WHERE IN THE WORLD IS *GECARCINUS QUADRATUS*? DISTRIBUTION OF AN ELUSIVE BUT INFLUENTIAL FOREST SPECIES

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Abstract: The land crab, *Gecarcinus quadratus,* influences sapling diversity in the 'crab zone', an area within 600 m of the beach bordering coastal neotropical rainforests. Despite their abundance and importance, little is known about the spatial population structure of this species because crabs are rarely seen. We suspected that intraspecific interactions would cause non-random crab distributions throughout the crab zone. We hypothesized that a sand-to-soil gradient would influence crab densities and hole structural characteristics. We tested these hypotheses by measuring crab spacing and density, as well as hole diameter and depth at varying distances from the beach. We found no evidence of intraspecific interactions affecting the spacing of crabs, but conclude that abiotic factors may affect the spacing of their holes. We also found that the density of holes decreases, the diameter of holes increases, and the depth of holes does not change with distance from the beach. We suggest that only larger crabs are able to dig through the non-sandy inland soil. The fact that *G. quadratus* is so abundant, yet so rarely seen, suggests that it experiences intense predation pressure.

Key words: crab zone, dispersion, hole structure, intraspecific interactions, land crab, substrate gradient

INTRODUCTION

The land crab, *Gecarcinus quadratus*, lives in holes dug in the coastal neotropical rainforest floor, in a zone extending 600 m inland from the beach. These crabs have been shown to affect plant community composition in this "crab zone" by selectively feeding on seedlings, thereby reducing the diversity and abundance of saplings (Sherman 2002). Despite the importance of this species in forest dynamics, little is known about the ecology of this crab. This is due, in part, to the shy nature of *G. quadratus*; it is rarely seen in the dry season despite the prevalence of its holes. In pilot studies we could not locate *G. quadratus*, and it seemed that some holes were occupied while others were empty. Because crab spatial distributions probably influence the surrounding plant community, we explored the spatial population structure of *Gecarcinus quadratus*.

We hypothesized that crab spatial population structure would be influenced by intraspecific interactions such as competition and territoriality. If crabs are territorial, the spatial distribution of crabs and their holes would be uniform. We also hypothesized that a gradient in soils from sand near the beach to fine mineral soil farther inland would affect crab distribution. It could be that only larger crabs can dig holes in the harder inland soil, in which case we would see decreased density of crabs and their holes, increased hole diameter, and decreased hole depth with increasing distance from the beach.

METHODS

We tested these predictions in a section of the crab zone at Corcovado National Park, Costa Rica, on 4 - 6 January 2004. We established eight 4 x 4 m plots haphazardly along the Sirena trail. The distance of each plot from the high water line (hereafter referred to as distance) ranged from 21 to 351 m. Each plot was divided into sixteen 1 x 1 m subplots, within which we counted the total number of crab holes. We determined whether holes were occupied by sprinkling beach sand around each hole in the afternoon and inspecting for tracks

Figure 1. Two holes dug by *Gecarcinus quadratus*, cleared of litter, sprinkled with beach sand and left overnight. We observed lizards, ants, spiders and hermit crabs crossing the sand, but these animals left no tracks. Therefore, holes with tracks coming from the entrance (left) were considered occupied by land crabs. Holes with no tracks (right) were considered unoccupied.

in the sand the following morning (Fig. 1). We haphazardly selected up to twelve crab holes in each 16 m^2 plot and measured depths and diameters. Depths were determined by inserting a vine as far as possible into each hole.

To test for nonrandom dispersion of crabs and crab holes, we calculated frequencies using a Poisson distribution calculated from the observed mean density of crabs (and crab holes) to compare to observed frequencies with a chi-square test. We also calculated crab and crab hole dispersion indices for each plot as variance/mean. A dispersion index of 1 indicated a random dispersion, while a value above or below 1 indicated a clumped or uniform dispersion, respectively.

We used correlation matrices to test the relationship between distance from the beach and crab hole characteristics. Crab abundance and number of crab holes were log transformed to correct for non-normality.

