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Radio tracking detects behavioral thermoregulation at a snail's pace

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ABSTRACT

The dynamic ebb and flood of tides makes the marine intertidal zone a habitat with temperatures that fluctuate rapidly in both space and time. This is problematic for slow intertidal organisms that cannot move at the speed of tidal fluctuations. The timing of low tides determines which days organisms may experience extreme body temperatures, controlling microclimate to a greater degree than weather patterns. When low tides occur midday, temperatures can exceed critical thermal maxima for many species. Although high shore areas experience the greatest environmental extremes, they often harbor untapped food resources. The periodicity of low tide timing creates a predictable cycle that marine animals can use to obtain food in risky areas while minimizing exposure to thermal extremes. Here, we use a two-part approach to assess whether the snail, *Nucella ostrina*, uses the predictability of the tidal cycle to obtain food in risky areas while minimizing exposure to thermal extremes. Radio tracking detected the presence/absence of snails in high shore feeding areas continuously for 14 weeks and physical thermal models approximated snail body temperature in those high shore areas. Snails were absent when extreme low tides occurred at times of high solar irradiance (midday). Comparing the subset of physical model body temperatures foraging snails experienced to all available body temperatures in the high shore environment showed snails in foraging areas disproportionately at 9–12 °C and absent at body temperatures > 31 °C, suggesting that *N. ostrina* is not present when and where thermal risk is greatest. These patterns demonstrate that censusing only at low tide yields an adequate picture of foraging behavior of this species in its natural habitat, and that migratory foraging behavior effectively moderates snail experience of environmental temperature in nature and may buffer this species from aerial warming.

1. Introduction

An animal's behavior modifies how it experiences its environment and can act as a filter of undesirable conditions (Buckley et al., 2013; Huey, 1991; Kearney et al., 2009; Lathlean, 2014; Sears et al., 2016; Sunday et al., 2014), therefore altering the temporal and spatial scales at which a species will be affected by climate change (Deutsch et al., 2008; Kearney et al., 2009; Sears et al., 2011; Woods et al., 2015). Correctly accounting for animal behavior is critical to relating environmental conditions to performance and risk in a changing world.

Organisms inhabiting marine intertidal zones are subjected to potentially stressful physical conditions whenever tides retreat. When the tide is low on warm, sunny days, organisms have a high risk of exposure to temperatures exceeding thermal maximums. Mobile intertidal organisms may change their behavior drastically to minimize thermal risks, for example, actively selecting thermally favorable microsites (Chapperon and Seuront, 2011a) or changing body orientation to regulate heat gain (Munoz et al., 2005). Intertidal zones have a gradient of thermal and desiccation stress: higher shore elevations are exposed to air for longer than lower elevations and therefore are more likely to reach high temperature and low humidity extremes. Mobile intertidal animals must choose between seeking food in exposed high shore areas that are accessible only to the most physiologically robust species (Connell, 1970), or taking refuge in cracks and lower on shore where food stocks may be depleted by competitors (Johnson et al., 1998). Organisms are constrained by the distance between high and low intertidal elevations, up to several meters in many systems, and by potential water loss if moving when emerged at low tide or across dry substrates. Fast organisms move into new foraging areas with a flooding tide and retreat with the receding tide (Holsman et al., 2006; Yamada and Boulding, 1996). For example, small shore crabs can run over ground up to 1.4 m s^{-1} (Martinez, 2001). The much slower locomotion and feeding of animals such as snails suggests they must adopt a different mechanism of balancing foraging with risk avoidance.

Thermal complexity created by tidal cycling controls benthic environmental conditions more than any climatic factor, creating a

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variety of microhabitats (Mislan et al., 2009). Low tide aerial exposure varies seasonally and geographically, occurring at different times of day. However, within season and location tidal patterns repeat on a two-week interval. Aerial exposure during midday subjects intertidal organisms to higher solar radiation, and therefore body temperatures, than they experience when low tide occurs at other times of day (Hayford et al., 2015; Helmuth et al., 2002). The air temperature may or may not be high on any given day, yet it can only reach maximum values on days with long midday low tides. This makes the two-week tidal cycle a potentially dependable feature of a stochastic environment. Tidal phase (high or low, ebb or flood), day-night, and seasonal cycles have often been considered in assessment of thermoregulatory behavior in tidal invertebrates (for example Garrity, 1984; Harper and Williams, 2001; Little, 1989; Takada, 1996). Less common are connections between the two-week tidal cycle and thermal risk (but see Burrows and Hughes, 1989, Moran, 1985, Spight, 1982), yet the two-week periodicity creates spatio-temporal thermal variation which may provide reliable cues for tidal organisms.

Slow intertidal animals can take advantage of both food and thermal refuge if they are selective in their foraging timing. Risk is reduced on days when low tides are timed such that most aerial exposure is at night or early in the morning (Hayford et al., 2015). It is therefore predicted that slow mobile organisms are most active in the high shore region on those days of the tidal cycle with minimal midday aerial exposure.

