Microhabitat Distribution of the Hermit Crabs *Calcinus haigae* and *Calcinus hazletti* (Decapoda: Anomura: Diogenidae)[1]

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Abstract: Two sympatric species of hermit crabs, *Calcinus haigae* and *Calcinus hazletti*, appear to have different microhabitat distributions in the subtidal. Several biotic factors may be influencing this microhabitat difference. We documented the field distributions of these two species as a function of coral species and investigated whether aggregation behavior, avoidance behavior, and/or shell exchanges are influencing the distribution patterns. Individuals of *C. hazletti* occurred predominantly on the cauliflower coral *Pocillipora meandrina*. In addition, individuals of *C. hazletti* aggregated toward conspecifics in the laboratory. Individuals of *C. haigae* avoided individuals of *C. hazletti* in the field unless the *C. haigae* were in damaged shells. Individuals of *C. haigae* did not initiate interspecific shell exchange attempts in the laboratory, but individuals of *C. hazletti* did initiate interspecific shell exchanges. Thus, both intraspecific and interspecific interactions affect the distributions of these crabs.

ONE OF THE MOST basic questions in ecology is what factors limit the distribution of individuals. The biotic and abiotic factors that affect where animals are found are of course extremely diverse. Among hermit crab species, as is the case for marine animals in general, zonation along a tidal gradient is very common (Wooster 1982, Haig and McLaughlin 1983, Reay and Haig 1990, Barnes and Arnold 2001). Within a tidal zone, the presence of conspecifics commonly affects microhabitat distribution patterns. Aggregated distributions have been shown for *Clibanarius tricolor* and *Calcinus tibicen* in the Caribbean (Hazlett 1966), *Clibanarius vittatus* in North Carolina (Rittschof et al. 1992), *Pagurus bernhardus* and *P. prideauxi* in the northern Atlantic (Meadows and Mitchell 1973),

and *Clibanarius digueti* in the Gulf of California (Snyder-Conn 1980).

Two common sympatric species of hermit crabs occurring in the Hawaiian Islands, as well as some other locations in the Indo-Pacific, are *Calcinus haigae* Wooster, 1984, and *Calcinus hazletti* Haig & McLaughlin, 1984 (Asakura and Tachikawa 2003). There has been very little published on the behavioral ecology of *Calcinus haigae* or *Calcinus hazletti* other than descriptions of the postures and movements of limbs during intraspecific social interactions (Hazlett 1972, 2009). Hoover (2006) suggested that *C. hazletti* occurs more often on living cauliflower coral, *Pocillopora merandrina*, than on other corals. Casual collections on the island of Hawai'i revealed that coral heads with *C. hazletti* present rarely had *C. haigae* present. Preliminary observations also indicated that these two species overlap in resource use because they utilize the same species of shells. Thus, it is of interest to explore how the potential interactions between these two species influence their microhabitat distributions.

In this study, we investigated four questions related to the microhabitat distributions of *Calcinus haigae* and *Calcinus hazletti*: (1) Are *C. haigae* and *C. hazletti* distributed at random in the field or do they have microhabitat preferences? (2) Do individuals of the two species

Species	n
Calcinus haigae	62
Calcinus hazletti	29
Calcinus elegans	13
Calcinus latens	12
Calcinus isabellae	2
Calcinus guamensis	2
Ciliopagurus strigatus	2
Dardanus sanguinocarpus	2

show aggregation behavior in the laboratory? (3) Do individuals of *C. haigae* avoid coral heads occupied by individuals of *C. hazletti*? and (4) If so, is the mechanism behind this avoidance related to shell exchanges?

MATERIALS AND METHODS

The work was done in Hōnaunau Bay on the west side of the island of Hawai'i during February and March 2008 and January 2009. Both species are subtidal, with individuals occurring on corals primarily below 2 m water depth. Although eight species of hermit crabs were found in field surveys at that site, *Calcinus haigae* (50% of the crabs collected) and *C. hazletti* (29%) were the most common species (Table 1). Comparing the three most commonly occupied shell species (*Nassarius papillosus*, *Coralliophila neritoidea*, and *Drupa morum*), these field surveys showed that *C. haigae* and *C. hazletti* did not differ in the shell species occupied ($\chi^2 = 2.02$, df = 2, $P = .36$). All crabs used were adult size, 6–10 mm cephalothorax length. All field experiments were carried out on coral bommies (distinct outcrops of corals) approximately 2 m by 2 m by 2 m high.

