Foraging behavior minimizes heat exposure in a complex thermal landscape

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ABSTRACT: Ectotherms use specialized behavior to balance amelioration of environmental temperature stress against the need to forage. The intertidal snail *Nucella ostrina* risks aerial exposure at low tide to feed on the barnacle *Balanus glandula*. We hypothesized that *N. ostrina* foraging behavior would be constrained by duration and timing of low tide exposure. We added snails to intertidal blocks on San Juan Island, Washington, USA, and forced them to choose between barnacles placed on the western or eastern face of each block, or to shelter and forgo foraging. Snail behavior and barnacle mortality were monitored daily for 8 wk during summer 2011. *N. ostrina* foraging peaked every 2 wk, when temperature was minimized by tidal cycling. Low tide timing determined which substrate orientation was coolest and coincided with the proportion of snails foraging on one substrate face or the other: snails foraged on the western faces on days with morning low tides and on eastern faces on days with afternoon low tides. Barnacle consumption rates mirrored this spatiotemporal foraging pattern. Our conceptual model predicted mobile organism presence and location: snails foraged during the days of the tidal cycle least likely to be hot and selected the coolest available surface when foraging. These results suggest that *N. ostrina* alters foraging behavior to minimize risk of exposure to high temperatures or other emersion stresses. Consequently, predation on barnacles varies over space and time. This spatiotemporal behavior may buffer warming air temperatures and should be considered in models of coastal population and community dynamics.

KEY WORDS: Thermoregulation · Intertidal ecology · Climate change · Tidal cycle · Predation · *Nucella* · Whelk

INTRODUCTION

The impact of climate change on natural ecosystems is dictated by the relationship between organisms and their environments. A key assumption in many climate impact models is that ectothermic organisms, lacking the ability to metabolically regulate body temperature, will be susceptible to the most extreme environmental conditions (Fuller et al. 2010). However, behavior is critical in determining which environmental conditions an ectothermic organism actually experiences (Huey & Tewksbury

2009, Kearney et al. 2009). To make the link between potential temperature and resulting organismal distribution, we must know to what extent animals regulate their exposure to environmental conditions (Huey 1991, Chapperon & Seuront 2011).

Organisms that live in extreme habitats often have specialized behavioral and physiological strategies for surviving stressful environments (Rothschild & Mancinelli 2001). The relative successes of these strategies can have a large impact on community ecology as species are differentially affected and therefore the dynamics between species changes

(O'Connor 2009, Yamane & Gilman 2009). The inter-tidal zone is a well-known example of a habitat with steep environmental gradients, where the transition from terrestrial to marine environment occurs in the space of a few meters (Doty 1946). Key emersion stressors, that generally co-occur, are air temperature (Wethey 1983), solar radiation (Przeslawski et al. 2005), and desiccation (Helmuth 1998). Even when not in danger of lethal exposure, organisms can suffer sublethal effects of extreme environmental factors at the cost of growth, reproductive success, and other components of fitness (Hand & Hardewig 1996). Organisms that live in this transition zone use a combination of strategies to cope with emersion stress, including: (1) physiological, such as the heat shock response (Somero 2002); (2) morphological, such as the specialized structure of cell walls and body plans which foster desiccation resistance and tolerance in algae (Bell 1995); or (3) behavioral, as in the minimization of aerial exposure by limpets when they forage within range of a protective 'home' indentation in the rock (Wolcott 1973).

Exposure regulation strategies must be balanced against energetic needs. For example, one important behavioral strategy used by ectotherms to self-regulate is to seek refuge from high temperature by moving to protected areas when not actively foraging (Cowles & Bogert 1944). In the intertidal, mobile consumers commonly seek food higher on shore where competition is relatively low and prey are more abundant (Connell 1961a, b, 1970), and take refuge at lower shore levels, in cracks in the rock, or beneath sheltering organisms (Spight 1982, Garrity 1984, Johnson et al. 1998). Whereas many mobile consumers such as crabs or fish can move in a matter of seconds to avoid unfavorable conditions, responses by slow-moving animals like gastropods or echinoderms may take hours. When foraging on shore, slow-moving animals risk exposure to emersion stress unless they time their movements carefully. Poor timing can increase risk of exposure to lethally and/or sublethally stressful conditions.

The duration of aerial emersion experienced by an animal during low tide depends on the magnitude and duration of the tide as well as the shore height of the organism and the relative wave height (Harley & Helmuth 2003). Periods of maximum (spring) and minimum (neap) tidal exchange alternate approximately weekly, yielding a 2 wk cycle. The timing of low tide progresses by approximately 50 min each day. The risk of emersion stress cycles with the tides. For example, the highest organismal body temperatures occur during spring tides that coincide with

midday aerial exposure (Helmuth et al. 2002), whereas cool organismal temperatures occur if aerial exposure occurs at night. Mesocosm studies have shown strong temporal patterns in foraging of *Nucella ostrina* that followed the biweekly tidal cycle, with snails feeding continuously for 2 to 4 d when low tides occurred during cool early morning hours (Carrington & Kull 2011, Vaughn et al. 2014). One goal of this study is to determine whether these cyclical patterns of foraging also occur under natural tides in the field.

