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FACTORS AFFECTING DISTRIBUTION OF *NERITA* SPECIES IN THE INTERTIDAL: EXPERIMENTS WITH MODELS

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ABSTRACT

A series of surveys were conducted to determine whether the position of snails (*Nerita* spp.) in the intertidal zone at San Salvador was predictable based on size and color. Hypothesizing that characteristics which reduced heat gain would be selected for, we predicted that larger and lighter-colored snails would be found farther from the water. Comparing shell characters of snails in horizontal transects five and ten meters from the low water line, we found larger and lighter-colored snails in the upper transect. We placed jars of seawater painted white, black, and tan on transects five and ten meters from the water during low tide, and measured their temperature after one hour. We performed similar experiments using snail-shaped plastic models under a sun lamp in the laboratory. In both cases, white containers remained the coolest, while black reached the warmest temperatures. These results suggest that both size and color can affect the distribution of tropical snails in the intertidal, and that temperature control may be the selective mechanism in their distribution.

INTRODUCTION

An animal living in the intertidal spends part of its day underwater and part exposed to air. Survival in such an environment requires unique adaptations of morphology and physiology not only to reduce the probability of desiccation, but also to withstand extreme temperatures while exposed to air. Shell size and color may both affect temperature change in molluscs. Lighter colors, which increase reflection of the sun's rays, would maintain cooler body temperatures than darker colors, which increase absorption. Previous studies have shown a latitudinal gradient in shell color in the mussel *Mytilus edulis*, with lighter forms predominating at lower latitudes and darker individuals more common at higher (Mitton, 1977). Body size has also been found to affect temperature regulation; Helmuth (1998) found that larger individuals of *Mytilus* sp. were better able to maintain body temperature because the greater tissue mass in larger individuals provided more water for evaporational cooling. Shell size alone might have an effect on heating and cooling, since smaller shells with a greater surface to body volume ratio would absorb more heat than would larger shells.

In the subtropics selection would favor mechanisms for maintaining lower temperatures while exposed at low tide. Since animals living farther from the low tide line are exposed for longer periods of time each day, we might expect adaptations for temperature control to occur in organisms living there. We would predict that related species and populations of conspecifics living higher in the intertidal would be lighter in color and larger than those living nearer the water's edge. Textbooks do cite the occurrence of lighter and larger mollusks higher in the intertidal, but no related experimental results are available (e.g. Nybakken, 1997).

At San Salvador three species of the genus *Nerita* occur in the intertidal: *Nerita peloronta* L., *Nerita versicolor* Gmelin and

Nerita tessellata Gmelin. According to the literature, each has a unique distribution. *N. tessellata* occurs in the upper half of the yellow zone; *N. peloronta* along the edge of the black and gray zones, and *N. versicolor* occurs in a zone intermediate between those occupied by the other two (Kaplan, 1988).

We conducted a series of laboratory experiments with shell models to determine how size and color might affect heat gain. We also conducted field surveys on San Salvador Island to verify that snail distributions fit our hypothesis. We predicted that larger and lighter-colored shells would resist heat gain, and snails with these shell characteristics would occur higher in the intertidal.

METHODS

Field Studies

We surveyed the occurrence at low tide of each of the three species of *Nerita* on 30-meter horizontal transects, five and ten m from the water. These observations were repeated at the following sites on San Salvador: North Point, Dump Beach and the Bluff. These sites are described by Diehl et al., (1988). We used a vernier caliper to measure shell height and recorded the color pattern of each individual in each species found in the transects.

We measured temperature changes after one hour in small containers of seawater, either left clear or painted white, tan or black five and ten m from the water line at low tide. We repeated this experiment three times, with two replicates of each color in each case.

Lab Studies

We used small snail-sized plastic models to determine temperature changes under a sun lamp. Models which were 7 mL in volume were painted black, white and brown, or left clear, and we recorded their temperatures after 2 hours under the lamp. We repeated this experiment five times. To determine the effect of size on heat gain, we conducted the same experiment, using black and white models with volumes of 1.5 mL, 3.5 mL and 7.0 mL.

RESULTS AND DISCUSSION

Field Studies

All 70 individuals of *N. tessellata* occurred in the five meter transects; *N. versicolor* occurred in both sets of transects; 17% of the 142 individuals were found at 5 m, and 83% occurred in the ten meter transects. All but one individual of *N. peloronta* occurred in the ten meter transects. Mean shell lengths of the three species were found to be significantly different from each other (Fig. 1). Since individuals of *N. tessellata* were found to be significantly smaller ($p < .01$) than either of the other two species, their occurrence nearer the water was as predicted. There was also a significant difference in body size between individuals of *N. versicolor* and *N. peloronta* ($p < .01$), although both were more common in the 10 m transect. There were no significant size differences between the 23 individuals of *N. versicolor* that occurred at five meters and the 119 snails that occurred at ten.

Nerita tessellata were the darkest of the three species in terms of shell color with the shell marked with either black and yellow or black and white checks. When the sizes of the two color forms were compared, we found that black and yellow individuals were significantly larger ($p < .0001$) than the black and white forms (Fig. 2); larger size might offset heat gain in darker-colored individuals. As the specific name implies, individuals of *N. versicolor* showed variable shell color patterns; *N. peloronta* had the lightest shell color. The findings on size and color with respect to both *N. tessellata* and *N. peloronta* were as predicted based on the locations where they occur.

Our experiments on snail models were designed to help us determine what effect size and color might have on temperature change within the shell.