Microhabitat Preference

We surveyed the microhabitat distribution pattern of individuals on corals to determine if the two species of crabs had preferences for coral species. It is not always possible to distinguish between individuals of the two species in the field when they are holding on to the substrate, and both species, but

especially *C. hazletti*, tend to drop down into crevices in the coral when approached (Hoover 2006). Therefore we collected specimens of both species and marked the shells with white correction fluid and dots of color to identify the species without disturbing them. We marked the crabs on one day, placed them on a distinct coral bommie, and the next day recorded the types of corals on which they were found. On day 1, we also estimated the percentage cover on the bommie of living *Pocillopora meandrina*, of other living coral species (primarily *Porites lobata*), and of dead coral.

We placed 17 marked *C. hazletti* and 20 marked *C. haigae* on two different bommies on 2 March 2008. Crabs were placed in the middle of the bommies on living *Porites lobata*. On 8 March (when all previous marks had worn off), we placed 19 marked *C. hazletti* and 20 marked *C. haigae* on the same bommies but alternating which species was placed on each bommie. The bommies were searched on 3 and 9 March, and the types of corals on which the marked crabs were found were recorded.

Aggregation in the Laboratory

Given preliminary observations that crabs were aggregating in the field, we tested for aggregation under more controlled conditions in the laboratory. We placed 10 crabs in a plastic container (15 cm by 30 cm by 10 cm deep) and placed the container in an aquarium with aeration. The container had marks on the outside dividing the substrate into 12 quadrants of equal size (7.5 cm by 6 cm). Ten crabs were distributed randomly in the container in the afternoon, and the number of crabs in each quadrant was recorded 6 hr later (at night) and 18 hr later (during the next day). In five replicates the 10 crabs were individuals of *Calcinus hazletti*, and in five replicates they were *C. haigae*. The observed distributions were used to calculate Morisita's Index of Dispersion, I_M (Hurlbert 1990) for each replicate. Wilcoxon signed-rank tests compared the observed index of dispersion values with the I_M value of 1.0 expected if crabs were distributed at random for each species during the day and at night.

Avoidance in the Field

The field distribution results showing that individuals of *C. haigae* were not found on living cauliflower corals (see Results) suggested the possibility that individuals of *C. hazletti* were keeping individuals of *C. haigae* away from living cauliflower corals in the field. In our releases of crabs to determine microhabitat preference, we had not removed crabs of either species from the bommies before placement of the marked crabs. To address this question of preference by individuals of *C. haigae*, we selected other bommies on which there were two living *Pocillopora meandrina* heads of similar size (about 20 cm in diameter) separated by about 30 cm of living *Porites lobata*. We removed all crabs from the bommies. On day 1, we placed five marked *C. hazletti* in one of the heads and placed 10 marked *C. haigae* equidistant between the two heads. This experiment was conducted at two sites on 14 March and two other sites on 18 March 2008. We sampled the location of the marked crabs 1 day later.

The apparent strong avoidance of coral heads with *C. hazletti* already in them by individuals of *C. haigae* (see Results) could be a resident effect, not a species effect. That is, individuals of *C. haigae* could just be avoiding a coral head that is already occupied by other hermit crabs. To test this possibility, in January 2009 we set up a second type of field experiment, again using four different bommies, but placed five marked *C. haigae* in one coral head and placed 10 *C. haigae* marked with alternate colors between the two heads. The next day the number of shells marked with alternate colors in each of the coral heads was recorded.

One possible reason that individuals of *C. haigae* might avoid *C. hazletti* could be that *C. haigae* does not get better shells from interspecific shell exchanges. If that were the case, one could predict that *C. haigae* in less-preferred shells (damaged, unpreferred species, wrong size) would be less motivated to avoid *C. hazletti*. To test this, in January 2009 we repeated the first experiment but used *C. haigae* in damaged shells. We damaged the shells of 20 *C. haigae* with pliers and at two sites placed 10 *C. haigae* between

two cauliflower coral heads, one with five *C. hazletti* and one with no crabs. We recorded the location of the *C. haigae* the following day.

