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The importance of behavior and morphological traits for controlling body temperature in littorinid snails

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Summary

For organisms living in the intertidal zone, temperature is an important selective agent that can shape species distributions and drive phenotypic variation among populations. Littorinid snails, which occupy the upper limits of rocky shores and estuaries worldwide, often experience extreme high temperatures and prolonged aerial emersion during low tides, yet their robust physiology—coupled with morphological and behavioral traits—permits these gastropods to persist and exert strong grazing control over algal communities. We use a mechanistic heat-budget model to compare the effects of behavioral and morphological traits on the body temperatures of five species of littorinid snails under natural weather conditions. Model predictions and field experiments indicate that, for all five species, the relative contribution of shell color or sculpturing to temperature regulation is small, on the order of 0.2 – 2 °C, while behavioral choices such as removing the foot from the substratum or reorienting the shell can lower body temperatures by 2 – 4 °C on average. Temperatures in central California rarely exceeded the thermal tolerance limits of the local littorinid species, but at sites where snails are regularly exposed to extreme high temperatures, the functional significance of the tested traits may be important. The mechanistic approach used here provides the ability to gauge the importance of behavioral and morphological traits for controlling body temperature as species approach their physiological thresholds.

Introduction

Within the narrow band of habitat between the low and high tidemarks on seashores, the distributions of individual species and the structure of ecological communities are dictated by a variety of biotic and abiotic factors (Connell, 1961; Lewis, 1964; Connell, 1972; Paine, 1974; Dayton, 1975; Menge and Branch, 2001). Biological interactions such as predation, competition, and facilitation play out on a background of constantly-shifting environmental conditions driven primarily by the action of tides and waves (Stephenson and Stephenson, 1972; Denny, 2006; Denny *et al.*, 2009). Changes in important environmental parameters such as light, temperature, and wave action can alter the suitability of the habitat for a given species at both small and large spatial scales (Wethey, 2002; Denny *et al.*, 2004; Harley, 2008). The capacity of organisms to persist under these varied environmental conditions is mediated by the interaction of a suite of behavioral, morphological, and physiological traits.

Snails in the family Littorinidae are important herbivores in mid- and high-shore intertidal communities around the world (McQuaid, 1996a, b; Reid, 1996), and often exert control over macroalgal and microalgal communities (Castenholz, 1961; Hawkins and Hartnoll, 1983; Norton *et al.*, 1990; Hidalgo *et al.*, 2008). These snails can experience large swings in temperature over the course of a single tide cycle and must often contend with multi-day aerial emersion periods when they live above the high tide line (Vermeij, 1972; Cleland and McMahon, 1986; McMahon, 1990; Judge *et al.*, 2009; Marshall *et al.*, 2010).

The importance of morphological and behavioral traits for managing body temperature has been demonstrated in many terrestrial ectotherms such as insects, reptiles, and gastropods (Schmidt-Nielsen *et al.*, 1971; Porter *et al.*, 1973; Stevenson, 1985; Huey, 1991; Kingsolver, 1996; Kearney *et al.*, 2009), and similar roles for morphological and behavioral variation have been hypothesized for littorinid snails and other intertidal gastropods. Variation in shell color across geographic scales has been hypothesized to be a response to climatic conditions, with dark-colored morphs inhabiting cooler sites, while light-colored morphs dominate warmer areas (Markel, 1971; Vermeij, 1971b; Etter, 1988; McQuaid and Scherman, 1988; McQuaid, 1992; Sergievsky, 1992; McQuaid, 1996a; Phifer-Rixey *et al.*, 2008), as has been argued for terrestrial gastropods (Jones, 1973; Heath, 1975; Heller, 1981). Shell shapes can vary from globular to high-spired, which affects heating by absorption of shortwave radiation from the sun and determines the internal volume of fluid that can be stored in the shell to withstand desiccation (Vermeij, 1972, 1973; Chapman, 1995). In addition, the outer surface of the shell may be smooth, or it may be sculptured, with ribs, ridges, and nodules that increase the surface area of the shell (potentially increasing convective heat flux) without a concomitant increase in the projected area of the shell that captures heat energy from the sun (Vermeij, 1973; Britton, 1995). While these morphological traits may impact body temperature, there are additional selective forces such as predation and wave action that may drive the variation in shell morphology (Struhsaker, 1968; Johannesson, 1986; Seeley, 1986; Johannesson *et al.*, 1993; Trussell, 1997b, 2002).

Mobile intertidal grazers often seek refuge from hot conditions in crevices or under algal canopies. In contrast, littorinids—which often exploit food resources on open rock faces where thermal refuges are absent—may employ additional behavioral strategies to avoid stressful high temperatures. As with terrestrial gastropods that must withstand prolonged unfavorable weather conditions (Stearns, 1877; Machin, 1967; Schmidt-Nielsen *et al.*, 1972), littorinid snails commonly remove the foot from the substratum and anchor the shell using a dried mucus holdfast (Wilson, 1929; Newell, 1958; Vermeij, 1971b; Garrity, 1984). For a gastropod sitting on a surface warmed by the sun, the large surface area of the foot allows for substantial conductive heat exchange between the foot and substratum (Vermeij, 1971a; Denny and Harley, 2006). The ability to remove the foot from the substratum reduces this conductive heat flux, keeping a snail several degrees cooler than the substratum (Schmidt-Nielsen *et al.*, 1972; Vermeij, 1973). Many littorinid snails can also re-orient the shell, lifting the aperture away from the substratum, leaving only the outer lip of the shell aperture attached to the substratum with dried mucus (Fig. 1A, B) (Denny, 1984). Thusly, reorienting the shell alters conductive and convective heat flux, and may change the projected area absorbing heat from the sun.

The relative importance of these morphological and behavioral characteristics for controlling body temperature can be estimated using a mechanistic heat-budget model (Porter and Gates, 1969; Gates, 1980; O'Connor and Spotila, 1992; Porter and Kearney, 2009), combining physical parameters of the organism with environmental data to estimate body temperature through time. From a high-resolution decade-long weather data set from Hopkins Marine Station, Pacific Grove, California (HMS), we create historical reconstructions of snail body temperatures to examine the effects of these morphological and behavioral changes, particularly during high-temperature aerial exposures. Specifically, we test four hypotheses: 1) light colored shells remain cooler than dark shells, 2) shells with surface ornamentation remain cooler than smooth shells, 3) removing the foot from the substratum lowers body temperature, and 4) reorienting the shell up off the substratum lowers body temperature. We compare the relative effectiveness of each trait for controlling body temperature during hot aerial exposures, and their effects on body temperature across the range of environmental temperatures experienced in the field.

Materials and Methods

To facilitate the manipulation of individual morphological and behavioral parameters, we developed heat-budget models for five species of littorinid snails (Figure 1C). The snails included four of the five common rocky intertidal *Littorina* species from the temperate western North American coastline: *Littorina keenae* Rosewater, *L. scutulata* Gould (both collected at HMS), *L. plena* Gould (collected from Tatoosh Island, Washington, USA), and *L. sitkana* Philippi (collected from San Juan Island, Washington, USA). The fifth common species on these shores, *L. subrotundata* Carpenter (not used in this study), is morphologically similar to *L. sitkana*, so model results for *L. sitkana* should be similar for *L. subrotundata.* The final species used in this study, *Echinolittorina natalensis* (formerly *Nodilittorina natalensis* Philippi, see Williams *et al.*, 2003), collected from Cape Vidal in the Natal region on the east coast of South Africa, provided an ornamented shell for comparison to the smooth-shelled *L. scutulata* and *L. plena*. Of the species used in this study, *L. sitkana* tends to live in low- to mid-intertidal zones (Boulding and Van Alstyne, 1993; Rochette and Dill, 2000), while the remaining species occupy the mid- and high-intertidal zone (Harger, 1972; Stirling, 1982; Behrens Yamada, 1989, 1992; Branch *et al.*, 2002).