RESULTS

Since we were unable to find *G. quadratus* during daylight, we searched for crabs several times at night by walking through the crab zone and by waiting quietly by crab holes for 30 min. However, no crabs were ever sighted between 2100 - 2300 or 0230 - 0400.

Number of holes per m^2 and crabs per m^2 varied widely among the 128 subsample plots (holes: zero to nine, crabs: zero to eight), and 78% of all holes were occupied. Hole diameter ranged from 2.18 - 14 cm, and depth of holes ranged from 7.5 - 107 cm. Correlation matrices (Tables 1 and 2, Fig. 2) show that hole diameter increased and crab and hole density decreased with distance from the beach, but there was no trend in hole depth. Occupied holes had signifi-

Table 1. Correlation matrix for crab hole measurements (n = 80).

	Depth (cm)	Diameter (cm)	Distance (m)
Depth (cm)	1.00		
Diameter (cm)	0.49	1.00	
Distance (m)	0.50	0.68*	1.00

* $P < 0.08$

cantly larger hole diameters than unoccupied holes ($F_{1,79}$ = 4.47, P = 0.04). A contingency analysis showed that the distribution of holes was significantly different from random (χ^2= 20.07, df = 5, P = 0.001). Relative to the Poisson distribution, there was a surplus of plots with zero holes and a surplus of plots with five or more holes, but a lack of plots with three or four holes (Table 3). In contrast, the dispersion of crabs did not differ from random (χ^2= 4.67, df = 5, P = 0.46). Dispersion indices did not vary with distance from the beach for holes or crabs (r = 0.33 and 0.01, respectively, df = 7, P > 0.40; Fig. 3).

Table 2. Correlation matrix for plot measurements (n = 8).

	Log(# holes + 1)	Log(# crabs + 1)	Distance (m)
Log(# holes + 1)	1.00		
Log(# crabs + 1)	0.99**	1.00	
Distance (m)	-0.72**	-0.66*	1.00

* P < 0.08
** P < 0.05

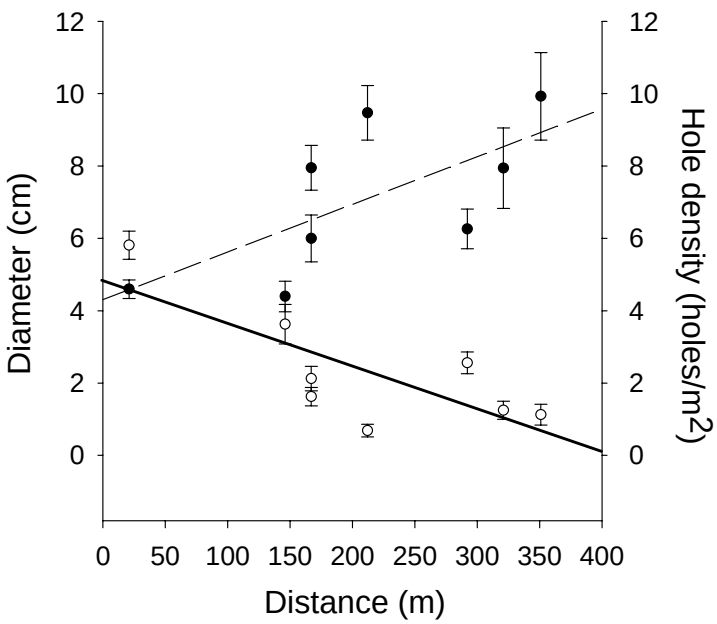

Figure 2. Hole diameter (filled circles) increased and hole density (open circles) decreased with distance from the high water mark. Means (± SE) are shown. The dashed line represents a regression of diameter with distance (r^2 = 0.59, df = 7, P = 0.03) and the solid line represents a regression of hole density with distance (r^2 = 0.47, df = 7, P = 0.06).

