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Field Experiments Demonstrate that Heat Spells Can Reduce Territory Defense in the Owl Limpet, Lottia gigantea

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FIELD EXPERIMENTS DEMONSTRATE THAT HEAT SPELLS CAN REDUCE TERRITORY DEFENSE IN THE OWL LIMPET, *LOTTIA GIGANTEA*

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Introduction

Global climate change is likely to put intertidal organisms dangerously near their thermal physiological limits (Harley, et. al., 2006). Hot days, which climatologists predict will increase in frequency and intensity (Diffenbaugh & Giorgi, 2012), are known to fatally overheat and desiccate intertidal species (Harley, 2008).

Less well known are the non-lethal effects of heat spells on the behavior of intertidal species. One high intertidal species, the owl limpet *Lottia gigantea,* uses aggressive behavior to maintain territories free of intra and interspecific competitors (Stimson 1970, 1973; Wright 1985, 1982). Because it excludes both mobile and sessile invertebrates, this territorial behavior strongly structures California's outer-coast rocky intertidal. We hypothesize that the territorial activities of owl limpets may be compromised by heat spells. We test this hypothesis by correlating field measurements and experimental manipulations of temperature with movement frequency and aggression in response to staged territorial challenges.

Figure 1: Test site at Inspiration Point (33.590519°, -117.870750°), Corona Del Mar, CA. View of boulder's more shaded northeastern face.

Materials and Methods

We conducted all tests and observations at Inspiration Point, a marine protected area in Corona Del Mar, CA. All limpets were located on a single long boulder (ca. 30 m long by 4 m wide; Figure 1) running approximately northwest to southeast, providing a sunny southwestern and a shaded northeastern side. We tagged limpets' shells using plastic labels embedded in waterproof epoxy glue.

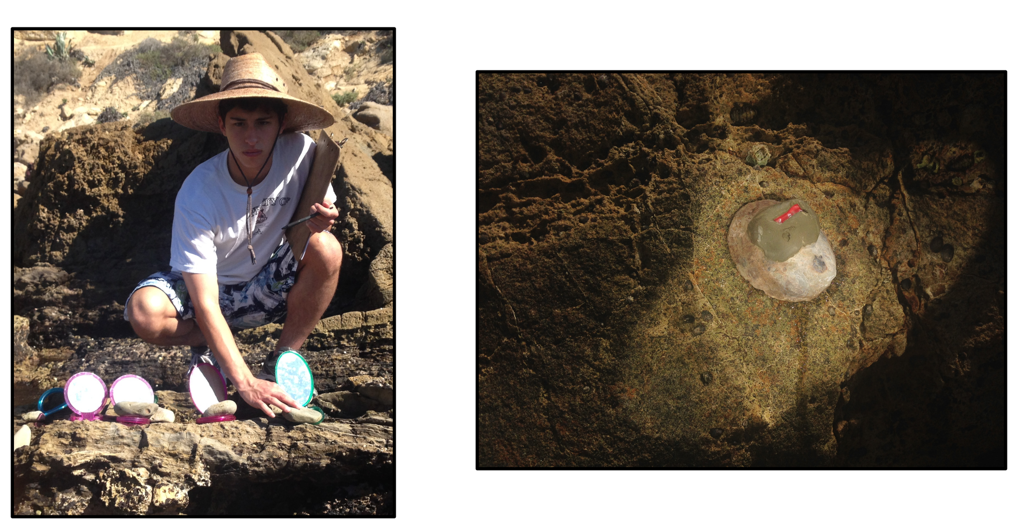

Figure 2. The experimental subject limpet (right) is illuminated with 4 hand mirrors (left). The control limpet remains in the shadow of the adjacent substratum.

During sunny daytime low tides, we identified pairs of test limpets in approximately the same location on the northeastern face and randomly chose one of each pair to be a control or experimental limpet. We heated the experimental limpets for 3-hours using 3-6 small (~20 cm) mirrors to increase the limpets' radiant temperature to between 30-35°C (Figure 2). We monitored temperature with a field-calibrated infrared "thermogun" every 15 minutes throughout the 3-hour period (Figure 3).

Figure 3. Measuring experimental and control limpet radiant temperatures with field-calibrated infrared "thermogun." Temperature measurements were taken every 15 minutes throughout the 3-hour heating period.

The night after heating, during the high-low tide, we returned to observe movement and test for territorial behavior. We determined movement by the presence of visible cephalic tentacles (Figure 4). We elicited a faux territorial encounter by placing a "bait limpet" taken from a nearby location in front of the test limpet (Wright, 1982; Figure 4). Once the limpet moved forward over one shell length it was counted as being territorial. A greater than 90° turn away from the bait limpet was deemed a retreat response.