Nucella ostrina (Gould, 1852) is a predatory snail common to intertidal shores throughout the Northeast Pacific. In the San Juan Islands, Washington, USA, *N. ostrina* feeds preferentially on the barnacle *Balanus glandula* (Connell, 1970). *N. ostrina* forages at all tidal heights when barnacle prey are available, however, prey at lower shore elevations are typically consumed by superior competitors of *N. ostrina* in the spring or early summer. By late summer the remaining available prey are located high on shore. The process of crawling (1.3 cm min^{-1} for a typical individual, data not shown), selecting, drilling, and ingesting a prey item (5.3 ± 0.37 h for drilling and ingesting an average sized barnacle) can exceed 24 h and typically takes longer than the duration of a high tide (Emlen, 1966). In experimental tests using caged snails in the laboratory and field (Vaughn et al., 2014 and Hayford et al., 2015, respectively), snails moved into exposed areas in the high intertidal during days of the two-week tidal cycle when thermal and desiccation risk were reliably low, and foraged for multiple consecutive days before retreating to thermal refuges (Fig. 1). Snails selected days of the tidal cycle when foraging areas were subject to reduced potential sun exposure. However, these manipulated conditions offered a dichotomous choice of food or refuge within a few cm of one another, and so only provided suggestive evidence of how snails behave in more heterogeneous natural habitats. Sampling only at low tide would have missed *N. ostrina* movement into high shore areas during high tides. Furthermore, measuring habitat temperatures likely wasn't as accurate an assessment of thermal risk as estimating body temperature (Gilman et al., 2006; Helmuth, 1998; Helmuth and Hofmann, 2001).

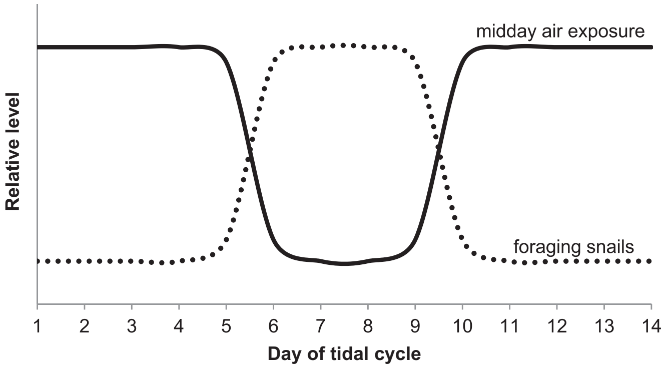

Fig. 1. Conceptual model of snail behavior during a two-week tidal cycle.
Midday aerial exposure (solid line) changes throughout the cycle due to low tide timing. The proportion of snails on a given shoreline that forage in sun-exposed, high-shore locations (dotted line) increases on those days of the tidal cycle where midday aerial exposure is minimized.

The objectives of this study were to determine whether: (1) natural populations of *Nucella ostrina* forage periodically as has been previously observed in experimental manipulations; (2) snail foraging behavior limits thermal risk; and (3) censusing only at low tide provides an adequate picture of snail foraging behavior. We predicted that *N. ostrina* would forage only on the few days of the two-week tidal cycle when the chances of high temperatures were reduced by timing of tidal cycling, thereby reducing thermal risk to the snail, and that surveying only at low tide would adequately assess snail populations if surveys were conducted on foraging days.

2. Materials & methods

2.1. Low tide surveys of microhabitat use

The intertidal snail *Nucella ostrina* was tracked to assess habitat use in nature and whether behavior moderated thermal experience within the wide range of natural thermal heterogeneity. Typically < 3 cm in length, *N. ostrina* is too small to carry a traditional temperature logger. Instead, a two-part approach was used: tracking with radio frequency identification (RFID) tags and estimating operative body temperature with physical thermal model loggers that approximated body temperature of live organisms. Snail censuses were conducted at multiple sites on the University of Washington Friday Harbor Laboratories Research Preserve (FHL, 48°33′ N, 123°00′ W) on San Juan Island, Washington, USA. The mean tidal range (difference between mean higher high water, MHHW, and mean lower low water, MLLW) for this NOAA station (#9449880, www.tidesandcurrents.noaa.gov) is 2.36 m, with a lowest recorded water level of − 1.27 m and highest water level of 3.40 m, relative to MLLW. Observed water levels and physical thermal model temperatures were used to assess the relationship between snail behavior, estimated body temperature, and tidal emersion. Three intertidal sites, separated from one another by approximately 100 m alongshore distance, were selected for their relatively steep, east-facing rock surfaces. This semi-vertical substrate was chosen from a variety of available substrate aspects because it decreased the horizontal distance that an animal would have to travel to change tidal elevation. Each site consisted of a rectangular census plot stretching 1.0 m alongshore and vertically from 1.0 m above mean lower low water (MLLW) to 2.25 m above MLLW, plus a larger RFID search area. Epoxy markers (#788, *Z*-spar Coatings, Kop-Coat, Inc., Rockaway, New Jersey, USA) were used to semi-permanently mark plots. RFID search areas consisted of the heterogeneous rocky region of approximately 20 m^2 surrounding each plot. These included horizontally and vertically-oriented surfaces, and were bounded by natural features such as crevices, which were included in searches. The total count of snails in each census plot plus any individual with an RFID tag in the surrounding search area was determined daily and averaged across all three sites. RFID tags enabled individuals to be detected even when they were in microhabitats with low visibility. Each snail was assigned a bivariate level of solar exposure: unprotected from sun (exposed) or in cracks or under algal canopy (refuge), microhabitats known to be cooler on this shoreline (Gilman et al., 2015); and a bivariate vertical tidal elevation: below 1.5 m (low shore) or 1.5 m or above (high shore). This elevation corresponds with the approximate peak barnacle density, yet is above mean elevation for the snails at these sites.

RFID tags (12 mm HDX + PIT, Oregon RFID, Portland, Oregon, USA) were affixed to the shells of *N. ostrina* that naturally occupied chosen survey sites and were 2 cm or greater in shell length (Supplemental Fig. S1). Half duplex (HDX) tags are resistant to electrical noise which allows for the transmission of radio signal through highly-conductive seawater and therefore the tracking of snails while

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