Discussion

The dispersion of *G. quadratus* did not show evidence of structuring from intraspecific interactions. Because the dispersion of holeswas non-random, but not clearly uniform or patchy, we posit that abiotic factors are influen-tial. For example, there may be coarse scale heterogeneity of substrate type in the crab zone. Patches of rocks or roots may cause clumping of crabs in soil where it is easier to dig. In areas where suitable substrate for digging is not limiting, intraspecific competition may still cause a more uniform spacing of crab holes. Future studies should look at larger scale plots to capture the effect of heterogeneous substrate on crab hole distribution and determine if and how intraspecific interactions are influential. Also, future studies should analyze substrate type in more detail to determine how it changes within

Table 3. Frequency of number of holes per m^2 as expected by the Poisson distribution and as observed, as well as the χ^2 value between them. The distribution of holes differs significantly from random.

# holes per m^2	# expected from Poisson	# observed	χ^2
0	12	21	6.37
1	29	29	0.00
2	34	33	0.01
3	26	18	2.68
4	16	7	4.68
> 4	11	20	6.31

the crab zone and whether it influences crab distribution.

A gradient of conditions from beach to forest may affect *G. quadratus* hole densities and hole diameters. Perhaps only large crabs have the strength to dig in a non-sandy dirt substrate, explaining the reduced abundance of holes and larger hole diameter when moving further and higher inland.

However, our prediction that hole depth would decrease with distance from the beach in harder soil was not supported. We suggest that hole depth may not depend on the sandiness of soil or the size of the crab digging the hole, but on other factors such as hole age. If crabs gradually dig deeper over time, the depth of holes would depend on how recently they were colonized, and not on the distance of holes from the beach. Future studies could test this by examining whether hole depths change through time.

We also found that occupied holes were larger than unoccupied holes, suggesting that large holes are more likely to be occupied than small ones. Assuming that hole diameter corresponds to crab size, perhaps the larger crabs in these holes are less susceptible to predation due to their size. In fact, we tended to see larger and more distinctive tracks coming from large holes. It would be informative to devise methods to capture crabs, and to examine the relationships between crab size, hole diameter, and hole occupancy. Perhaps crabs move further inland as they grow, to feed on preferred sapling types towards the edge of the crab zone, or perhaps they expand their holes as their own size increases.

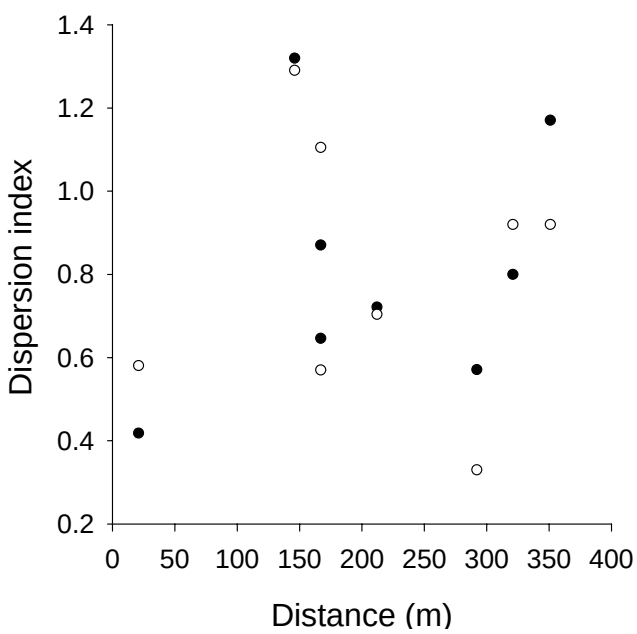

Figure 3. Dispersion indices for holes (filled circles) and crabs (open circles) displayed no relationship distance from the high water mark.

We were unable to find crabs either by watching holes throughout the day and night or by digging or flushing out holes. Given that *G. quadratus* is so difficult to locate, we speculate that there is strong predation pressure on this species, perhaps by animals such as large birds or raccoons. This pressure may limit the amount of time crabs spend above ground, and thus limit their impact on the plant community.

G. quadratus plays an important role in the dynamics of coastal sections of neotropical rainforests, yet the characteristics of their spatial population structure are poorly understood. Predation pressure and variation in substrate may explain patterns in crab abundance, hole structure, and diel activity patterns.

LITERATURE CITED

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