Heat-budget model

The heat-budget model estimates an organism's body temperature by balancing the heat fluxes (*W*) into and out of the body (see Gates, 1980; Campbell and Norman, 1998).

$$W_{\mathrm{sw}} \pm W_{\mathrm{conv}} \pm W_{\mathrm{cond}} \pm W_{\mathrm{evap}} + W_{\mathrm{met}} \pm W_{\mathrm{lw}} = W_{\mathrm{stored}} \qquad (1)$$

The basic heat-budget model (1) considers fluxes due to short-wave solar radiation, W_{sw}; convective heat exchange with the air, W_{conv}; conductive heat exchange with the substratum, W_{cond}; heat lost or gained due to evaporation or condensation, W_{evap}; metabolic heat production, W_{met}; and long-wave radiative exchange between the organism and its surroundings, W_{lw}. The sum of these fluxes equals heat energy stored in the organism, W_{stored}. Our model was modified from a heat-budget model originally developed for the intertidal limpet *Lottia gigantea* (Denny and Harley, 2006), calculating the same heat flux components as the limpet model, but adding in a behavioral component by altering the area of conduction, surface area for convection, and projected area facing the sun depending on the modeled shell orientation and foot position (see below).

Because littorinid snails have a small mass and are uninsulated, we treat stored heat energy, W_{stored}, as negligible and set it equal to zero. Metabolic heat production and evaporative heat flux for small littorinids are approximately 0.07% and 1% as large as the heat flux due to short-wave radiation at midday, respectively (Newell, 1976; Kronberg, 1990; Miller, 2008). Based on these estimates, we treat metabolic heat production and heat flux due to evaporation as negligible terms in the model, and therefore remove W_{met} and W_{evap} from the model. The simplified heat-budget model used for this study is

$$W_{\mathrm{sw}} \pm W_{\mathrm{conv}} \pm W_{\mathrm{cond}} \pm W_{\mathrm{lw}} = 0. \qquad (2)$$

The methods used for the parameterization of the model are described in detail in Denny and Harley (2006) and Miller (2008). We made empirical measurements on a pair of snail shells from each species, except for *L. plena*, for which we only had a single shell. Projected area and substratum contact area were measured using size-referenced digital images analyzed in Image-J

(Rasband, 1997-2010), and surface area was similarly estimated from digital images using the method of Johnsen and Widder (1999). To estimate the heat transfer coefficient of each shell, we used silver casts of each shell to measure rates of convective heat exchange in a wind tunnel for shells both sitting down on the substratum or rotated up onto the lip of shell, allowing us to incorporate the effects of wind speed and shell orientation on the convective flux component of the model. Short-wave absorptivity (i.e. color) was measured using shell fragments mounted in an integrating sphere attached to a Li-Cor 1800 spectroradiometer (LI-COR Biosciences, Lincoln, Nebraska, USA). The thickness of any mucus attachment was treated as negligible and was not present in the model, so that heat flux was modeled as occurring directly between rock and shell surfaces. The rate-limiting step in conductive heat flux is assumed to be between the rock surface and the foot when the snail is crawling, while conduction from the rock surface through the shell is assumed rate-limiting when the snail is withdrawn into the shell. Shell thickness values are given as "conductive distance" in Table 1, with the greater conduction distance through the lip of the shell reflected in the greater distance given when the shell is elevated from the substratum. The snail body and any mantle water trapped in the shell are assumed to be at a single temperature due to blood circulation.

Model verification

Temperature predictions from the model were ground-truthed against temperature measurements of live snails and silver-epoxy-filled shells in the field and laboratory. Live *L. keenae* were close in size to the modeled *L. keenae* shells were fitted with polyurethane-coated 0.08 mm diameter thermocouple leads (Omega Engineering Inc., Stamford, Connecticut, USA) inserted through a hole ground in the shell and covered with cyanoacrylate glue. The hole was positioned so that the thermocouple entered the main body whorl near ground level when the shell sat down on the substratum, and was designed to put the thermocouple tip in contact with the snail body when the snail was withdrawn into the shell. Measurements of body temperature of a live *L. keenae* were carried out in a temperature-controlled wind tunnel (see Miller *et al.*, 2009) with the snail actively crawling or with the foot withdrawn into the shell. For field measurements, we took each of the shells used for the size measurements described above, filled the shells with thermally-conductive silver epoxy (two parts ground silver shavings, one part epoxy by volume; Devcon 2 Ton Clear Epoxy, ITW Devcon, Danvers, Massachusetts, USA), and fitted a 0.08 mm thermocouple into a hole drilled in the epoxy filling. We deployed these shells on a high-shore granite rock at approximately 2.5 m above mean lower low water at HMS during two warm periods in April and June 2007. In addition, we fit thermocouples into two live *L. keenae* to be deployed in the field alongside the silver-epoxy-filled shells during the June experiment. Temperatures were monitored at 1-minute intervals by a datalogger (23X, Campbell Scientific Inc., Logan, Utah, USA) while concurrently monitoring air temperature (Viasala HMP45C, Campbell Scientific Inc.), wind speed (Wind Sentry, R. M. Young Co., Traverse City, Michigan, USA), and solar irradiance (LI-200SB, LI-COR Biosciences, Lincoln Nebraska, USA). The field site was not submerged during high tide and thus represented a "worst-case scenario" for snails on the shoreline.

Model comparisons

For long-term reconstructions of snail body temperatures in the field at HMS, we used a 10 year record of weather and sea-state data from HMS, spanning August 1, 1999 through July 31, 2009. This data set included air temperature, solar irradiance, wind speed, tide height, significant wave height, and water temperature, all measured or interpolated at 10 min intervals

(Denny and Harley, 2006). After specifying the shore height, wave exposure, and shell orientation for a model snail, the heat-budget model calculates a body temperature for each 10 min time step based on the co-occurring environmental conditions. When the tide height exceeds the specified shore height, the snail body temperature is set equal to sea surface temperature, and when the tide and waves recede below the modeled shore height, the snail heats or cools according to the sum of the heat fluxes to and from the surrounding environment. The heat-budget model was employed to analyze the effects of behavioral or morphological changes on predicted body temperatures for the snail species under a variety of weather conditions. Because the focus of the study was to examine the effects of these traits under a "worst-case" scenario, all species were modeled resting on a horizontal surface 2.0 m above mean lower low water, a height which is 0.4 m above the mean higher high water line at HMS and thus is only submerged during spring tides or when large waves are present. The predicted temperatures for pairs of snails of each species were generally within a fraction of a degree Celsius, and so we only report results from a single representative shell of each species. The model was implemented in MATLAB 7 (The Mathworks Inc., Natick, Massachussetts, USA). Analyses were carried out in MATLAB and R 2.12.1 (2010).

Two behavioral manipulations were carried out with the model. First, the effect of removing the foot from the substratum was simulated by changing the contact area of the snail with the rock while leaving other parameters constant. The modeled snail either kept the foot in contact with the rock constantly, or withdrew the foot into the shell after three hours of aerial emersion, mimicking the behavior of snails that close the operculum as the rock surface becomes dry. Second, the effect of reorienting the shell up onto the aperture lip was tested by using a further-reduced value of contact area and simultaneously altering values for the projected area facing the sun and the surface area of the shell, as the aperture of the shell is exposed to the air rather than being held against the substratum (see Table 1 for representative values for each shell).