Figure 4. *Left:* Limpet showing cephalic tentacles, the determinant of movement. *Right:* Baiting a limpet to induce a response (territorial, retreat, or no response) from a moving subject limpet. The bait limpet (upper left) is held in front of the subject limpet (lower right).

Results

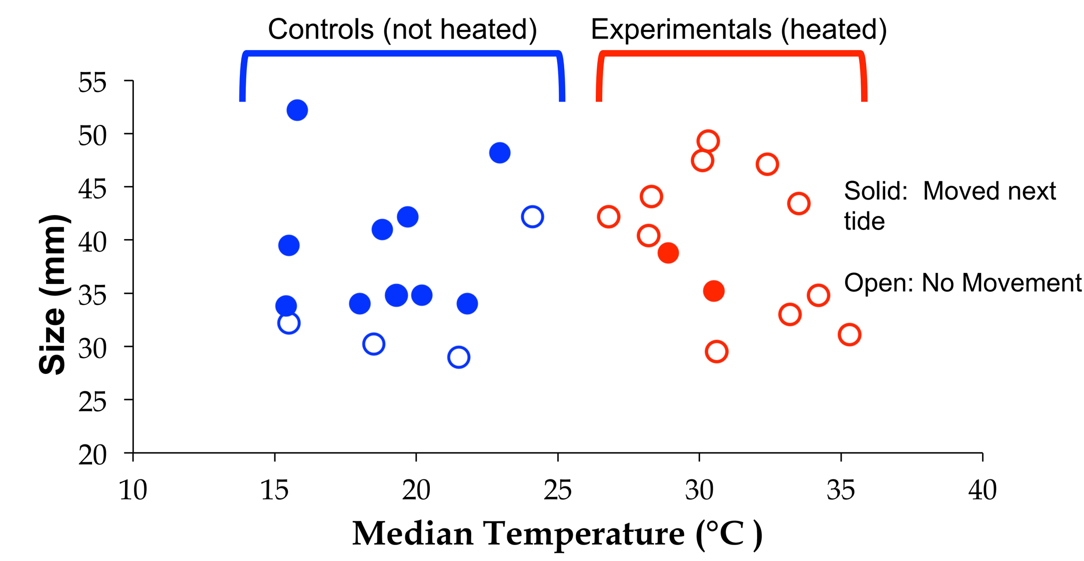

Figure 5. Experimentally heated limpets (red) were less likely to move during the next high-low tide than were unheated control limpets (blue; Fisher Exact Test, P ≤ 0.005). Solid circles show animals which were moving, open circles were animals not moving.