Animals may also reduce emersion stress by selecting less stressful microhabitats. In particular, locations that differ in solar aspect may differ not only in UV radiation, but also in temperature and relative humidity under the same tidal conditions (Miller et al. 2009, Helmuth & Hofmann 2001, Denny & Gaylord 2010). In this study, we focused on temperature as a tractable representation of these correlated factors. The location and timing of highest temperature change throughout the tidal cycle (Fig. 1). When low tide occurs in the morning, eastern faces of substrates are exposed to solar warming, whereas western faces are shaded, remaining cooler and moister. When the low tide occurs around midday, east and west faces receive about the same solar irradiance. When low tides occur during afternoon, western faces are most exposed to solar irradiance, warming, and drying. Fine-scale exposure gradients are therefore established on intertidal shores by the daily progression of the timing of the lower low tide. If an animal exhibited a preference for foraging in certain microclimates, we would expect to see a shift in the proportion of the population foraging on one side or the other as the low tide timing progressed through the lunar cycle (Fig. 1).

We chose a common mobile predator that lives on shorelines of the Northeast Pacific Ocean: the whelk *N. ostrina*. The genus is known for its impact on habitat-forming barnacles and mussels (Connell 1961a, b). *N. ostrina* preys upon the acorn barnacle *Balanus glandula* by drilling through the opercular ligament and ingesting the contents, commonly taking from 3 to 24 h per barnacle (Emlen 1966, S. E. Gilman & E. Carrington, unpubl. data). As the dominant *B. glandula* zone in the Northeast Pacific is aerially exposed for 5 to 21 h d^{-1}, even when *N. ostrina* begins foraging at high tide, it will likely be exposed to aerial conditions at some point in the foraging process. As low-tide substrate temperatures commonly exceed known lethal limits (LD$_{50}$) for some populations of *N. ostrina* (LD$_{50}$ = 34°C for 80 min at 100% relative humidity or for ~250 min at 0% relative humidity,
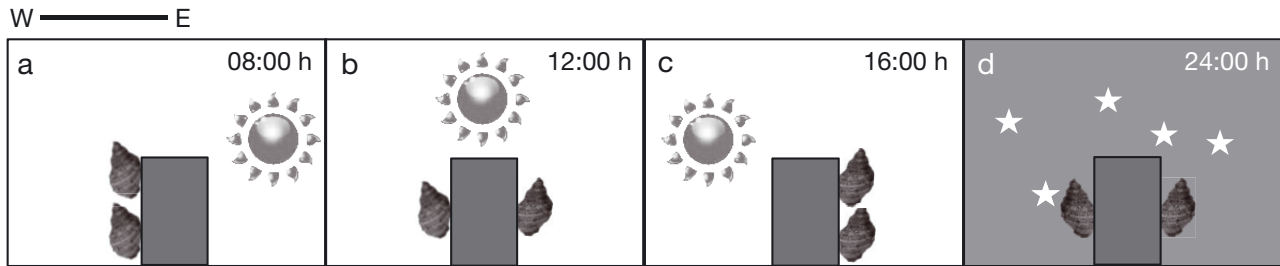
Fig. 1. Conceptual model of how interactions between tide timing and solar radiation influence microclimate and behavior of a mobile predator. Timing of low tide determines solar radiation received by surfaces of different orientations, which in turn determines emersion stress risk. In each panel, a central block represents habitat with prey available only on surfaces facing directly east (right) and directly west (left). Panels show predictions for when low tide occurs (a) in the morning, (b) at midday, (c) in the afternoon, and (d) at night. Snails are predicted to forage on the side more sheltered from direct solar radiation: west and east for morning and afternoon tides, respectively. When the risk on both faces is equal, when low tide occurs at solar noon or at night, snails may be found on either side

Bertness & Schneider 1976), we predicted that snails would avoid the hottest temperatures and show a preference for foraging on the cooler surface.

We hypothesized that: (1) snails would follow a predictable biweekly pattern of increased foraging during periods of cool temperatures and reduced aerial exposure, occurring during neap tide weeks for our study season and location; (2) snails would preferentially forage in cooler microclimates, shifting foraging from the west to the east to follow tidally created shifts in surface warming; and (3) as a result of these choices, snails would experience a cooler subset of the range of habitat temperatures encountered by their barnacle prey. To experimentally test these hypotheses, we corralled *N. ostrina* on artificial rocky outcrops in the intertidal and observed daily foraging.

