

Too hot to handle? Diel variation in hermit crab distribution and abundance in beach and forest habitat

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Abstract: Abiotic factors such as temperature, tides, and habitat type strongly affect the diel migrations of many organisms. Hermit crabs in a shoreline habitat in Corcovado National Park, Costa Rica inhabit the beach and bordering forest area at different densities within a 24 hour period. We hypothesized that substrate surface temperature would limit hermit crab distribution within these habitats. We found that hermit crab density decreased with increased substrate temperature. We also found more hermit crabs on the beach at night than during the day, consistent with temperature differences. These findings were supported by an experimental manipulation in which hermit crabs showed signs of extreme heat stress when exposed to mid-day beach conditions. Because hermit crabs were found on the beach at night, there may be benefits associated with the beach habitat, such as increased foraging and mating opportunities. However, we found significantly more hermit crabs in the forest than beach habitat overall, suggesting that the forest habitat may also have additional benefits such as protection from predators.

Key Words: desiccation, heat-stress, Paguridae

INTRODUCTION

The daily migrations of many organisms are influenced by both abiotic and biotic factors. Hermit crabs (Paguridae) are one of many species that make diel migrations. Although hermit crabs are generally considered beach and intertidal species, they are also found in forest habitats near the shore. While the beach may be their preferred habitat for finding food and mates, crabs may be forced to take refuge from desiccation, and possibly predation, in the forest (Fenster 1984). The costs and benefits associated with this trade-off change throughout the day as the temperature and tidal conditions vary. At night, lower surface soil temperatures and lower exposure to visual predators may allow the crabs to take advantage of beach resources.

We hypothesized that the distribution of hermit crabs would be affected by temperature, time of day, and habitat type. We predicted that as surface soil temperature increased, the density of hermit crabs would decrease. High daytime temperatures may limit the crabs' access to the beach. Therefore, we predicted that there would be more hermit crabs present on the beach at night than during the day.

We conducted our observations and experiment on 4–6 February 2003 on the beach at the end of the airstrip at Sirena Biological Station in Corcovado National Park, Costa Rica. We sampled at mid tides over a 24 h period, at 08:00, 14:00, 20:00, and 02:00. We set up two 60 m transects from the waterline up the beach, extending approximately 25 m into the forest. At each time, we sampled 1 x 1 m plots every 5 m along each transect, for a total of 13 plots per transect. In each plot we recorded the surface temperature of the substrate, estimated percent shade, recorded habitat type, and counted all hermit crabs.

We then ran two enclosure experiments. Using *Heliconia* leaves, we constructed one large (1 x 1 m) enclosure, and two small (0.5 x 0.5 m) enclosures. One of the small enclosures was set up in the sun and the other in the shade. The large enclosure was half in sun and half in shade. We took the surface soil temperature in each small enclosure and both halves of the large enclosure. We put 15 hermit crabs in the middle of the large enclosure and then counted how many were in each half after 15 m. We put 7 crabs in each of the small

METHODS

enclosures and observed their behaviors.

RESULTS

We found a significant correlation between temperature and hermit crab density (Fig. 1; Spearman's $Rho = -0.21$, $P = 0.03$). We also found significant differences in crab density on the beach among sample times (Fig. 2; $F = 4.67$, $df = 60$, $P = 0.005$). We found a much higher density of hermit crabs at 20:00 (evening) than at 14:00 (afternoon) (Tukey-Kramer).

We found a significantly higher density of crabs in the forest than on the beach overall (Fig 2; $F = 2.52$, $df = 96$, $P = 0.02$). There was a peak in crab density between about 30–45 m, at the beach-forest interface (Fig. 3).