Shell Acquisition

The acquisition of appropriate gastropod shells is critical for all species of hermit crabs, and it is possible that the avoidance of individuals of *C. hazletti* by individuals of *C. haigae* could be related to avoidance of interspecific shell exchanges. The two species clearly occupy similar arrays of shells, yet when the two species of crabs were observed in aquariums together there were no interspecific shell exchange attempts. In the case of *C. haigae*, no intraspecific attempts were observed despite over 50 hr of observation (Hazlett 2009), but there were a number of intraspecific attempts by individuals of *C. hazletti*. *Calcinus haigae* behaved as if all individuals were in well-fitting shells.

To further investigate shell exchange behavior between these two crab species, 10 individuals of each species of similar sizes were placed together in an aquarium. Five individuals of each species had their shells damaged with a pair of pliers before placement together. We then watched sets of crabs for an hour, recording who got into the opposed position (shell apertures facing, the first act leading to a shell exchange attempt) with whom. Any occurrence of rapping behavior, the characteristic bringing together of shells by the initiator (Hazlett 1966), was also recorded. The crabs were then left together overnight with five empty shells of the appropriate size range and species. Shell occupation was recorded the next morning. This experiment was conducted twice in 2009.

RESULTS

Microhabitat Preference

The field surveys showed that *C. haigae* and *C. hazletti* had different distributions on the coral bommies, and neither crab species occurred on the coral types in proportion to their availability (Figure 1). Although living *Pocillopora meandrina* made up only 5% of
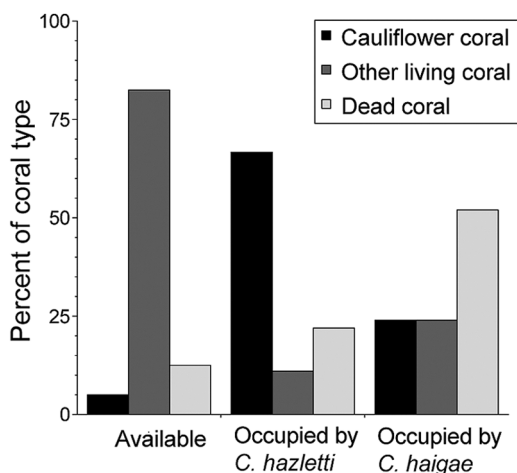
FIGURE 1. Percentage of coral types (cauliflower coral, other living coral, and dead coral) available on coral bommies, occupied by *C. hazletti*, and occupied by *C. haigae*. For available coral types, the percentage is the mean of the two coral bommies, whereas for the crab occupation, percentage is the percentage of crabs for both bommies combined. Sample sizes of the number of crabs found were as follows: *C. hazletti* ($n = 27$) and *C. haigae* ($n = 25$).

the cover, the majority of individuals of *C. hazletti* were found on living cauliflower coral heads. The majority of the *C. haigae* were found on dead coral even though that made up only 10%–15% of the cover. Both species tended to avoid the most common coral, *Porites lobata*. Comparing the number of individuals found on the different coral types with the number expected if the crabs were distributed in proportion to the available percentage cover showed that the distributions of both species differed very significantly from random ($\chi^2 = 232.8$, df $= 1$, $P < .001$ for *C. hazletti*; $\chi^2 = 61.1$, df $= 1$, $P < .001$ for *C. haigae*).

In the case of *C. hazletti*, the crabs did not seem to be distributed evenly among the heads of *Pocillopora meandrina* on the bommies. There were four coral heads on each of the bommies and there were 0, 1, 3, and 4 individuals of *C. hazletti* on individual heads on one bommie and 3, 3, 3, and 1 on individual heads on the other bommie. These numbers are too small to analyze statistically and although this "pattern" could be due to vari-

ance in some qualities of the heads, it is suggestive of some degree of aggregation.