MATERIALS AND METHODS

Study species

Nucella ostrina Gould, 1852 is a muricid gastropod ranging from Yakutat, Alaska, to Point Conception, California (Vermeij et al. 1990), with a typical vertical range of 0.6 to 1.9 m above mean lower low water (MLLW) at our study locale, San Juan Island, Washington ('SJI,' Connell 1970). *N. ostrina* was collected from Cedar Rock Preserve, Shaw Island (48° 33′ N, 122° 57′ W), Washington, and Friday Harbor Laboratories (FHL) Preserve, SJI, Washington (48° 32′ N, 123° 00′ W). Snails of 15.2 to 26.9 mm in length, with no difference in mean size across all experimental plots (1-way ANOVA, $F_{4,140} = 0.034$, p = 0.998), were housed in aquaria and allowed to self-regulate aerial exposure by crawling up and down aquaria walls. Post collection snails were fed *Balanus glandula* ad

libitum for 0.5 to 6 wk prior to being transferred to experimental plots. Initial surveys were conducted after a 2 wk adjustment period. Each *N. ostrina* was tagged with a vinyl cloth wire marker (20 × 5 mm, Smart Sign) affixed with cyanoacrylate to its shell. These tags allowed identification in refuges without disrupting snail behavior. New snails were sporadically introduced throughout the experiment when densities dropped below the minimum of 5 individuals per plot.

Experimental set-up

Feeding preference experiments were conducted on a south-facing gravel beach at FHL. Concrete slab islands (Fast-Setting Mix no. 1004, Quikrete) were used to mimic the natural bench habitat of *N. ostrina* while constraining the variability in topography. Five square islands (0.76 × 0.76 × 0.10 m) were aligned at +0.95 m above MLLW, separated from each other by 0.5 m (Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). A standard cinder block (0.40 × 0.15 × 0.20 m) was placed in the center of each island, with the greatest surface areas facing east and west. Cobble spacers were used to create moist cool crack refuges beneath each block while enabling snails to move up the walls of the block. Each island was surrounded by a barrier of 15 cm high stainless wire mesh (73.6% open area, McMaster Carr) to deter *N. ostrina* escape. The mesh did not shade the block faces during hours of sunlight exposure.

Barnacle (*B. glandula*) bait shells were created from mussels *Mytilus trossulus* (collected from Argyle Pier, SJI, 48° 31′ N, 123° 00′ W) with barnacle epibionts. Mussels were shucked and drilled to facilitate attachment to the cinder block. Barnacle prey

(*B. glandula*) were placed ad libitum at +1.25 m (±0.03 m) tidal elevation on both the eastern and western faces of each block. Barnacles placed on each face ranged from 8 to 35 individuals, with opercular sizes from 2 to 8 mm. Barnacle bait was exchanged when fewer than 8 living barnacles remained on a block face, except when snails were actively feeding on that face.

Substrate temperature and tidal cycle

Temperatures of the eastern and western faces of each block were recorded at 2 min intervals by one Hobo Tidbit v. 2 datalogger (Onset Computer) per face, adjacent to barnacle prey. Dataloggers were correlated to block temperature, measured by a thermocouple ($y = 1.02x$, $R^2 = 0.78$, n = 126 samples ranging from 34 to 47°C; data not shown). We assume block temperature is the primary driver of snail temperature, as has been shown for limpets (Denny & Harley 2006). However, datalogger temperatures likely overestimate snail body temperatures because live snails cool through evaporation. Observed tidal elevations (NOAA station #9449880, Friday Harbor) were used to distinguish exposed (low-tide) temperatures. Mean daily maximum temperatures and net daily difference between maximum face temperatures were averaged per block across 4 complete lunar tidal cycles (56 d).

Temporal foraging behavior

Foraging surveys were conducted opportunistically during daytime low tide, except for 4 done at night when plots were completely submerged by day. Individual snails were recorded as foraging if they were on the same block face as the bait. Most 'foraging' snails were on barnacles (Fig. S4 in the Supplement at www.int-res.com/articles/suppl/m518 p165_supp.pdf); we chose to include those nearby on block faces because those individuals (<15%) were also exposed to higher emersion stress risk. Dead barnacles were counted daily on each face to assess the number newly consumed by snails. Snail consumption was evidenced by a barnacle test that was completely intact, but lacking tissue inside. Barnacles on faces with actively foraging snails were skipped so as not to disturb behavior. They were assessed on the following day and missing values for daily barnacle consumption were estimated by linear interpolation between known values.

Snails occasionally escaped the plots; most were found within 1 d and returned to their enclosure. Foraging behavior and barnacle consumption were standardized to the total number of *N. ostrina* present in each plot each day. Plots were removed from analysis on days when fewer than 5 *N. ostrina* were found.

Periodicity in foraging behavior and barnacle consumption was examined using autocorrelation (ACF) and cross-correlation (CCF) analyses, with significance assigned to correlation coefficients outside the 95% confidence intervals. These analyses were conducted with SPSS v.19 (IBM).

Microclimate temperature and behavior

Based on the relative length of aerial exposure before and after solar noon, we predicted *N. ostrina* presence on either the eastern or western face of each block. Trees on either side of the beach shaded the plots for approximately 2 h immediately after sunrise and 2 h immediately before sunset. We calculated the proportion of time blocks were exposed from the NOAA observed tides and used the total minutes of aerial exposure in the afternoon subtracted from aerial exposure in the morning to predict the location of foraging snails. Specifically, we tested for an association between the relative number of minutes of aerial exposure in the afternoon and the proportion of foraging snails found on the west face of each block using logistic regression in SAS Proc GLIMMIX (SAS v9.3, SAS Institute). Block and snail identity were included as random effects.

