ENVIRONMENTAL CUES DRIVING THE DIEL ACTIVITIES OF THE TERRESTRIAL HERMIT CRAB *COENOBITA COMPRESSUS*

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Abstract: Hermit crabs at Corcovado National Park, Costa Rica migrate each day from the beach to the forest to seek shelter, and each night from the forest to the beach to forage. We hypothesized that the hermit crabs use environmental cues including beach slope, body temperature, ambient temperature, and light gradients to orient themselves during these diel movements. We used four separate experiments to test our predictions. Our results are inconclusive concerning the effects of slope and temperature, but are strongly supportive of light gradients as cues driving the diel movement of hermit crabs.

Key words: spatial orientation, inter-tidal zone, foraging behavior, behavioral cues, phototaxis, geotaxis

INTRODUCTION

Organisms use environmental cues to orient themselves toward food sources, mating grounds, and shelter. These cues have been extensively studied for many animals; hatchling sea turtles use the light of the ocean to find their way towards the water (Lohmann and Lohmann 1996), songbirds use temperature as a cue to begin seasonal migration (Jenni and Kéry 2003), and snails use geotaxis and phototaxis to move towards the tops of rocks (Warburton 1973). While it has been documented that land hermit crabs (*Coenobita* spp.) spend daytime hours in shelter, and forage after dusk on the beach (Simon et al. 2003), it is unclear what environmental conditions influence this behavior. To determine how land hermit crabs use environmental cues to direct their diel movements, we experimentally tested four hypotheses: (1) depending on the time of day, crabs use the slope of the sand as a cue to orient themselves upslope or downslope; (2) foraging activity depends on the ambient temperature of food sites; (3) the body temperature of crabs influences movement patterns; and (4) crabs use light gradients differently depending on the time of day.

First, we predicted that crabs would move upslope to the nearby forest during the day to seek shelter from the sun, and downslope after dusk to forage along the beach. Second, we predicted that crabs would forage during the day if a shaded pathway was provided toward a food source, but would not move toward a food source in direct sunlight. Third, we predicted that crabs that had been maintained in a cool, shaded location would spend more time roaming the sand in the sun before returning to the more shaded forest line, compared to crabs that had been left in the sun prior to the experiment. Fourth, we predicted that crabs would orient themselves toward darker areas during the day (i.e. to shady refuges, avoiding overheating) and toward lit areas during the night (i.e. toward the ocean and food sources).

METHODS

We conducted our experiments on 3-5 February 2007, during low tide, on the land hermit crab *Coenobita compressus,* on the Pacific coastline of El Parque Nacional Corcovado, Costa Rica. Crabs were haphazardly selected from forest shelters during the day and from the beach at night. A crab was never used for more than one trial.

Slope Experiment: To determine the effect of beach slope on day and nighttime movements, we constructed a sand pyramid with four slopes (Fig. 1), facing the forest, the ocean, the north beach, and the south beach. We used this arrangement to analyze slope independently of destination (i.e., ocean, forest, north beach, south

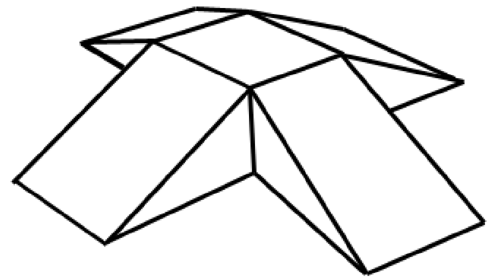

Figure 1. Sand pyramid constructed for the slope experiment, to test response of hermit crabs to slope and slope direction, in day and night trials in Corcovado National Park, Costa Rica. All slopes were approximately 27 degrees, and the four directions were used to control for destination bias (i.e., ocean, forest, south beach, north beach).

beach). For each trial, we placed a hermit crab in the middle of the slope and recorded the direction of its movement (up or down slope) after 10 seconds. We also noted the crab's destination, defined as movement towards the forest or the ocean. We conducted 25 trials on each slope of the pyramid, for a total of 100 trials, at both 0900 and 2030.