Effects of shell color on body temperature were tested by altering the short-wave absorptivity of the shell (α, a dimensionless value) while leaving all other characteristics constant. Four shell colors were compared, nominally referred to as "black" ($\alpha = 0.85$), "green" ($\alpha = 0.82$), "brown" ($\alpha = 0.80$), and "white" ($\alpha = 0.67$). Shell color differences were also compared for snails over a range of substratum contact areas to illustrate the relative contributions of color and conduction to the overall heat budget of the snail. Black and white *L. keenae* were modeled with contact areas that scaled from full foot contact to having only the outer lip of the shell glued to the substratum. Shell ornamentation comparisons were carried out by comparing temperature predictions for *L. scutulata* and *E. natalensis*. These two high-spired species grow to similar overall sizes, but *E. natalensis* has rows of nodules on the shell surface, increasing the total surface area for convection while only slightly increasing the projected area for absorbing solar irradiance. Both snails were modeled with a brown shell to remove effects of color differences.

Effects of morphological and behavioral manipulations were compared by examining predicted body temperatures. Maximum body temperature or body temperature differences between model scenarios were calculated for the 10 yr time series. Because the heat-budget model is deterministic, we report calculated temperatures and standard deviations for the temperatures rather than standard errors.

In addition to the ten year hindcasts for HMS, we modeled body temperatures with different foot and shell positions for *L. scutulata* at ten additional sites (Table 2) along the west coast of North America between August 2007 and August 2009 to gauge the effects of these behaviors at sites that might be more thermally stressful than HMS. Data for *L. scutulata* are reported because it is found throughout the west coast of the US (Reid, 1996), although modeled estimates of body temperatures for the other species at each site are very similar. Tide height, water temperature, air temperature and wind speed data were obtained from tide monitoring stations run by the U.S. National Oceanic and Atmospheric Administration's Center for Operational Oceanographic Products and Services, available through an online database (http://tidesandcurrents.noaa.gov/). When several hours or days of data were missing for a station, water temperatures were filled in from the nearest oceanographic buoy available in the NOAA database, while air temperature and wind speeds were obtained from the nearest weather station available in the MesoWest database maintained by the Department of Atmospheric Sciences at the University of Utah (http://mesowest.utah.edu/). Data for La Jolla, CA, were obtained from the Scripps Institute of Oceanography (http://meteora/ucsd.edu/weather/observations/sio-pier/dat/). Solar irradiance estimates for each site were obtained from NOAA's National Environmental Satellite, Data, and Information Service, which produces a map of satellite-derived hourly down-welling shortwave radiation for North America, available through the Department of Atmospheric and Oceanic Science at the University of Maryland (http://www.atmos.umd.edu/~srb/gcip/). All data were linearly interpolated to a 10-minute period. Predictions for 15 December 2008 to 8 January 2009 were discarded due to unavailable solar irradiance data. We predicted *L. scutulata* body temperatures for a black snail either with the foot extended at all times, the foot withdrawn into the shell resting on the rock, or the foot withdrawn and the shell rotated up onto the edge of the shell lip. Effects of wave surge were removed from the model due to uneven availability of data for the sites. We used the granite substratum characteristics from HMS for all sites. Because the vertical extent of the tide varies between sites, we modeled the snail at the high water mark for each site, which represents a likely worst-case scenario for thermal stress.

Live snail color comparisons

To complement the heat-budget model predictions, a comparison of shell color effects on body temperature was carried out with live *L. keenae* during a heat wave on May 14-16, 2008 at HMS, when the air temperature exceeded 27, 36 and 35 °C respecitvely. Three pairs of similar-sized *L. keenae* were collected from the field. The shell of one snail from each pair was naturally black, the other, white. Shell length was within 0.2 mm and total mass was within 0.05 g for each pair of snails. Maximum shell length was 13.25 mm, minimum shell length was 11.13 mm. A 0.08 mm diameter thermocouple wire, coated with a thin layer of polyurethane glue, was inserted into a hole ground in the main body whorl of the shell. The hole in the shell was then covered in cyanoacrylate glue to minimize evaporative water loss. Instrumented snails crawled normally in aquaria for the 24 hrs prior to deployment in the field. The snails were placed on a high-shore granite rock at midnight, May 14, 2008. The rock was wetted with seawater and the snails were allowed to crawl. As the rock dried, all snails withdrew the foot and glued the shell to the rock, but kept the shell aperture down against the rock surface. A datalogger recorded body temperatures once per minute for the subsequent 68 hr.

Results

Model parameters

The measured shell parameters for the snails used in the study are given in

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Table **1**. *L. keenae* was the largest snail used, with a maximum shell length of 10.8 mm from the spire tip to the outer edge of the aperture lip. *L. plena* was the smallest snail, at a maximum length of 5.7 mm. Parameters used for calculating heat exchange between the rock surface and the snail shell, or between the sky and the snail shell, are the same as those given in Denny and Harley (2006) and Miller (2008).

Model verification

The heat-budget model predicted temperatures for silver-epoxy-filled shells from all five species and for live *L. keenae* deployed in the field that were typically within 1.5°C of the measured temperatures at each time point, while predictions for the hottest 1% of time points were within 0.64 °C of measured temperatures (Table 3, Figure 2). The largest deviations between predicted and measured temperatures occurred during foggy conditions at night because our weather records do not record the incidence of fog. The altered long-wave heat-flux during foggy periods should keep snails slightly warmer than predicted by our model. Temperature predictions for the live *L. keenae* measured in the temperature-controlled wind tunnel agreed closely with measured temperatures. The difference between measured and predicted temperatures was 0.18 °C ± 0.27 (mean ± SD) while the snail was actively crawling, and was 0.02 °C ± 0.40 when the foot was withdrawn and the shell rested on the substratum.

Effect of foot position

The effect of withdrawing the foot into the shell and leaving only portions of the shell in contact with the substratum was estimated by calculating the average temperature difference between the foot-out and foot-withdrawn positions during the hottest 1% of all 10-minute time periods in the 10 yr dataset (*n* = 5260). Snails modeled with the foot withdrawn were 2.3 – 3.2

°C cooler on average during these hot periods than snails that kept the foot attached to the substratum, with a maximum difference of 5.4 °C for the smallest species, *L. plena* (Figure 3A). When the foot was left in contact with the surface, the maximum predicted temperature at HMS for all five species was between 40.4 and 40.7 °C. When the foot was withdrawn into the shell during low tide, the maximum temperature experienced by the five modeled species during the 10 yr model run ranged from 38.4 to 39.0 °C. The smallest snail modeled, *L. plena*, stayed the coolest, and the largest species, *L. keenae*, reached the highest temperatures. The daily maximum body temperature for each day in the 10 year time series (n = 3652) was generally higher for a snail with its foot in contact with the rock, as shown for *L. keenae* (Figure 4A).

Effect of shell position

Standing the shell on edge yielded body temperatures that were on average 1.5 to 2.3 °C cooler during the hottest 1% of time points when compared to the same shell sitting down against the substratum with the foot withdrawn (Figure 3B). For all species, the maximum temperature difference between the two shell orientations was between 2.2 and 3.5 °C. While snails in either orientation generally start from similar body temperatures in the pre-dawn hours, the difference in temperatures grows through the day and typically becomes largest during the hottest part of the day. Maximum temperatures reached by snails with the shell elevated off the substratum ranged from 36.9 °C (*L. plena*) to 37.8 °C (*L. keenae*). Daily maximum body temperature for every day in the 10 year time series was higher for snails that left the shell on the substratum, except during occasional cooler periods when the elevated shells became warmer (Figure 4B).

Latitudinal comparison

During 2007-2009, *L. scutulata* was predicted to reach the highest maximum temperatures near the edges of its latitudinal distribution (Figure 5), both in the north at Friday Harbor, WA (42.9 °C, 6 days > 40 °C) and Toke Point, WA (40.7 °C, 2 days > 40°C), and in the south in Los Angeles (41.9 °C, 2 days > 40 °C) and La Jolla, CA (42.7 °C, 4 days > 40 °C). In all cases, a snail with the foot in contact with the rock reached the highest temperatures, while removing the foot from the rock reduced the predicted maximum temperature by 1.18 ± 0.53 °C (mean ± SD), and elevating the shell reduced maximum temperature by an additional 1.56 ± 0.34 °C.