We compared the maximum daily temperatures of all substrate faces to the subset of maximum substrate temperatures on the days and locations of snail foraging to determine whether behavior was shifting snail exposure towards cooler temperatures.
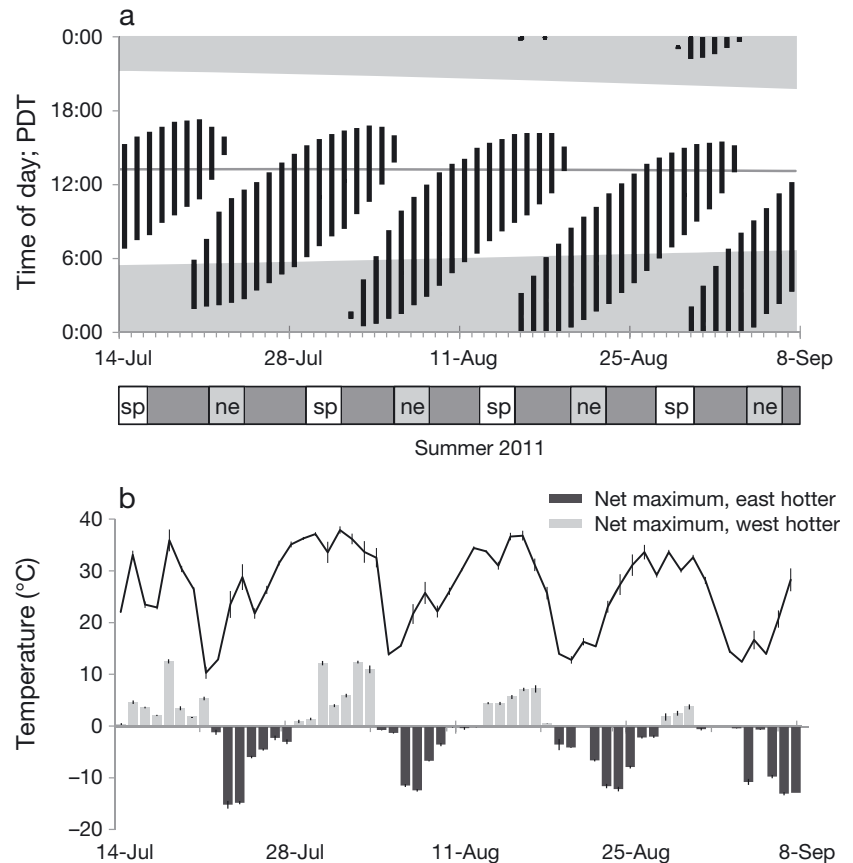
RESULTS

Substrate temperature and tidal cycle

Averaged across both faces, cinder block face temperature fluctuated periodically with the lunar tidal cycle (Fig. 2). The highest maximum temperatures occurred when the blocks were exposed to long low tides in the middle of the day (spring tides and transitions), whereas cooler maximum temperatures occurred when low tides were during the night, early

Fig. 2. Tidally driven temporal and spatial variation in temperature in intertidal microhabitats. (a) Vertical black bars: daily timing and duration of low tide aerial exposure at +1.25 m tidal elevation. Shaded areas: night; horizontal line: solar noon. The bar below shows the phases of the lunar tidal cycle as spring (sp, unshaded), neap (ne, lightly shaded), or transition between the two (darkly shaded). Note that spring tides have long periods of daytime exposure, whereas neap tides have primarily nighttime exposure. PDT: Pacific Daylight Time. (b) Black line: Daily mean maximum substrate temperature averaged over both eastern and western faces. Note temperatures are highest when aerial tidal exposure has longer midday intervals (spring tides). The bar graph below shows the mean difference between the mean maximum temperatures of eastern and western faces. Bars represent days with higher temperatures on the (dark grey) east and (light grey) west. Peak temperatures differ little between the 2 faces when tidal exposure is at night or midday. Whiskers represent SEM, n = 5 blocks

morning, or for only brief periods during midday (neap tides).

The daily progression of the tides through the lunar cycle led to temperature differences between eastern and western substrate surfaces. Generally, periods of higher maximum temperatures on the east were followed by higher temperatures on the west a few days later. This shift corresponded to the gradual transition of low tide from morning to afternoon (Fig. 2). When averaged over the whole experiment, mean daily maximum temperatures were not significantly different between the faces (paired $t = 1.403$, p = 0.255); however, as predicted, there were significant differences during specific tidal phases (Fig. 2b, Table S1 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). On average, eastern faces were 3.7°C warmer during neap tides (paired $t = 8.015$, p = 0.004) and 8.3°C warmer during neap-to-spring transitions (paired $t = 5.988$, p = 0.009), while western faces were 4.8°C warmer during spring-to-neap transitions (paired $t = -3.451$, p = 0.041). During spring tides both surfaces were relatively hot (>30°C) and did not differ significantly (paired $t = -1.529$, p = 0.224). The highest mean daily maximum substrate temperature (32.6°C) occurred on western faces during spring tides, when afternoon

low tide exposure was greatest (Fig. 2b, Table S1 in the Supplement).