Foraging Experiment: To examine the daytime foraging activity of hermit crabs in shade and sun, we constructed an awning covering a 1.75 m-long transect that extended from natural shade onto the sunlit beach. We placed several pieces of coconut and canned tuna, preferred foods of hermit crabs (Hanke et al. 1990), under the awning, and along a similar transect in the sun (Fig. 2). Both the shaded

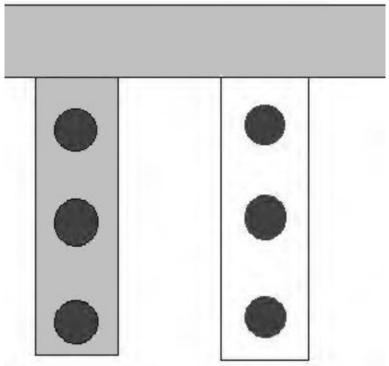

Figure 2. Layout for foraging experiment (not to scale), to determine whether light and temperature affect hermit crab movement toward food sources in Corcovado National Park, Costa Rica. The horizontal gray bar represents a natural crab shelter. The vertical gray bar is the shaded foraging transect, and the white bar is the sunny transect. The three black dots per transect represent places where we placed bait. The transects were 1.75 m long and the distance between transects was 1.75 m.

and sunny transects originated in the same sheltered area and were therefore available to the same population of foraging crabs. We started the experiment at 1030 and counted the number of crabs present at each bait station after 1, 5, 30, 60, and 120 minutes. We simultaneously replicated the entire arrangement using a transect that was naturally shaded by a tree. Because sunlight provides both light and heat, two variables that are difficult to separate in the field, we evaluated them jointly in our experiments.

Pre-heating Experiment: To test for a relationship between initial crab temperature and direction of movement, we placed 20 hermit crabs in a cardboard corral in open sunlight (39.9 ^{o}C sand temperature; hot crabs) and 20 hermit crabs in a shaded corral (31.1 ^{o}C sand temperature; cool crabs) for 1.5 hours. We assumed crab temperatures were similar to sand temperatures in the corrals. We placed each crab in the sand 4 m from the forest and measured the time it took for the crab to move towards the shaded forest. Eighty percent of the crabs in this experiment began moving toward the forest within 5 minutes.

Phototaxis Experiment: To determine the effect of light gradients on crab movements, 8 daytime and 8 nighttime trials were conducted in a 1 x 1 m cardboard corral on the beach, with a cardboard awning shading half of the corral. In daylight trials, unshaded areas were illuminated by sunlight. At night we used a small LED flashlight to simulate moonlight in the unshaded area. For each trial, we placed 10 crabs in the center of the corral and left them for 2 minutes, after which we calculated the percentage of crabs in shaded and unshaded areas. To control for any directional bias, we rotated the cardboard awning after each trial so that it covered a different half of the corral.

Statistical methods: For the slope experiment, we used a Wald Chi-Square test to determine the relative effects of time of day and destination (i.e., ocean, forest, north beach, south beach), and their interaction, on the direction (i.e., upslope, downslope, horizontal) that the crab moved on the slope. We used Chi-Square tests to further determine if the effect of destination outweighed the effect of slope on crab movement. Because the data for the foraging experiment were paired between the shaded and sunny bait stations at each time interval, we used paired t-tests to compare the shaded and sunny foraging sites by trial. To determine whether we could combine the number of crabs at the experimental and natural bait stations, we used a t-test to compare the differences between them. For the pre-heating experiment, we used t-tests to analyze the differences in the time that it took until hot and cool crabs headed upslope. For the phototaxis experiment, we used t-tests to compare the number of crabs in the shaded and unshaded areas.

RESULTS

Time of day did not affect the direction of crab movement in the slope experiment (Wald $\chi^2_2 = 0.34$, $P = 0.84$). However, there were significant effects of destination (Wald $\chi^2_6 = 12.55$, $P = 0.051$) and time of day x destination (Wald $\chi^2_6 = 28.20$, $P = 0.0001$) on the direction of crab movement.

During the day, significantly more crabs moved toward the ocean than toward the forest (Pearson $\chi^2_{2,45} = 9.74$, $P < 0.0062$, $r^2 = 0.10$, Fig. 3) and

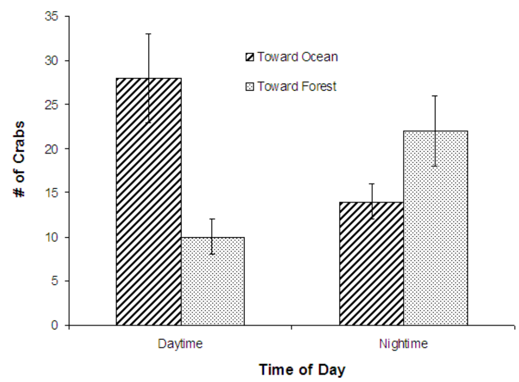

Figure 3. Number of crabs moving toward ocean or forest on the artificial slope (see Fig 1) during both day and night on the beach of Corcovado National Park, Costa Rica. Each crab was placed in the center of a sloping rectangle and the movement toward either destination was recorded after 10 sec. N = 25 individual crabs on each slope for a total n = 100 trials.