Aggregation in the Laboratory

The distribution of individuals of *C. haigae* in the laboratory did not differ from random either during the day ($I_M = 0.99$, Wilcoxon $Z = 0.96$, $P = .34$) or at night ($I_M = 0.92$, Wilcoxon $Z = 0.35$, $P = .89$). The distribution of individuals of *C. hazletti* did not differ from random during the day observations ($I_M = 1.32$, $Z = 0.94$, $P = .34$), but at night they were significantly aggregated ($I_M = 3.90$, $Z = 2.02$, $P = .043$).

Avoidance in the Field

In the field experiments testing whether *C. haigae* avoids coral heads occupied by *C. hazletti*, between 60% and 80% of the *C. hazletti* remained in the coral heads in which they were placed. At all four bommies, individuals of *C. haigae* readily colonized coral heads not occupied by *C. hazletti*, whereas not a single individual colonized heads with *C. hazletti* (Figure 2, Expt. 1). This preference for coral heads not occupied by *C. hazletti* was very significant (14 versus 0, $\chi^2 = 13.0$, df $= 1$, $P < .01$). These results suggest that individuals of *C. haigae* avoid heads of living cauliflower coral only when those heads have individuals of *C. hazletti* in them.

In the field experiments testing whether *C. haigae* avoids coral heads occupied by *C. haigae*, a total of 12 individuals of *C. haigae* was found in the coral heads with resident crabs and 11 in the unoccupied heads (Figure 2, Expt. 2); this pattern is clearly not different from an even distribution ($\chi^2 = 0.043$, $P = .835$). Thus it appears that individuals of *C. haigae* do not avoid heads occupied by conspecifics but do avoid heads occupied by individuals of *C. hazletti*.

The field experiments with *C. haigae* in damaged shells resulted in no avoidance of *C. hazletti*. Of the 11 *C. haigae* found in the target coral heads, six were in the coral head with *C. hazletti* and five in the coral head without *C. hazletti* (Figure 2, Expt. 3). Clearly
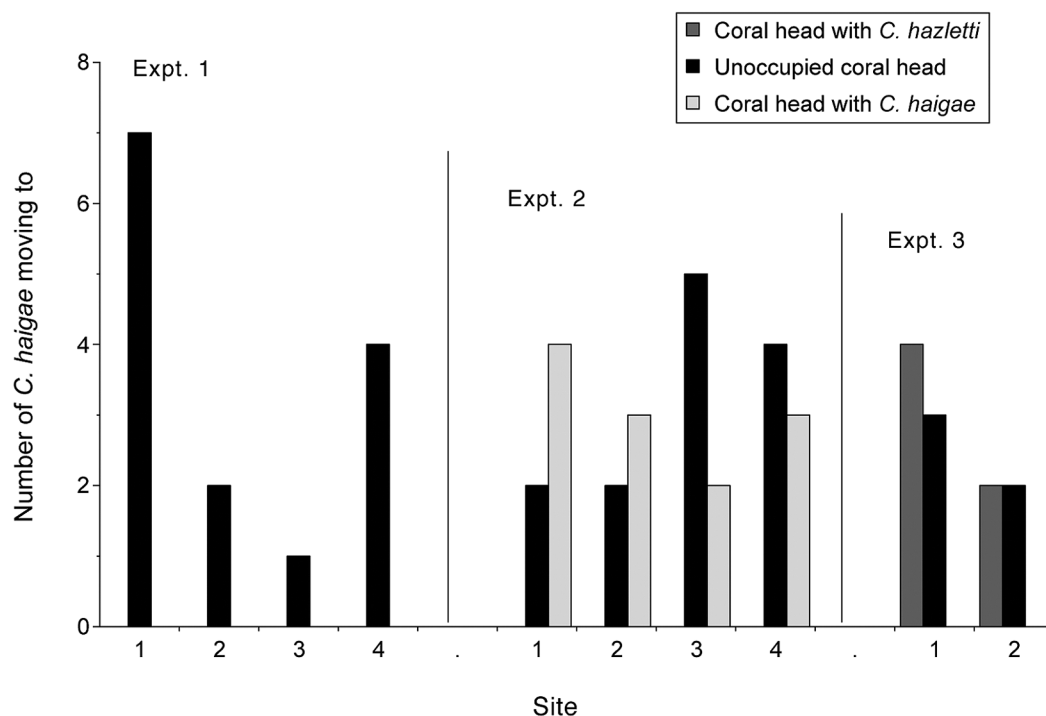
FIGURE 2. Number of *Calcinus haigae* moving to different coral heads in choice experiments in the field: Expt. 1, choice of coral head with *C. hazletti* or unoccupied coral head; Expt. 2, choice of coral head with *C. haigae* or unoccupied coral head; Expt. 3, choice of coral head with *C. hazletti* or unoccupied coral head by *C. haigae* in damaged shells. Each site represents a separate coral bommie.