Temporal foraging patterns

The mean proportion of *Nucella ostrina* foraging each day varied substantially, from 0 to 0.50 (Fig. 3a). Prevalence of foraging varied with day of the tidal cycle (1-way ANOVA, $F_{3,12} = 6.672$, p = 0.007): foraging peaked during neap tides and spring-to-neap transitions, but was rare during spring tides and neap-to spring transitions (Tukey's HSD, $\alpha = 0.05$; Table S1 in the Supplement). Both peaks and troughs of foraging occurred at regular 14 d intervals (significant autocorrelation coefficient = 0.464, Fig. 4a). Barnacle consumption matched snail foraging behavior (Fig. 3b) and trended towards a similar 14 d cycle, with a significant negative correlation after 7 d (autocorrelation coefficient = −0.251, Fig. 4a). Cross-correlation analysis of the proportion of snails foraging to barnacle consumption per snail showed the greatest significance at a lag of 0 to 1 d (cross-correlation coefficient = 0.550 to 0.592; Fig. 4b), indicating that barnacles were eaten within 1 d of observed snail foraging bouts.
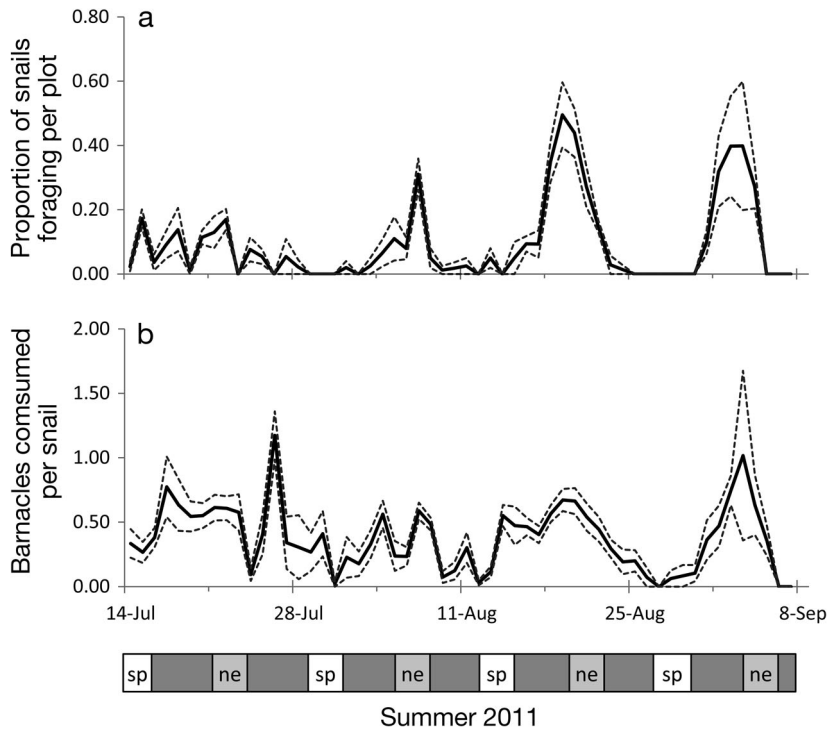
Fig. 3. Summary of temporal patterns in *Nucella ostrina* foraging. (a) Solid line: mean proportion of snails foraging for all plots; dashed lines: ± SEM. The bar below shows the phases of the lunar tidal cycle as spring (sp, unshaded), neap (ne, lightly shaded), or transition between the two (darkly shaded). Note that periods of high and low foraging alternate weekly; highest foraging occurs during the neap tides. (b) Solid line: mean number of barnacles consumed per snail since previous day; dashed lines: ± SEM. Note that pattern of peaks and troughs aligns with snail foraging behavior