significantly more crabs moved toward the south beach than the north beach (Pearson $\chi^2_{2,46} = 28.56$, $P < 0.0001$, $r^2 = 0.33$). There was no significant difference among destination chosen at night, either between ocean and forest (Pearson $\chi^2_{2,44} = 1.86$, $P = 0.39$, $r^2 = 0.019$) or between north and south beach (Pearson $\chi^2_{2,50} = 2.28$, $P = 0.32$, $r^2 = 0.021$).

There was no significant difference in the time elapsed before heading upslope between hot and cool crabs ($t_{37} = 0.66$, $P = 0.26$).

We combined the data from the experimental and natural baits, since there was no significant difference in the total number of crabs at each ($t_8 = 1.39$, $P = 0.20$). The number of foraging crabs was significantly greater at shaded food (paired $t_9 = 3.39$, $P = 0.004$) across all times (Fig. 4). The number of foraging hermit crabs at shaded bait steadily increased over the course of the two-hour observation period, reaching 71 total individuals, while the number of hermit crabs at sunny bait peaked at 10 before decreasing to 0 (Fig. 4). The temperature of the beach in the sun increased by 4.5°C over the two-hour observation period.

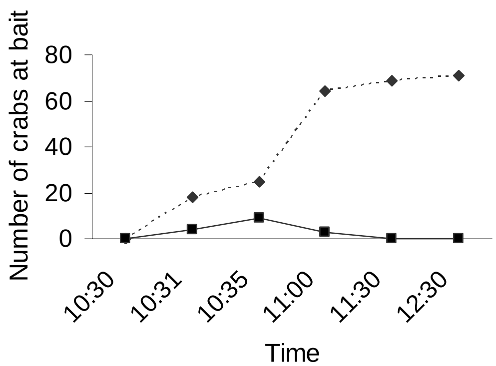

Figure 4. Number of crabs at a foraging experiment (Fig. 2) conducted from 1030 to 1230 on the beach of Corcovado National Park, Costa Rica. The shaded bait station is represented by a dashed line, and the sunny bait station by a solid line.

Crabs showed negative phototaxis (chose shaded habitat) 79% of the time during the day, and positive phototaxis (chose unshaded habitat) 81% of the time at night (t_{14} = 11.40, $P < 0.0001$, Fig. 5).

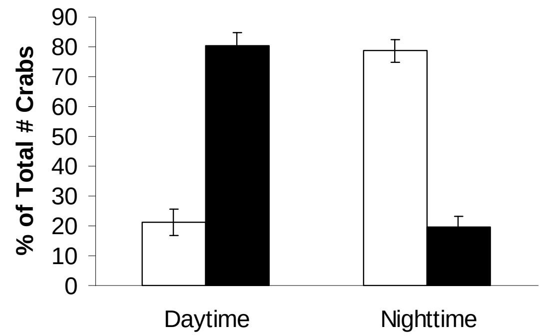

Figure 5. Average percent of hermit crabs in the light or dark half of an experimental corral on the beach of Corcovado National Park, Costa Rica. We conducted phototaxis trials during both day and night. Each trial consisted of ten crabs; N = 8 trials per treatment. White bars represent percent crabs in the light half of the corral, and black bars represent percent crabs in the dark half of the corral.

Discussion

Our results are inconclusive concerning the effect of temperature on crab behavior. The bait experiment showed that crabs foraged less in sunny areas, but we could not disentangle the effects of increased light intensity and ambient temperature. We also found no difference in the behavior of crabs with presumed different body temperatures, despite results from other studies showing that hermit crabs can become heat stressed (Simon et al. 2003). This discrepancy may be due to a failure to induce heat stress in our study.

We found that destination instead of slope was driving crab movement. Because we failed to control for destination, we could not determine the extent to which crabs use geotaxis. Future studies could analyze the effect of slope on crabs in a more controlled setting.

Hermit crabs oriented themselves using negative phototaxis during the day and positive phototaxis at night, supporting our prediction. Our finding that crabs used negative phototaxis during day was also supported by the bait experiment, in which crabs avoided foraging in sunny transects. Phototaxis in crabs is probably important for avoiding heat stress during the day and finding food at night. While it is likely that the high temperatures of the beach are an important driver in the diel migrations of hermit crabs (Simon et al. 2003), more research is needed for definitive evidence.

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