Effect of shell color

For black *vs.* white comparisons, the model predicted average temperature differences of 0.38 to 0.54 °C during the hottest 1% of times in the data set, with maximal differences of 0.8 °C (Figure 3C). Black shells were always predicted to be warmer than white shells when exposed to the sun, while brown and green shells fell closer to black shells. The magnitude of the temperature difference between shell color morphs was influenced by conductive heat flux through the shell or foot, and greater conductive flux with the rock tended to homogenize body temperatures (Figure 6). At colder environmental temperatures, a similar pattern in temperature differences between black and white shell color morphs was maintained. For daylight low tides when air temperatures were less than 15 °C, black morphs of *L. keenae* were 0.44 ± 0.2 °C (mean ± 1SD, for all seasons, *n* = 80,476 time points) warmer than white morphs when snails were modeled elevated off the substratum (Figure 7A), and for snails modeled with the foot always in contact with the substratum, the average predicted difference between black and white morphs was reduced to 0.03 ± 0.03 °C across all seasons (Figure 7B).

Temperature differences measured between pairs of live black and white *L. keenae* were similar to those predicted by the model. Among the three pairs of snails, the average temperature difference between live black and white snails was less than 0.5 °C during daylight hours (Table 4). The maximal difference between black and white shells was 2.39 °C, though there were periods during the day when the white shell in each pair was hotter than the black shell.

Effect of shell sculpture

The influence of shell sculpturing of *E. natalensis* on body temperature during warm periods was minimal. The heat transfer coefficient was greater for the nodulose *E. natalensis* shell compared to the smooth-shelled *L. scutulata,* but the convective flux difference was greatest at high wind speeds (Figure 8A), which rarely occur during the hottest days (see Denny and Harley, 2006, materials and methods for the calculation of the heat transfer coefficient). On calm, hot days, the small difference in heat transfer coefficient resulted in an average predicted body temperature for *L. scutulata* 0.2 ± 0.3 °C (mean ± SD, $n = 5260$) warmer than a similarly-sized and identically-colored *E. natalensis* shell modeled in the same weather conditions (Figure 8B).

Discussion

Littorinid snails often occupy the highest reaches of the intertidal zone, remaining exposed to terrestrial conditions for hours to days. As a result, these species may reach high body temperatures when weather and ocean conditions combine to create hot low tide periods. Although littorinids can move to refuges to avoid high temperatures and desiccation stress, this study has focused on littorinid snails living on open rock faces, where they may be the only species exerting grazing control over algal communities (Norton *et al.*, 1990; McQuaid, 1996b). The behavioral and morphological traits of these species, combined with their physiological tolerance to heat and desiccation stress, permits them to occupy these habitats and survive extreme weather conditions.

Most rocky intertidal gastropods must keep their foot attached to the substratum to maintain their position on the shore, but this comes at the expense of increasing conductive heat flux between the foot and a potentially hot substratum (Denny and Harley, 2006). The propensity for littorinid snails to anchor their shell to the rock with mucus and withdraw the foot into the shell provides a reduction in body temperature not available to most other intertidal gastropods (Vermeij, 1971a, 1973; McQuaid and Scherman, 1988), and results in body temperatures for the five species studied here that can be 3-5°C lower than when the foot is left in contact with the rock. Withdrawing the foot into the shell has the added benefit of allowing the snail to seal the operculum, thereby reducing water loss (McMahon and Britton, 1985; Britton and McMahon, 1986). As a result, littorinid snails typically have very slow evaporative water loss rates, permitting survival of multi-day aerial exposures (Broekhuysen, 1940; Cleland and McMahon, 1986; Britton, 1995; Marshall *et al.*, 2010). The use of a mucus holdfast does, however, introduce a trade-off in terms of stability and attachment strength relative to the snail foot (Miller, 1974; Denny, 1984; Ohgaki, 1988), increasing the chance of dislodgement. However, survival of dislodged snails is typically high and they are commonly able to navigate back to their preferred high shore habitats (Evans, 1961; Bock and Johnson, 1967; Miller *et al.*, 2007).

Reorienting the shell so that only the outer lip of the shell is in contact with the substratum further enhances littorinid snails' ability to minimize body temperature on warm days. Although we lack quantitative data on the frequency of this behavior in the field, the shell-lifting behavior has been observed in all five species discussed here (L. Miller, personal observations), as well as in numerous other littorinid snail species (Garrity, 1984; Britton, 1995; Lang *et al.*, 1998; Wada and Ito, 2000). Lifting the shell from the substratum further reduces the surface area in contact with the substratum over the initial reduction achieved by pulling the foot into the shell (Table 1), but also changes other important heat flux components. The reoriented shell exposes a greater surface area to the surrounding air, increasing the rate of convective heat exchange, which cools a snail that is warmer than the air, as is often the case on hot days (Marshall *et al.*, 2010), while also lifting the shell higher into faster-flowing air in the boundary layer over the rock. Together, the reduction in conduction and increase in convection help minimize body temperature, as has been shown in many terrestrial organisms (Stevenson, 1985). Changing shells' orientation could also change the projected area facing the sun, potentially minimizing absorption of shortwave radiation. Although some species of littorinid snails have been shown to orient parallel to the sun when resting against the substratum (Muñoz *et al.*, 2005), there is no evidence that the species studied here consistently orient the shell spire towards the midday sun (Miller, 2008).

The role of shell morphology in avoiding high body temperatures is relatively small. Within the range of shell colors tested, the reduction in body temperature created by having a white *versus* a dark shell is on average less than 0.5 °C, both for model snails of all five species and for live *L. keenae*. The complementary hypothesis—that dark shells should be advantageous in cool conditions by helping to warm these ectothermic animals—also receives minimal support (Jones, 1973; Phifer-Rixey *et al.*, 2008). Due to the substantial influence of conductive heat flux between the snail foot and the rock substratum, an actively grazing littorinid snail does not deviate from the substratum temperature appreciably, so that differences in short-wave absorptivity between shell colors result in temperature differences of less than 0.5 °C in the model, while the range of reported temperature differences between color morphs of other species of intertidal snails is on the order of 0 – 2 °C (Markel, 1971; Cook and Freeman, 1986; Reid, 1987; Phifer-Rixey *et al.*, 2008), with differences of 3 – 5 °C in some larger snails species on certain substrata (Etter, 1988). The high thermal conductivity and heat capacity of seawater effectively homogenizes temperatures in the intertidal zone during high tide and when waves splash during rising and ebbing tides, removing any effect of shell color on body temperature during these periods. Thus, while thermal melanism may be important for warming the body in some terrestrial organisms (Kingsolver, 1996; Clusella-Trullas *et al.*, 2007), the importance to gastropods in intertidal systems is less clear. Differences in shell colors among intertidal snail populations could be driven by other factors such as visual predation by crabs and fishes (Reimchen, 1979; Hughes and Mather, 1986; Reid, 1987; Johannesson and Ekendahl, 2002; Manríquez *et al.*, 2009).