there was no difference and no avoidance of *C. hazletti* in the field when the *C. haigae* were in damaged shells.

Shell Acquisition

When we damaged shells and recorded attempted shell exchanges in the laboratory, there was a total of 23 instances of one crab getting into the opposed position with another crab. Of these, nine were individuals of *C. haigae* in damaged shells being the initiator and of those cases, all nine were with individuals of *C. haigae*. Individuals of *C. hazletti* got into the opposed position six times with conspecifics and eight times with individuals of *C. haigae*. Rapping by individuals of *C. hazletti* occurred in three cases (one *C. haigae*, two *C. hazletti*). As was the case with the results from the field experiments, in-

dividuals of *C. haigae* appear to avoid interactions with individuals of *C. hazletti*. Individuals of *C. hazletti* do not avoid contact with heterospecifics. After being left overnight with empty shells, six empty shells were occupied by *C. hazletti* and one empty shell was occupied by *C. haigae*.

DISCUSSION

The microhabitat distributions of individuals of *C. hazletti* and *C. haigae* within the subtidal zone are affected by a number of biotic factors. Individuals of both species seem to avoid the dominant coral in the area, *Porites lobata*, probably because the smooth surface of that species does not offer many hiding places. *Calcinus hazletti* prefers the cauliflower coral, *Pocillopora meandrina*, as suggested by Hoover (2006). The branches of this coral afford hid-

ing places that presumably protect the hermit crabs from predators.

In addition to its preference for *Pocillopora meandrina*, the microhabitat distribution of individuals of *C. hazletti* tends toward a clumped distribution, with crabs often maintaining very short distances between individuals. This pattern of aggregation has been reported for other hermit crab species, such as *Clibanarius tricolor*, *Pagurus miamensis*, and *Calcinus tibicen* (Hazlett 1966). Clumped distributions have also been reported in *Clibanarius digueti* (Snyder-Conn 1980), *Clibanarius vittatus* (Rittschof et al. 1992), *Clibanarius virescens* and *Calcinus laevimanus* (Gherardi and Vannini 1989), and *Pagurus bernhardus* and *P. prideauxi* (Meadows and Mitchell 1973). It has been suggested that clumping facilitates shell exchange opportunities (Rittschof et al. 1992) and may help retain moisture when crabs are exposed at low tide (Snyder-Conn 1980). The latter function would not apply to a subtidal species such as *C. hazletti*.

The avoidance of one species of hermit crab by individuals of another species is more unusual. Individuals of *C. haigae*, when in their normal, field-occupied shells, clearly avoid *C. hazletti*. This occurred in the settlement patterns in the field and in shell exchange attempts in the laboratory. In fact, the presence of *C. hazletti* seems to prevent *C. haigae* from occurring on some cauliflower corals. The fact that making shells suboptimal by clipping with pliers eliminated that avoidance suggests that interspecific shell exchange is what individuals of *C. haigae* are avoiding because they might lose the good shells they occupy.

In most reported instances of interspecific shell exchange, the negotiations model (Hazlett 1978, 1996) seems to best describe the process of resource exchange. That is, crabs exchange shells interspecifically only when both individuals gain in shell fit (Hazlett 1980, 1983). Studies on other pairs of Hawaiian hermit crabs showed both gaining in shell fit in most cases, although in the case of individuals of *Calcinus laevimanus* interacting with *Clibanarius zebra*, this was not the case (Hazlett 1990). Obviously further studies of *C.*

hazletti and *C. haigae* and their patterns of interaction are needed, but it would be interesting if individuals of *C. hazletti* did not follow the model of shell exchange proposed by Hazlett (1978)!

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