When placed along the five and ten-meter transects for one hour, white jars stayed coolest, and black jars took in the most heat. Temperatures were higher overall for the ten-meter transect than for the five-meter one (Fig. 3).

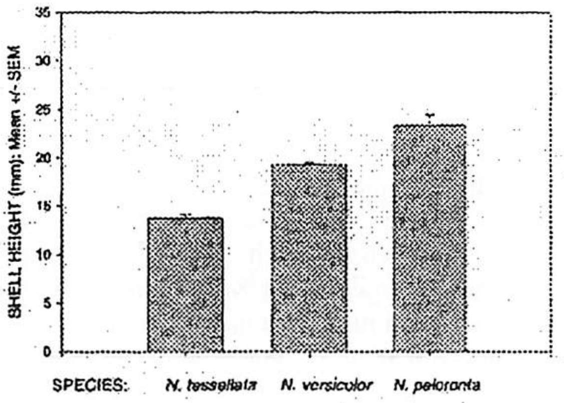

Figure 1. Differences in size among the three species of *Nerita* studied in the field. *N. tessellata* averaged 13.73 +/- 0.39 mm in shell height; *N. versicolor* was 19.18 +/-0.22 mm in height, and *N. peloronta* 23.38 +/-1.08 mm. The shell height of each species was significantly different from that of each of the others.

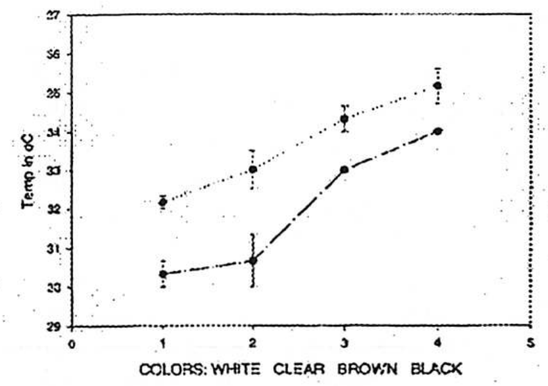

Figure 3. Temperature differences among jars of seawater painted white, brown or black, or left clear. Temperatures reported are the means after one hour in the intertidal, calculated for three separate experiments with two replicates of each color in each experiment. Jars were placed along transects five meters above the low tide line (dashed line) and ten meters above the low tide line (dotted line). There were significant differences in temperature between the white jar and the black and the white and the brown in both transects ($p < .05$).

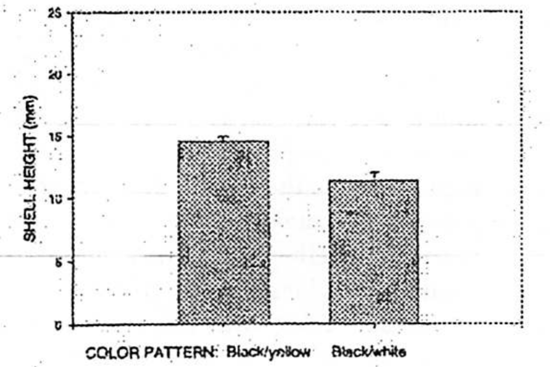

Figure 2. Difference in size between the two color forms of *N. tessellata*. Black and yellow snails were significantly larger than black and white snails ($p < .0001$).

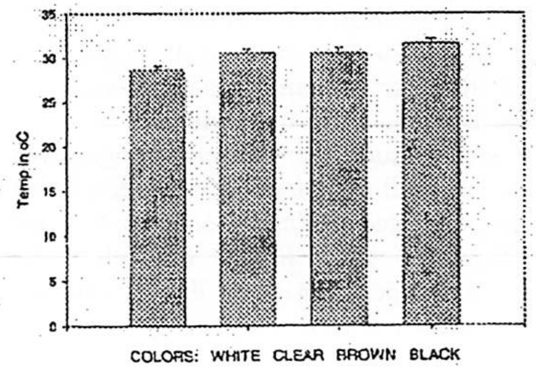

Figure 4. Temperature differences among snail models, 7 mL in body volume, painted white, black, or brown or left clear. Temperatures reported are the mean values after 2 hours under a sun lamp, calculated for five experiments. There were significant differences in final temperature between the white and black, white and brown and white and clear models.

Lab Studies

Plastic shell models, 7.0 mL in volume, that were white, clear, brown or black were filled with seawater and left for up to 2 hours under a sun lamp; white containers remained the coolest after two hours (Mean +/- SE = 28.62 °C +/- 0.48), and black were the warmest (31.60 +/- 0.52 °C). The differences were significant ($p < .003$); Fig. 4).

Our studies on the relationship of volume to warming in the models were confounded by the fact that the three kinds of models used had different shapes. White models that were 3.5 mL in volume were significantly cooler than models that were 1.5 mL ($p < .03$), but there were no significant differences between either of these groups of models and the largest models (7 mL). The same was true for the three different sized models when painted black; smallest models were significantly warmer than the 3.5 mL ones ($p < .003$), but the largest models were actually significantly warmer than the medium sized ones. We attribute these anomalous results to the fact the three kinds of containers differed in shape and therefore in the amount of surface area exposed to the heat source.

Conclusions

Distributions of the three *Nerita* species were as predicted based on color and size, with the small dark species, *N. tessellata* occurring nearest the low tide line, and *N. peloronta*, which is the largest and lightest in color, occurring in the upper zones. Our experiments on the effects of color on warming both in the field and in the lab, indicate the selective role of lighter shell color in maintaining cooler temperatures in the intertidal. While the results of our experiments on shell size were inconclusive, they do indicate that shell size, too, may play a role in temperature control.

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