The functional significance of shell shape in intertidal snails has received substantial attention. Shell shape and size influence drag forces imposed by waves during high tide (Denny *et al.*, 1985; Boulding and Van Alstyne, 1993; Trussell, 1997a; Denny and Blanchette, 2000; Pardo and Johnson, 2005) determine the volume of fluid retained in the shell during emersion (Vermeij, 1973; Britton and McMahon, 1986), and provide protection from predators (Seeley, 1986; Trussell, 2000; Trussell and Nicklin, 2002; Johannesson, 2003). The importance of shell shape for mitigating stress due to exposure to extreme high temperatures in these small species is less clear. We have shown that when comparing *L. scutulata* and *E. natalensis,* the addition of nodules on the outer surface of *E. natalensis* shells produces a negligible reduction in body temperature on hot days. These results mirror the minor contribution of shell sculpture to convective cooling found in intertidal limpet species (Harley *et al.*, 2009). Additionally, estimated temperatures for the globose, ribbed *L. sitkana* do not differ markedly from the other high-spired species examined here. Despite the relatively small effect of shell shape and shell sculpturing on body temperature in the temperate climate conditions used here, the trend within tropical intertidal gastropods, and particularly littorinids, is generally towards increased sculpturing and higher-spired shells at higher shore heights (Vermeij, 1973). The nodulose littorinids such as *E. natalensis* are primarily found in tropical or sub-tropical regions, so the importance of these characteristics to controlling body temperature may take on a greater importance at low latitudes where the frequency of high temperature exposures is greater.

Though body temperature changes created by the behavioral choices and color differences described here are only a few degrees, they may be sufficient to help littorinid snail populations avoid substantial mortality due to thermal stress. The reported physiological thermal tolerances of *L. keenae* and *L. scutulata* (> 42-44°C, Somero, 2002) exceed the body temperatures predicted for snails in the field at HMS, but snails at other sites along the coast may approach or exceed these temperature limits. The frequency and severity of thermal stress events are driven by the timing of the tides and the coincidence of calm, warm weather conditions with midday tides (Helmuth *et al.*, 2002; Helmuth *et al.*, 2006; Denny *et al.*, 2009; Mislan *et al.*, 2009). Our model predicts that littorinids living throughout the species' latitudinal ranges could occasionally experience prolonged aerial emersion at midday during weather conditions hot enough to push body temperatures close to 42 °C. Under these circumstances, the additive benefits of removing the foot from the rock, reorienting the shell, and having lighter shell colors could keep body temperatures several degrees below those lethal temperatures and help limit sublethal temperature stress. Work on the physiology of related littorinid snails has shown that as temperatures approach lethal limits, there is often an attendant decrease in aerobic respiration, increases in anaerobic metabolism, and eventual heart failure (McMahon and Russell-Hunter, 1977; Sokolova and Pörtner, 2003; Marshall *et al.*, 2010), along with the added energetic cost of repairing cellular-level damage through avenues such as heat shock protein expression (Tomanek, 2010).

Although lighter shell colors help avoid temperature stress, the native snail populations in many of the warmer sites on the west coast of North America highlighted here contain a substantial fraction of dark-colored individuals (L. Miller, personal observations). All of the *Littorina* species discussed here, except *L. sitkana*, have a pelagic larval dispersal phase (Reid, 1996, 2002), so that mixture among populations may counteract any selection for lighter shell colors at hot sites. In sub-tropical and tropical habitats the role of shell color may be more important, as evidenced by experiments with black-painted littorine snails in South Africa that demonstrated that darker colors did result in acute thermally-induced mortality on hot days (McQuaid, 1992). At sites with higher peak air and substratum temperatures, the small reduction in body temperature created by a light colored shell may make the difference between survival and death on hot days, especially after the more effective behavioral options have been exhausted.

Based on the long-term weather records for our central California coast site, it appears unlikely that acute high temperature exposures regularly cause significant mortality in *Littorina* populations at HMS. However, when considered over the lifetime of an organism, the cumulative benefits of the small temperature reductions afforded by the behavioral and morphological traits examined here could be important for allowing littorinids to exploit high littoral habitats. Sub-lethal temperatures will still incur metabolic costs that can be partially mitigated by having a lighter colored shell or minimizing conductive heat flux from a hot substratum. The attendant reduction in desiccation stress provided by these traits may also help contribute to the success of littorinids in the high intertidal zone (Chow, 1989). While these behaviors or shell morphologies may have little effect on the occurrence of single-day thermal mortality events at HMS, on other shores, particularly tropical shores and sites where mid-day low tides frequently coincide with warm weather, these traits may be key in allowing littorinids to avoid thermally-induced mortality.

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Table 1. Measured shell parameters for the five littorinid species used in this study.

Parameter	Units	*Littorina keenae*	*Littorina scutulata*	*Littorina plena*	*Littorina sitkana*	*Echinolittorina natalensis*
Shell length	mm	10.8	6.1	5.7	6.6	6.3
Area for conductive flux, foot extended	mm^2	58.5	10.3	10.9	15.5	11.4
Area for conductive flux, foot withdrawn	mm^2	2.20	1.02	0.84	1.02	0.71
Area for conductive flux, shell up	mm^2	0.34	0.14	0.10	0.29	0.25
Area for convective flux, shell down	mm^2	287.4	69.9	65.4	106.9	67.2
Area for convective flux, shell up	mm^2	347.8	81.1	77.0	123.1	85.6
Maximum projected area	mm^2	104.8	24.6	22.9	37.1	25.5
Minimum projected area	mm^2	65.8	14.3	13.0	22.4	16.5
Conduction distance (shell down)	mm	0.42	0.31	0.32	0.63	0.55
Conduction distance (shell up)	mm	2.57	1.41	1.25	1.44	1.32

Table 2. Sites on the west coast of North America used to model maximum body temperature for *L. scutulata* from August 2007 to August 2009. The relevant NOAA tide monitoring station ID from which data were obtained is given for each site, except La Jolla, CA, where data were obtained from the Scripps Institute of Oceanography archive. Maximum water level is the highest measured tide height during the survey period, referenced to mean lower low water.

Tide Station	NOAA Station ID	Latitude (°N)	Longitude (°W)	Maximum water level (m)
Friday Harbor, WA	9449880	48.522	123.025	2.93
Neah Bay, WA	9443090	48.367	124.612	3.29
Toke Point, WA	9440910	46.707	124.042	3.65
Newport, OR	9435380	44.625	124.042	3.25
Charleston, OR	9432780	43.345	124.322	2.95
Crescent City, CA	9419750	41.745	124.182	2.67
Point Arena, CA	9416841	38.913	123.706	2.43
San Francisco, CA	9414290	37.806	122.465	2.26
Pacific Grove, CA	9413450	36.622	121.904	2.21
Los Angeles, CA	9410660	33.720	118.272	2.30
La Jolla, CA	*SIO	32.867	117.257	2.26

Table 3. Comparison of measured temperatures of epoxy-filled shells and live snails in the field with predicted model temperatures using weather data from the same time period.

Species	Mean difference between all modeled and measured temperatures (°C ± SD)	Mean difference between modeled and measured temperatures for top 1% of temperatures (°C ± SD)
Shell mimic, shell down		
Littorina keenae	-1.13 (± 1.51)	0.64 (± 0.63)
Littorina scutulata	0.20 (± 1.31)	0.05 (± 0.46)
Littorina sitkana	-0.75 (± 0.95)	-0.09 (± 0.19)
Littorina plena	0.17 (± 0.88)	-0.07 (± 0.24)
Echinolittorina natalensis	-0.21 (± 1.07)	0.00 (± 0.41)
Shell mimic, shell up		
Littorina keenae	-1.47 (± 2.40)	0.45 (± 0.78)
Littorina scutulata	-1.03 (± 1.14)	0.11 (± 0.63)
Littorina sitkana	-0.10 (± 0.79)	-0.21 (± 0.28)
Littorina plena	-0.73 (± 1.28)	0.16 (± 0.81)
Echinolittorina natalensis	-0.55 (± 0.89)	-0.17 (± 0.62)
Live snails, shell down		
L. keenae 1	-0.56 (± 1.50)	-0.06 (± 0.86)
L. keenae 2	-1.00 (± 1.50)	0.17 (± 0.29)

Table 4. Summary of temperatures of three pairs of similarly-sized live black-shelled and white-shelled *Littorina keenae* deployed on a high intertidal rock during a heat wave on May 14 – 16, 2008. Temperature differences between each black and white pair are calculated for times from one hour after sunrise to one hour before sunset, and during the four hottest hours of the day.