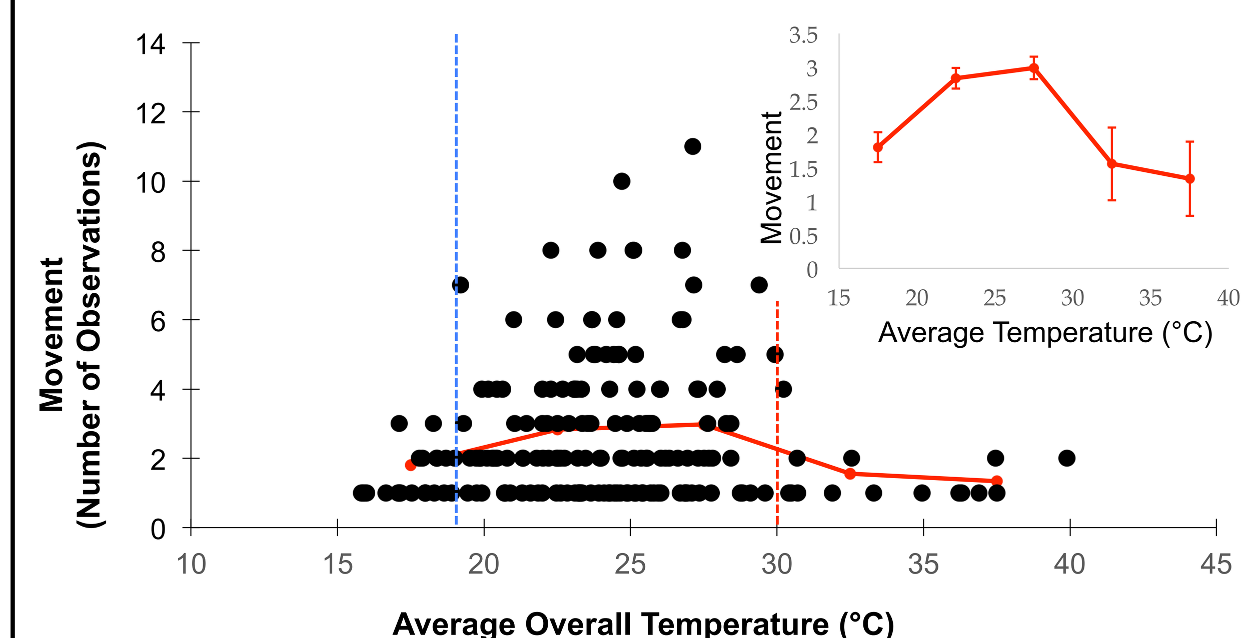

Figure 6. Movement frequency as a function of average daytime low-tide temperature. Movement data from 13 nights (Nov. 2013-June 2014), in which we observed and tested each limpet for movement and territorial behavior. Each dot represents the number of times a specific limpet moved, as a function of average temperature (4-6 sunny low tides during the same time period). Limpets in moderate microhabitats (22-28° C) moved more often than did those in warm (27-40° C) microhabitats (N = 177). Insert plots the average movement frequency (± standard error of mean) at 5-degree intervals.

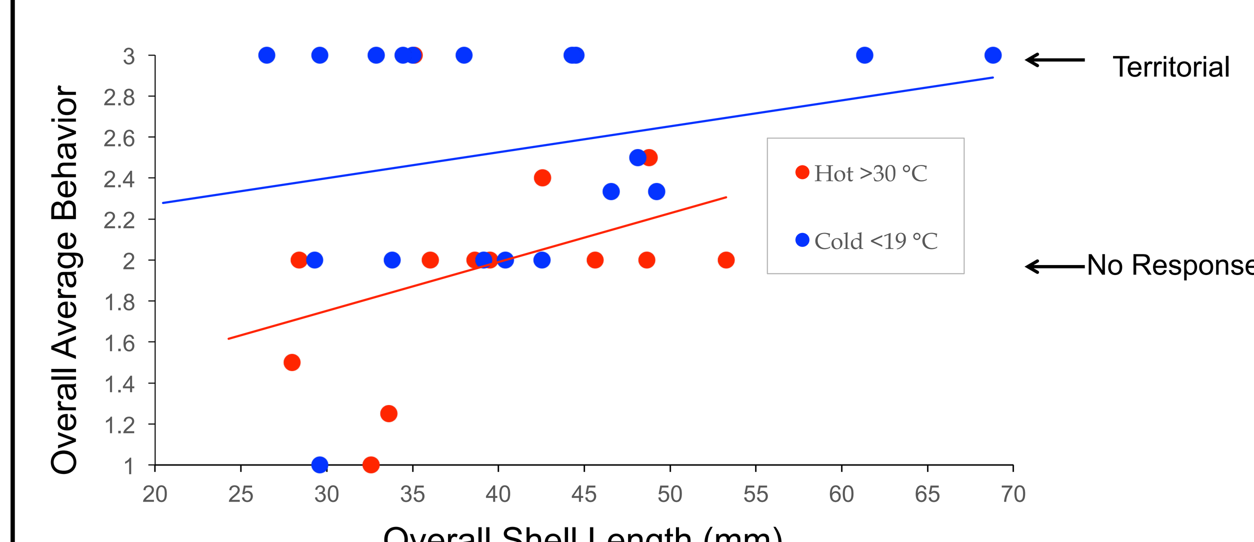

Figure 7. Cooler limpets (blue, < 19°C, see blue dotted line, Figure 6) were more aggressive than warmer limpets (red, > 30°, see red dotted line, Figure 6). Behavior: 1-Retreat, 2-No Response, 3-Territorial Response. Mann-Whitney U-test, P = 0.026.

Conclusions

1. **Experimentally heated limpets were less likely to move during the following high-low tide (Figure 5)**
2. **Limpets in naturally hotter microhabitats move less often than those in more moderate microhabitats (Figure 6)**
3. **Cooler limpets (< 19°C) were more likely to show a territorial response than warmer limpets (> 30°C; Figure 7)**

Significance

The behavioral maintenance and defense of a feeding territory by the owl limpet, *Lottia gigantea*, contributes significantly to the structure of its intertidal community. We showed inhibited foraging behavior in experimentally heated limpets (Figure 5). Furthermore, we also observed few moving limpets in naturally warm microhabitats (Figure 6). Finally, limpets in those warm microhabitats were less aggressive in response to intruding limpets than were those from naturally cool microhabitats (Figure 7). These observations suggest that predicted increases in frequency of extreme heat spells (Diffenbaugh & Giorgi, 2012) may compromise the impact of this limpets territorial behavior on community structure. They also raise the possibility that global climate change may have similar behavioral effects on other "keystone" or "ecosystem engineer" species, even in the absence of observable effects on those species' densities.

Acknowledgements

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