Microclimate temperature and behavior

More snails foraged when low-tide temperatures were cool on both faces (neap tides), with very few snails observed foraging on hot days (Figs. 2b & 3a). Mean daily maximum temperature varied periodically with the tidal cycle (significant autocorrelation coefficient = 0.449 at 14 d lag, Fig. 4a) and was negatively correlated with the total proportion of snails foraging (significant cross-correlation coefficient = −0.481 to −0.673 at 0 to 1 d lag; Fig. 4b). The proportion of snails foraging on east versus west faces did not differ when averaged over the duration of the experiment (t = −0.682, p = 0.506) or tidal phase (Table S1 in the Supplement), but trends toward short-term preferences for east or west faces on certain days of the tidal cycle were evident (Fig. 5). Logistic regression revealed, as predicted, that the probability that a foraging snail would be found on the west side of block was greatest when the majority of the low tide exposure occurred in the morning ($F_{1,177}$ = 4.16, p = 0.043). For every 10 min of increase in morning tide, there was a 2.9% increase in the odds ratio of a snail being on the west side (versus the east).
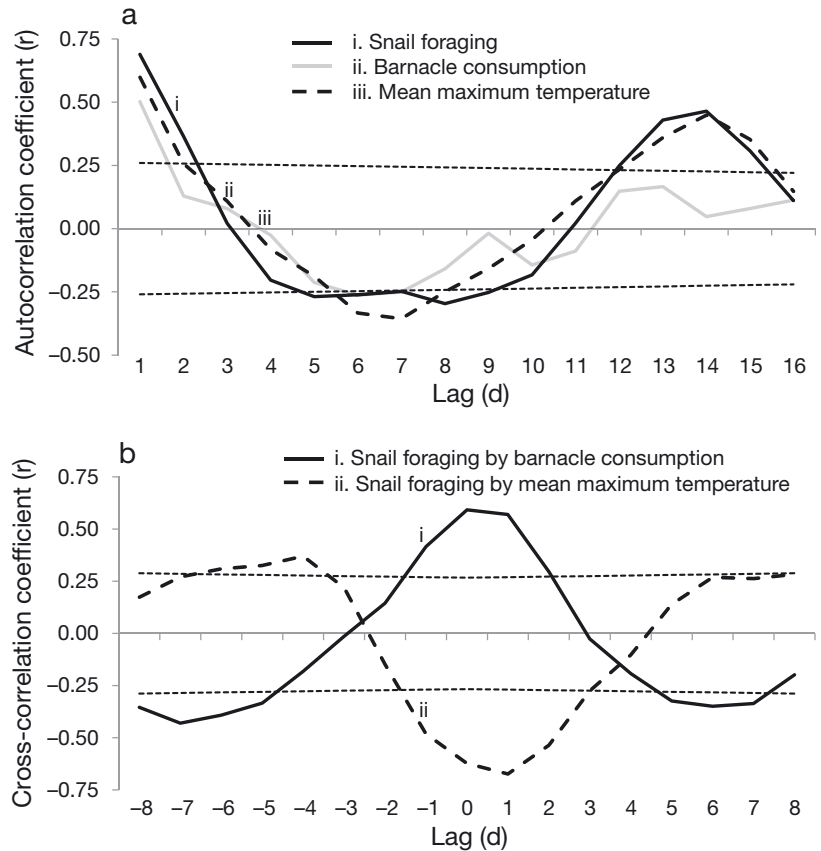
Snails foraged on only a subset of days and substrate faces, therefore experiencing only a subset of the possible emersion conditions. During periods when no snails foraged, the mean maximum daily

substrate temperature was 30.9°C ±6.02 SD; whereas during peak foraging times (>25% of snails foraging) the temperature was only 17.3°C ±5.31 SD. Snails were present for only some of the maximum substrate temperatures experienced by their barnacle prey (Fig. 6). Selectively choosing microhabitat increased the likelihood a snail foraged below its likely lethal limit (e.g. 34°C and up, Bertness & Schneider 1976); on 11 d, substrate temperatures were above 34°C on one side of the block, but not the other. Snails were exposed to a higher proportion of cooler maximum substrate temperatures (≤34°C) and a lower proportion of temperatures above 34°C when they restricted foraging to certain days of the lunar tidal cycle (χ_1^2 = 8.10, p = 0.004). The effect was even more striking when snails chose both restricted days and the cooler of the 2 substrate faces (χ_1^2 = 10.61, p = 0.001).

DISCUSSION

Snails are small, slow-moving ectotherms that need hours to react to environmental changes. Snail decisions to be active or take refuge must thus anticipate whether environmental conditions on a given low tide might reach stressful levels. If they are caught high on shore during a long daytime low tide, they may suffer from heat, desiccation, and UV stress

Fig. 4. Time series analyses of *Nucella ostrina* foraging. Correlation coefficient (r) versus lag number (d). Horizontal dashed lines: 95% confidence interval for all correlations. (a) Autocorrelation coefficients of (i) proportion of *N. ostrina* foraging, (ii) *Balanus glandula* consumed per snail, and (iii) mean daily maximum temperature, showing a significant 2 wk periodicity in snail foraging behavior and mean daily maximum temperature, and a trend towards a 2 wk periodicity in barnacle mortality due to consumption. (b) Cross-correlation coefficients of proportion of *N. ostrina* foraging by (i) *B. glandula* consumed per snail, and (ii) mean daily maximum temperature, showing that snail foraging and barnacle consumption cycle within 1 d of one another, while snail foraging and temperature are negatively correlated, or are out of phase by approximately 7 d

before they can reach an adequate refuge. Tide cycles are the most predictable driver of temperature and humidity in the intertidal zone (Mislan et al. 2009). On predictably high risk days of the tide cycle, snails should therefore avoid high shore activity and either forage lower or stay in refuges. Careful selection of microclimate when foraging high on shore can further buffer the risk of extreme emersion stress. We found both temporal and spatial preferences for foraging in *Nucella ostrina* that are consistent with

emersion risk avoidance. In this study, we measured temperature as one of many correlated emersion stresses.