Temperature difference (°C) black – white shell 6:00 – 18:00	Pair 1		Pair 2		Pair 3	
Average ± 1 SD, n = 2160	0.11 ± 0.69		0.43 ± 0.41		0.10 ± 0.71	
Maximum	2.29		2.39		2.15	
Minimum	-1.40		-0.78		-2.17	
Temperature difference (°C) black – white shell 11:00 – 15:00						
Average ± 1 SD, n = 720	-0.08 ± 0.54		0.48 ± 0.33		0.31 ± 0.66	
Maximum	2.06		2.12		2.02	
Minimum	-1.08		-0.78		-1.61	
Cumulative data, May 14-16	Black	White	Black	White	Black	White
Maximum temperature (°C)	43.8	42.5	43.4	42.7	43.7	42.9
Time above 30°C (hr)	18.7	18.5	19.2	19.1	19.4	19.1
Time above 40°C (hr)	1.5	1.25	2.05	1.47	2.38	2.0

Figure legends

Figure 1. Littorinid snails can often be found (A) with the foot withdrawn into the shell and the shell glued to the substratum, or (B) with the shell elevated up off the substratum, perched on the outer lip of the shell aperture. C) Representative shells of the five species used in the heat-budget model. From left to right: *Littorina keenae, L. scutulata*, *L. plena*, *L. sitkana, Echinolittorina natalensis*.

Figure 2. Measured *vs.* predicted temperatures for silver-epoxy-filled shells set out in the field. The left column shows the relationship when the shells were positioned with the aperture down against the substratum. The right column shows data for the same shells re-oriented up onto the edge of the shell lip. Data were collected during April 23-29 and June 3-7, 2007, at HMS.

Figure 3. Mean temperature differences (± 1 SD) between modeled snails during the hottest 1% of all time periods in the 10 yr weather data set (n = 5620). Maximum differences are denoted by the + symbol above each bar. A) Comparison of snails modeled with the foot always on the rock, or withdrawn into the shell during hot periods. Snails with the foot in contact with the rock reach higher temperatures. B) Comparison of snails modeled with the foot withdrawn into the shell, and the snail either resting aperture-down on the substratum or perched on the outer lip of the shell. Leaving the shell resting on the substratum results in higher body temperatures. C) Temperature differences between a black shell and alternate shell color morphs. Each color morph was modeled with the foot withdrawn and shell perched on the outer lip of the shell. Black shells are always warmer than the alternate color morphs.

Figure 4. A) Predicted daily maximum body temperatures for a black *L. keenae* modeled with the foot out in contact with the substratum at all times or withdrawn into the shell during low tide. B)

Predicted daily maximum body temperatures for the same *L. keenae* with the foot withdrawn and the shell sitting down on the substratum or with the shell tipped up on the edge of the aperture lip. Temperatures were predicted using environmental data for HMS from 1999-2009 (n = 3652 days). The snail was modeled on horizontal substratum at 2.0 m above mean lower low water. A line of unity is plotted in both panels.

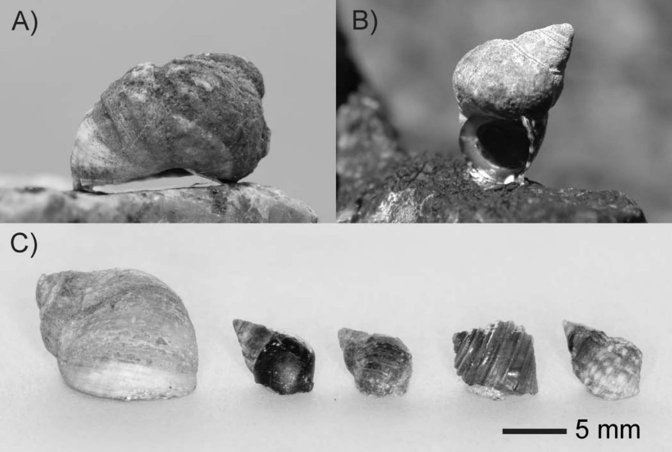
Figure 5. Maximum predicted body temperatures for a black *L. scutulata* at eleven sites along the west coast of North America, using environmental data from 1 August 2007 through 1 August 2009. Temperatures are given for the same snail in three positions: with the foot out on the rock at all times, with the foot withdrawn into the shell at low tide, and with the shell tipped up on edge during low tide. All models were run with the snail sitting on a horizontal surface at the height of the maximum still tide level for each site.

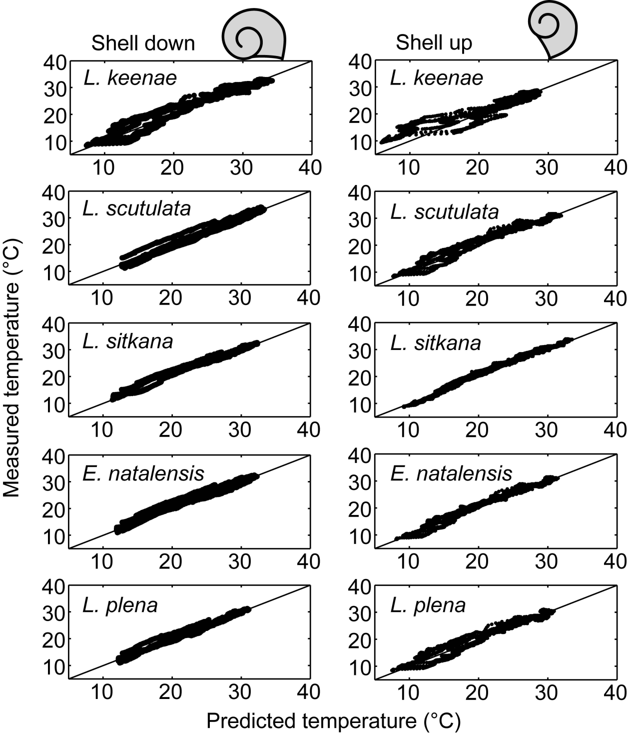
Figure 6. Maximum predicted body temperatures for a black snail shell (solid line) and white snail (dashed line) modeled with a range of contact areas on the substratum, using environmental data from HMS for 1999-2009. The shaded areas represent the typical range of contact areas for littorinid snails with only the lip of the shell glued to the substratum (1 point), resting on the lip and main whorl of the shell (2 points), or attached by the foot. As contact area increases, conductive heat flux reduces the effect of shell color differences on body temperature.