DISCUSSION

Our results indicate that temperature contributes strongly to diel variation in hermit crab distribution. Hermit crabs clearly avoided hot substrates. They were conspicuously absent from the beach during the hottest part of the day (Fig. 1). Our experiment strongly supported our hypothesis that temperature limits hermit crab distribution during daylight hours. In the choice experiment, hermit crabs clearly preferred the shady area and in the fully shaded box, the crabs behaved normally. In contrast, the crabs in the sunny enclosure showed signs of acute heat stress. Within minutes, two out of seven crabs had left their shells, and the remainder produced a foamy substance, which presumably indicates either physiological damage or a cooling mechanism. We immediately aborted the experiment.

However, when surface soil temperatures decreased at night, hermit crabs were present on the beach (Fig. 2). We found higher crab density on the beach at night than during the day, suggesting that there

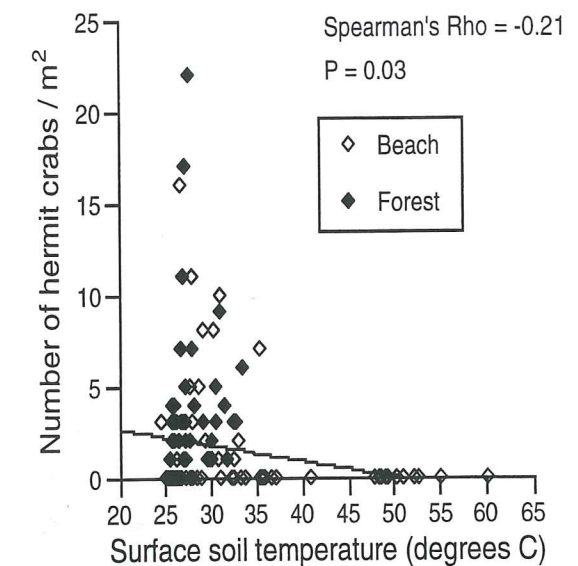


FIG. 1. Correlation between hermit crab density and temperature in two habitats at Sirena Biological Station, Corcovado National Park, Costa Rica. Data are from 1x1 m plots along 60 m transects over a period of 24 hours ($n = 104$).

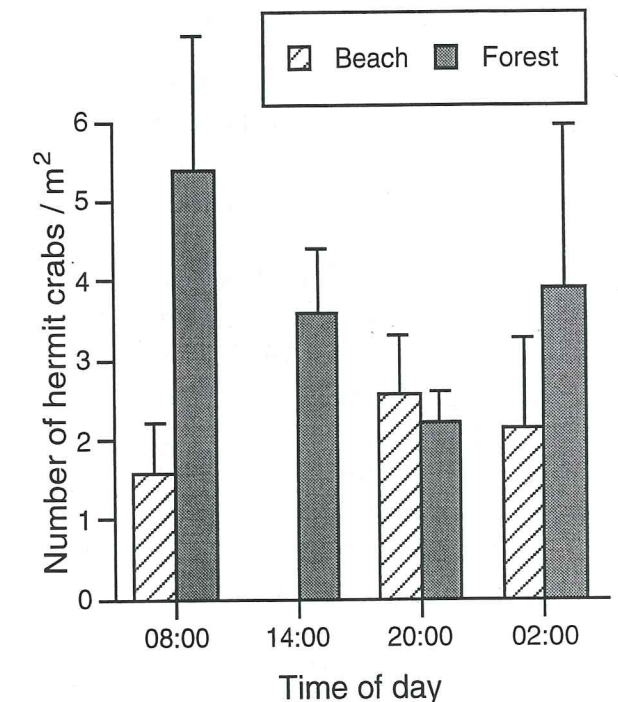


FIG. 2. Hermit crab density in beach and forest habitats throughout the day at Sirena Biological Station, Corcovado National Park, Costa Rica (mean \pm SE). Data are from 1x1 m plots along a 60 m transect ($n = 251$).

may be benefits associated with beach habitats. Hermit crabs are scavengers, and forage on organic matter washed in by the tides. We observed more hermit crabs on the beach during the outgoing tide at 20:00