Biweekly foraging excursions of *N. ostrina* populations peaked on days when lower low tides were in the early morning hours and barnacle prey were submerged during the warmest times of day (neap tides). Barnacle mortality was highest at the same time as snail foraging, supporting our assumption that snails present on block faces were engaged in barnacle
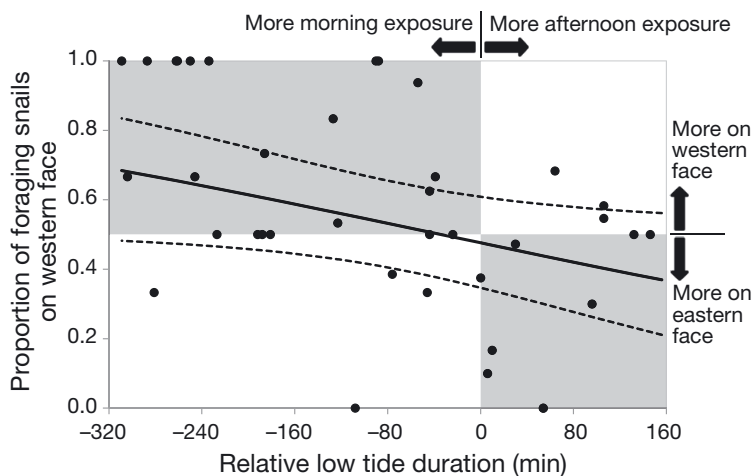

Fig. 5. Microclimate and foraging location with tidal shifts. Proportion of all foraging *Nucella ostrina* found on the western block face versus relative duration of afternoon low tide. Proportions below 0.5 denote a majority of snails on the eastern faces, whereas those above 0.5 represent a majority on the western faces. Relative low tide duration is the total time (min) of afternoon low tide minus the total time of morning low tide. A zero indicates that low tide exposure was equally distributed between morning and afternoon. Solid line: Best significant model fit; dashed lines: upper and lower 95% confidence intervals. Shading denotes expected cooler substrate orientation for given tidal exposure: west during morning low tides, east during afternoon low tides. In general, snails were found on the predictably cooler face during low tide
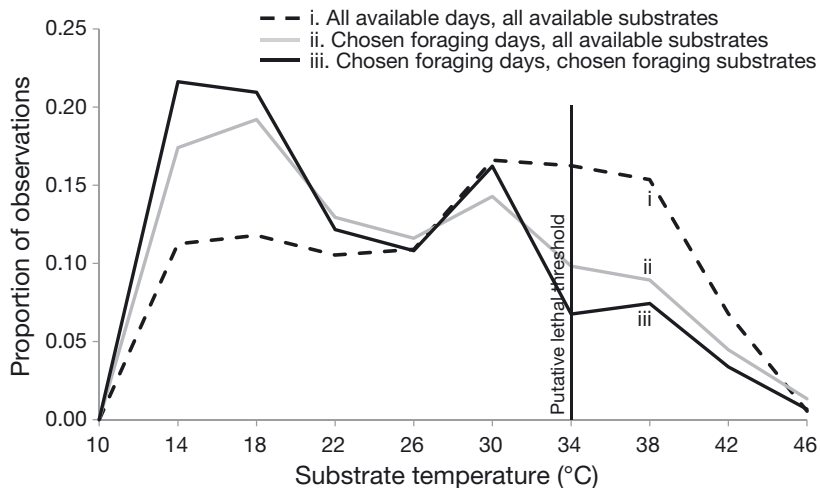
Fig. 6. Distribution of temperatures *Nucella ostrina* experiences for different foraging scenarios. (i) Proportion of daily maximum temperatures (N = 56 d) pooled from eastern and western block faces, (ii) subset of the pooled temperatures for days when snails chose to forage on either eastern or western block faces, and (iii) subset of the pooled temperatures for days and faces when and where snails chose to forage. Horizontal axis values represent upper bounds of each temperature bin. Snail behavior of preferring cooler days and faces increased the proportion of time spent below 26°C and reduced the proportion of time spent above the putative lethal limit for pro-longed exposure, 34°C, marked by the vertical line

consumption. Increased foraging activity during these periods of reliably cool temperatures effectively minimized thermal risk. This temporal pattern of activity relative to tidal conditions was previously described in *N. ostrina* in laboratory mesocosm studies (Carrington & Kull 2011, Vaughn et al. 2014), but this is the first field-based experiment. A similar pattern was observed in field studies of an Atlantic congener, *N. lapillus,* though it was dependent upon wave action (Burrows & Hughes 1989), and in an Australian muricid, *Morula marginalba* (Moran 1985). Natural populations of *N. ostrina* also decrease foraging during spring tides (Spight 1982, H. A. Hayford unpubl. data).

We observed shifts in *N. ostrina* foraging between eastern and western surfaces that matched our prediction that snails would forage preferentially on cooler surfaces. Thus snails have the ability to regulate thermal exposure on small spatial scales (Miller et al. 2009, Denny et al. 2011). The hottest overall substrate temperatures occurred during the afternoon low tides when western faces were directly exposed to the sun. This led to predictable shifts in snail foraging to the cooler eastern surface. Similar behavioral use of microclimates have been reported in other marine and terrestrial species, as differences in solar heating throughout the day create east and west microclimates potentially useful to thermoregulating ectotherms (Huey et al. 1989, Pringle et al. 2003, Harley 2008). This study is unique in its ability to predict spatial and temporal shifts in both predator behavior and predation rates from the biweekly tidal cycle. Risk avoidance mirroring temporal tidal cycling suggests that snails are responding to a tidal cue. Possible cues include sensitivity to water pressure, moonlight, and/or changes in temperature or desiccation (García-March et al. 2008, Chabot & Watson 2010).