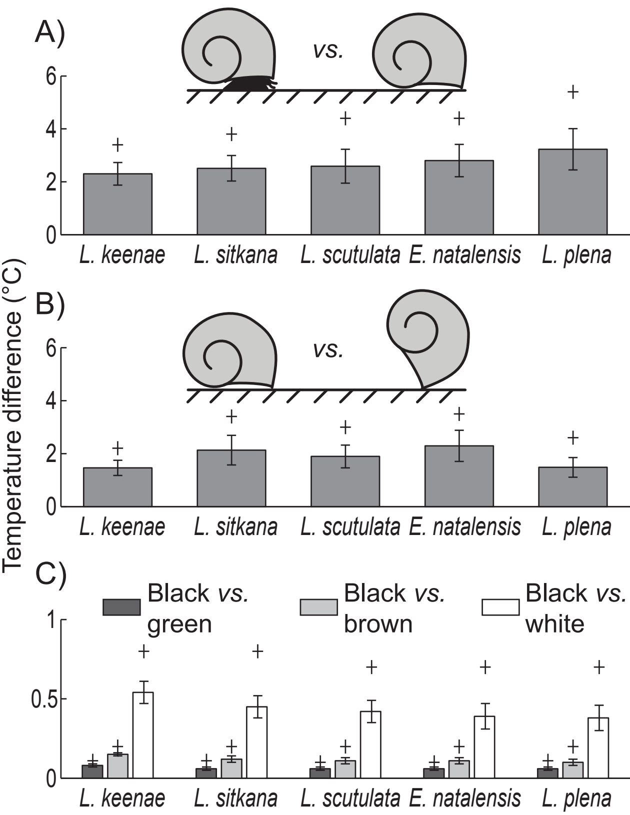
Figure 7. Temperature differences between black and white morphs of *L. keenae,* for all daytime low tide periods when air temperature was less than 15 °C. A) Temperature differences for snails modeled with the foot withdrawn and the shell elevated up onto the outer lip of the aperture. Black shells were warmer than white shells. B) Temperature differences for black *vs.* white snails modeled with the foot always in contact with the substratum. Comparisons were made for

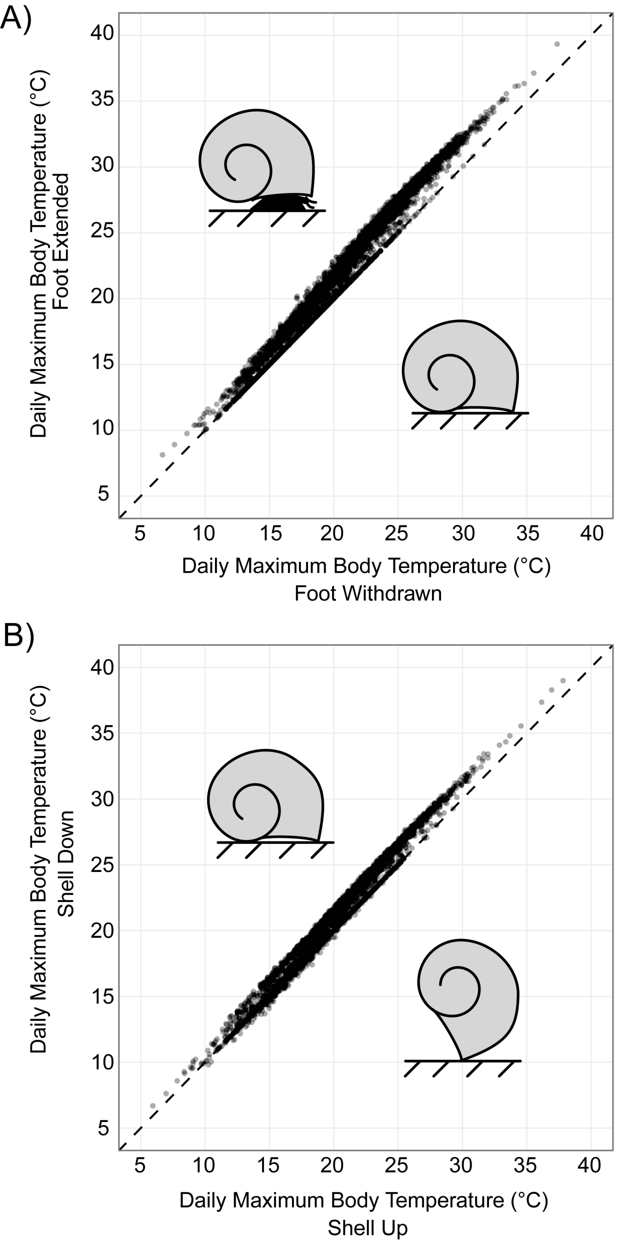
each meteorological season using weather data from HMS for 1999-2009. The center line in each box represents the median temperature difference between the two color morphs at each time point, and the upper and lower bounds of each box denote the 1st and 3rd quartiles, respectively. Crosses above a boxplot represent outliers. Box width represents the relative sample size in each season (Spring = 29,918 samples in both panels). Sample size varies between seasons due to the timing of low tides, wave action, and day length.

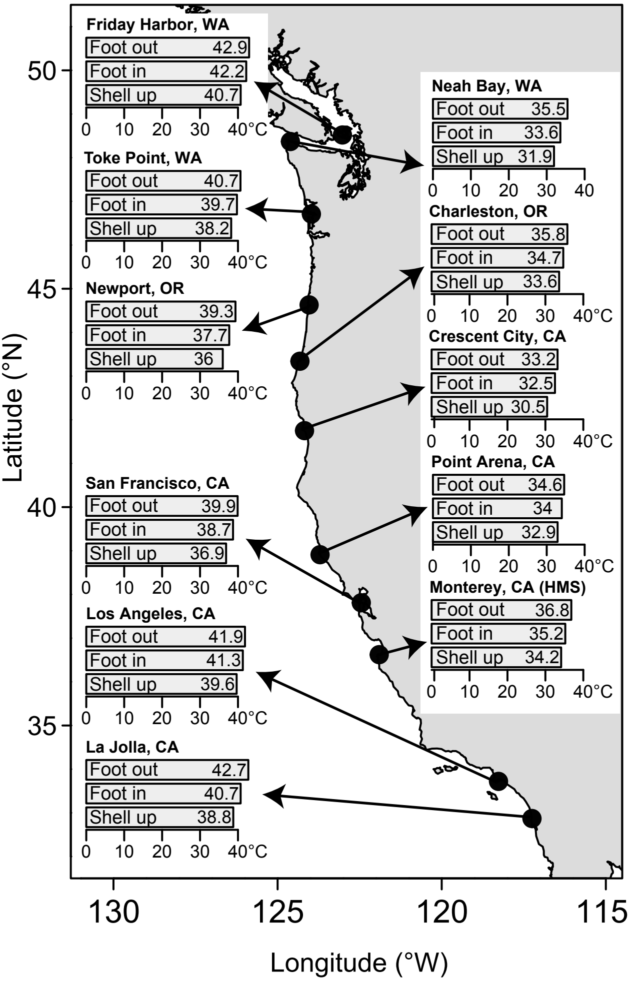
Figure 8. A) Calculated heat transfer coefficients for similarly-sized *E. natalensis* (black line) and *L. scutulata* (gray line). Higher values increase the convective heat exchange with the surrounding air. Values are calculated for 25°C air temperature and shells sitting with the aperture against the substratum. B) Predicted body temperatures for a representative hot day, for brown snails of each species modeled with the foot withdrawn and shell resting on the substratum. The sculptured shell of *E. natalensis* was 0.2°C cooler on average compared to the smooth shell of *L. scutulata* under identical weather conditions. The wind speed on this day was 1.2 ± 0.6 m s^{-1} (mean ± 1SD).