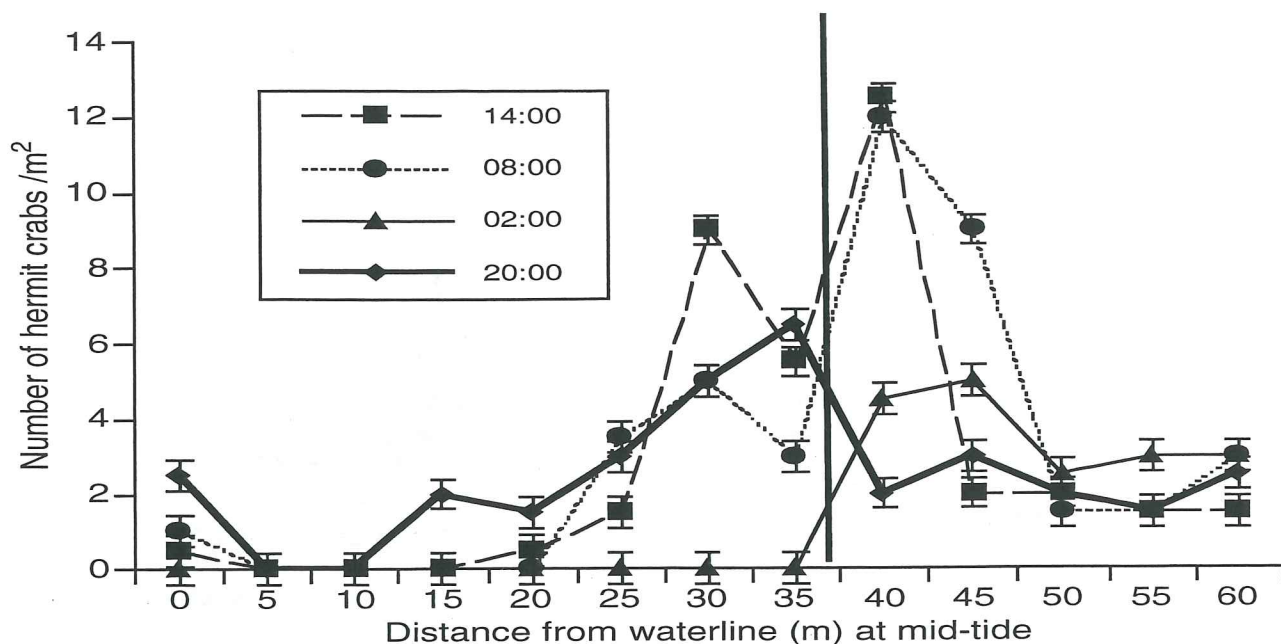


FIG. 3. Distribution of hermit crabs on the beach at Sirena Biological Station, Corcovado National Park, Costa Rica, through a 24 hr period (mean \pm SE). Vertical line represents the transition between forest and beach habitats. Data are from 1x1 m plots along a 60 m transect ($n = 251$).

when food had probably been deposited, than during the incoming tide at 02:00, suggesting a role of tidal cycles and food availability in hermit crab distribution. Due to interspecific competition for food resources, hermit crabs may differentially distribute themselves across the beach (Karlsberg and Hubbard 1995, Biedron and Theoharides 2003). We observed much feeding activity on the beach at night after the tide had fallen, further implicating the beach as an important foraging site.

We found the most hermit crabs in the transitional zone between beach and forest habitats, regardless of time (Fig. 3). This area may be preferred because it provides protection from desiccation and predators and is close to foraging sites along the high tide line. We found that overall hermit crab density was higher in the forest than the beach, which may be due to less variable temperatures in this habitat.

Environmental conditions in hermit crab habitats vary greatly over a daily cycle. We found that hermit crabs make clear habitat choices over the course of a day in order to avoid severe and potentially lethal heat stress. It is possible that hermit crabs

make other choices that may further mitigate the effects of daily temperature fluctuations. For example, crabs choose shell colors ranging from nearly white to black. Future studies could examine whether shell color affects hermit crab distribution in relation to spatial and temporal temperature variation.

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