Barnacle distribution was controlled in our experiment by placing equal numbers on eastern and western faces, thus emphasizing snail responses to abiotic factors. We recognize that natural barnacle distributions are unlikely to be homogenous (Lathlean et al. 2013), possibly with increased abundances on substrates with lower emersion stress. Barnacle distribution is determined by settlement preference and post-settlement survival, therefore barnacles can only respond to microclimate differences maintained over relatively long periods of time (mo, yr). In our 8 wk study, we observed no difference in temperature between eastern and western faces. In contrast, snail choices are made on the relatively short timescale of tidal cycle (d). We therefore predict the influence of barnacle distribution on spatiotemporal patterns of snail foraging to be minimal.

Predation by *N. ostrina* on *Balanus glandula* varied in both space and time. Tidal dynamics predicted locations and time periods when interaction strength was intensified. In a scenario of global warming, these results suggest behavioral thermoregulation may give this predator an initial thermal advantage over its sessile prey, but decreased thermal risk comes at a cost: decreased feeding. Foraging peaks could become even more infrequent, with feeding occurring only when risk is at an absolute minimum (fewer days per tidal cycle). These consequences are likely to be exacerbated by the increased metabolic demands that accompany increased temperature: snails can reduce foraging to decrease heat exposure or increase foraging to compensate for increased metabolic demands, but in either case may suffer lower growth, reproductive success, and/or survival, as resources in survivors are allocated to cellular repair. Thus *B. glandula* may experience a release from predation pressure if air temperatures warm

(Menge et al. 2002, Yamane & Gilman 2009, Pince-bourde et al. 2012). These temporal fluctuations of interaction strength could shape future communities; quantification may be critical to the goal of predicting functional response to environmental change (Wootton & Emmerson 2005, Gilman et al. 2010).

These effects may be seen at other trophic levels. Our conceptual model assumes *N. ostrina* alters foraging activity primarily to avoid exposure to risky temperatures. However, *N. ostrina* and *B. glandula* are not the only species in this complex coastal food web; *N. ostrina* must also avoid predation. During the experiment we saw signs of predation by the red rock crab *Cancer productus* (Zipser & Vermeij 1978). Predation on *N. ostrina* peaked approximately every 13 d, 2 to 3 d after peak snail foraging, just before the start of the spring tide (Fig. S5 in the Supplement at www.int-res.com/articles/suppl/m518p165_supp.pdf). It is possible that the crab predator follows the snail prey's movement and/or that predation risk is the impetus for snail migration (Yamada & Boulding 1996). However, crab movement is also consistent with our hypothesis that the mobile predator minimizes its aerial exposure. *C. productus* is nocturnal and forages underwater. Therefore, the ideal conditions for vertical migration onshore are likely to be different from those of *N. ostrina*: crab activity should be highest on nights with long tidal immersion. These periods coincide with low tides occurring just before the spring tide series. Crab predation risk cannot explain the shift seen in snail preference for east versus west microclimates; crabs had equal access to both block faces and were foraging primarily when the plots were immersed in cool, benign water.

We were able to test the effect of emersion stress on snail foraging behavior in a natural setting because of the midday low tides in the San Juan Islands during the summer months. We would predict the same pattern of biweekly foraging during the winter months, when low tides occur in the night, but for slightly different reasons. Water, with its high specific heat capacity, is far more resistant to thermal change than air and immersion in water therefore serves as an effective thermal insulator for intertidal organisms. When aerial temperatures dip below freezing, mobile organisms should minimize their time in air. In the winter in the San Juan Islands, this means minimizing exposure to air at night and we would expect to see selection of the same part of the lunar cycle to avoid freezing stress. In other regions of the world, we would also expect to see this pattern of minimizing daytime aerial exposure during summertime low tides. In locations such as California,

however, where spring low tides occur in the predawn hours in summer, only eastern faces would be exposed to sunlight during low tide emersion. We would therefore expect to see more foragers on western than eastern faces, with minimal migration from one face to another.

Our observed shifts in the spatiotemporal pattern of *N. ostrina* foraging demonstrate the importance of selecting not only the right time to forage, but also the right place. For intertidal snails, the most appropriate selection criteria shift over the course of the lunar cycle. These findings have important implications for the design of population surveys, as foraging snails are easily visible compared to those in refuges. Many mobile organisms are bounded by the same principles of resource acquisition versus refuge (Connell 1961a, b, Huey et al. 1977, Stevenson 1985), and are therefore likely to make precisely timed migrations. Censuses, if not properly designed, may incorrectly yield apparent differences in abundance that are, in fact, due to periodic foraging behavior — especially if the sites differ in orientation.

Our results support behavior as an important factor for predicting distribution and predation pressure based upon temperature, important goals of both ecologists and physiologists (Huey 1991, Menge et al. 2002, Kearney et al. 2010). Although individuals may exhibit complex behavior, close examination of the population's spatiotemporal distribution yield predictable patterns of foraging that can be used in mechanistic models to predict changes in distribution and abundance with climate change.

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