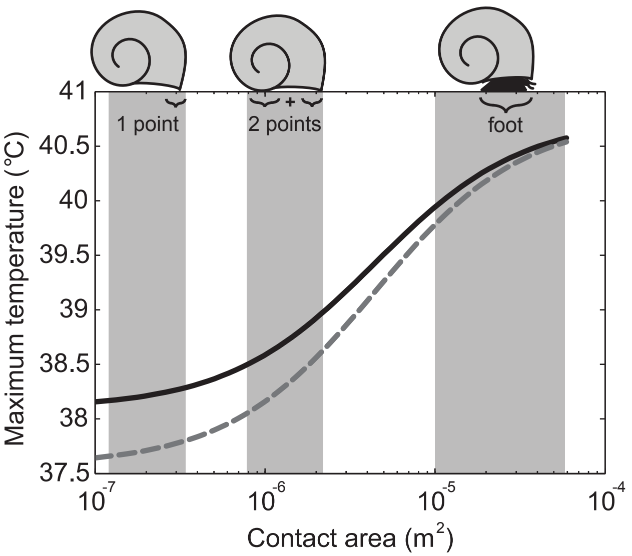

A)
B)
C)
5 mm

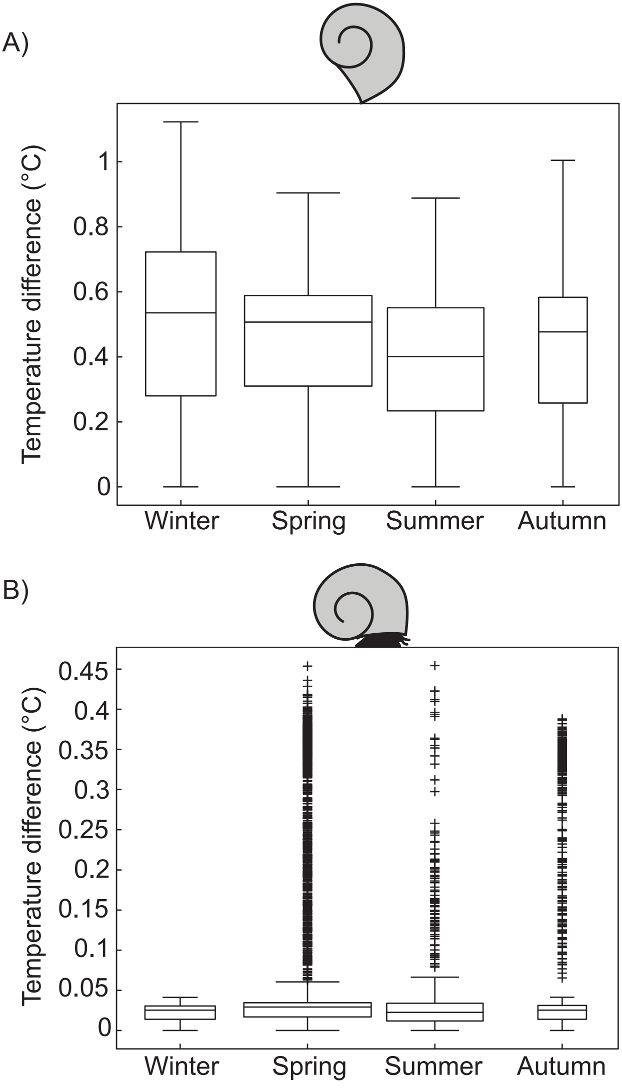

Shell down
Shell up
L. keenae
L. scutulata
L. sitkana
E. natalensis
L. plena
10
20
30
40
Measured temperature (°C)
Predicted temperature (°C)

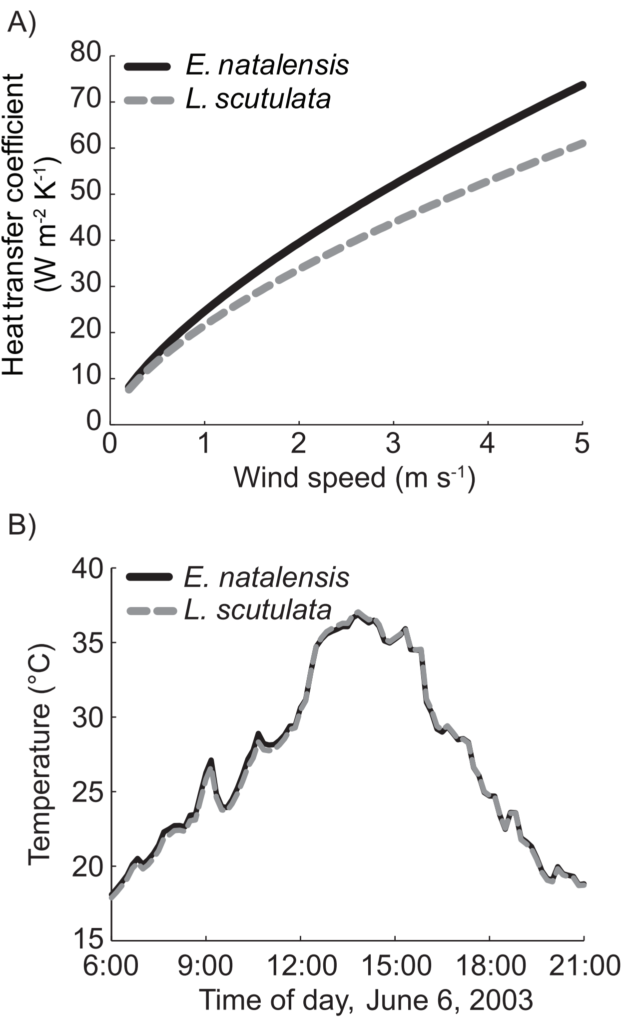

A)
vs.
6
4
2
0
L. keenae
L. sitkana
L. scutulata
E. natalensis
L. plena
Temperature difference (°C)
B)
vs.
6
4
2
0
L. keenae
L. sitkana
L. scutulata
E. natalensis
L. plena
C)
Black vs. green
Black vs. brown
Black vs. white
1
0.5
0
L. keenae
L. sitkana
L. scutulata
E. natalensis
L. plena


A)
Daily Maximum Body Temperature (°C)
Foot Extended
Daily Maximum Body Temperature (°C)
Foot Withdrawn
5
10
15
20
25
30
35
40
B)
Daily Maximum Body Temperature (°C)
Shell Down
Daily Maximum Body Temperature (°C)
Shell Up
5
10
15
20
25
30
35
40


Friday Harbor, WA
Foot out 42.9
Foot in 42.2
Shell up 40.7
0 10 20 30 40°C
Neah Bay, WA
Foot out 35.5
Foot in 33.6
Shell up 31.9
0 10 20 30 40
Toke Point, WA
Foot out 40.7
Foot in 39.7
Shell up 38.2
0 10 20 30 40°C
Charleston, OR
Foot out 35.8
Foot in 34.7
Shell up 33.6
0 10 20 30 40°C
Newport, OR
Foot out 39.3
Foot in 37.7
Shell up 36
0 10 20 30 40°C
Crescent City, CA
Foot out 33.2
Foot in 32.5
Shell up 30.5
0 10 20 30 40°C
San Francisco, CA
Foot out 39.9
Foot in 38.7
Shell up 36.9
0 10 20 30 40°C
Point Arena, CA
Foot out 34.6
Foot in 34
Shell up 32.9
0 10 20 30 40°C
Monterey, CA (HMS)
Foot out 36.8
Foot in 35.2
Shell up 34.2
0 10 20 30 40°C
Los Angeles, CA
Foot out 41.9
Foot in 41.3
Shell up 39.6
0 10 20 30 40°C
La Jolla, CA
Foot out 42.7
Foot in 40.7
Shell up 38.8
0 10 20 30 40°C
50
45
40
35
Latitude (°N)
130
125
120
115
Longitude (°W)


1 point
2 points
+
foot
Maximum temperature (°C)
41
40.5
40
39.5
39
38.5
38
37.5
10^{-7}
10^{-6}
10^{-5}
10^{-4}
Contact area (m^2)


A)
Temperature difference (°C)
0
0.2
0.4
0.6
0.8
1
Winter
Spring
Summer
Autumn
B)
Temperature difference (°C)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
Winter
Spring
Summer
Autumn


A)
E. natalensis
L. scutulata
Heat transfer coefficient (W m^-2 K^-1)
0
10
20
30
40
50
60
70
80
Wind speed (m s^-1)
0
1
2
3
4
5
B)
E. natalensis
L. scutulata
Temperature (°C)
15
20
25
30
35
40
Time of day, June 6, 2003
6:00
9:00
12:00
15:00
18:00
21:00