water loss during a daytime low tide than a nighttime low tide support the findings that they are more active and able to feed at night. However, the ability of *L. irrorata* to be active for long periods at night and stay within its desiccation tolerance is contingent on emersion beginning after sundown or when its body temperatures are low. Since emersion at the site most frequently begins from 0:00–8:00 h during summer months, *L. irrorata* should be able to be more active at night, as the model predicts. This has been confirmed by observations of increased nighttime activity at a nearby site (Gómez-Cornejo, 1993).

The total amount of time *L. irrorata* can maintain activity during the summer months follows similar trends to what has been measured and observed in its energy consumption (Cammen et al., 1980; Kemp et al., 1990) and reproduction (Bingham, 1972b; Baxter, 1983). These findings indicate that *L. irrorata*'s life history traits of energy uptake and output may be partially dictated by microclimate conditions. Specifically, monthly averages of air temperature and solar radiation at the height of the snails, and the number of submerging tides, account for most of the constraint to their calculated monthly activity times. Pinpointing the environmental parameters that have the most impact on *L. irrorata*'s body temperatures and activity times will be useful for predicting how it will cope with changing climate conditions (IPCC, 2007). Climate change scenarios can be applied to heat budget models to provide an understanding of how close ectotherms will be to their thermal tolerance limits (Denny and Harley, 2006; Gilman et al., 2006) and how constrained their activity will be due to desiccation. As the current model reveals, further limitations to activity times of *L. irrorata* may have an effect on its life history patterns.

The largest discrepancy between the snails' behavioral patterns and predicted activity times was in May. During this month, total duration of activity was calculated by our model to be one of the longest during the summer, along with September. In contrast, respiration (Shirley et al., 1978) and nitrogen assimilation (Kemp et al., 1990) measurements reported in the literature reflected increasing activity levels from May onward. However, *L. irrorata* energy flow measured in the same marsh as nitrogen assimilation rates (Kemp et al., 1990) showed consistently high levels of energy flow from May to August (Odum and Smalley, 1959). As we had observed with monthly activity time calculations, trends between the summer months were not the same each year, though we found significant differences between the averaged months. Therefore, studies quantifying energy uptake and flow within the time scale of a year may be highlighting short-term trends and not more general patterns.

Activity times of ectotherms mechanistically relate microhabitat conditions to the life history phenotypes that influence their population dynamics. Ectotherms have to partition their available activity time into resource uptake and output behaviors that affect their fecundity and survival (Grant and Porter, 1992). While abiotic conditions limit activity when outside of the fundamental niche of an organism (Hutchinson, 1957; Porter and Gates, 1969; Porter et al., 1973), realized niche parameters such as resource availability and predation can also constrain activity and affect population dynamics (Grant and Porter, 1992). Therefore, a more complete understanding of the constraints on *L. irrorata*'s life

history behaviors would need to incorporate biotic interactions. For instance, *L. irrorata* is known to migrate up stalks of *S. alterniflora* with tidal inundation to avoid crab predation (West and Williams, 1986; Vaughn and Fisher, 1992). Vertical migration would introduce the snails to a different microclimate and could lead to different energetic behaviors. Activity time calculations based solely on abiotic parameters provide a physiological framework in which ectotherms can be active, while biotic parameters may provide a more fine-tuned understanding of how organisms behave within their activity times.

## 5. Conclusions

*L. irrorata*'s daily and seasonal behavioral patterns are reflected in its ability to be active within its desiccation tolerance limit. The heat budget model and water loss calculations accurately predicted our field observations, as well as those of others (Gómez-Cornejo, 1993; Graca et al., 2000). Furthermore, the activity time predictions corresponded with observations that *L. irrorata* is more active at night (Shirley et al., 1978; Gómez-Cornejo, 1993; Graca et al., 2000) and that it feeds more as the summer progresses (Cammen et al., 1980; Kemp et al., 1990), in concordance with its reproductive behaviors (Bingham, 1972b; Baxter, 1983). This strongly suggests that *L. irrorata*'s behavioral patterns are controlled in large part by the microclimate conditions within the *S. alterniflora* canopy and by the snail's ability to tolerate desiccation. The results of this study help to explain *L. irrorata*'s behavioral patterns in a quantitative manner that has not yet been achieved with observational approaches. Furthermore, the heat budget model enables quantitative predictions to be made about the future health of salt marsh snail populations.

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## Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtherbio.2011.10.003.

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