Capistrán Barradas, Ascención; Defeo, Omar; Moreno Casasola, Patricia
Density and population structure of the red land crab gecarcinus lateralis in a tropical semi-deciduous forest in Veracruz, Mexico
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throughout their evolution, land crabs have acquired behavioral, physiological and biochemical adaptations that allow them to be almost completely independent of aquatic systems (Burggren and McMahon, 1988). In coastal ecosystems, these crustaceans determine the recruitment rate of some plant species by means of propagule predation, recycling of nutrients stored in the ecosystem by consuming leaf litter and increase of soil aeration through burrow construction (Louda and Zedler, 1985; Bertness, 1986; Robertson and Daniels, 1989; O’Dowd and Lake, 1991; Killman and Delfosse, 1993; Green et al., 1997; Green et al., 1999).

Crab abundance can be remarkable. In Christmas Island, Gecarcoidea natalis occurs in densities of 1.3 ind/m² and 1.8 burrows/m² (Hicks, 1985; O’Dowd and Lake, 1991; Green, 1997). Gecarcinus planatus and G. quadratus (considered a synonym of G. lateralis) in Clippertown Atoll and Costa Rica reach densities of up to 6 ind/m² (Turkay, 1973, Wolcott, 1988; Sherman, 2002). G. lateralis has been reported to have 2 burrows/m² and 3 ind/m² in Florida and Central America, respectively (Bliss et al., 1978; Britton et al., 1982). Some studies have attempted to explain the association between crab density and physical environment. For example, the distribution of some species of the genus Uca is associated with the amount of litter and soil texture (Murai et al., 1982), whereas the density of plant cover seems to be more important for G. planatus, G. lateralis, G. natalis, and water content in the burrows for Cardisoma guanhumi (Herreid and Gifford, 1963; Taissoum, 1974; Bliss et al., 1978; Britton et al., 1982; O’Dowd and Lake, 1991; Jiménez et al., 1994). However, few studies have explored the relationship of crab density and population structure with the heterogeneity of the environment; as it has been demonstrated for Aratus pisonii, which is positively and significantly correlated with mangrove productivity (Conde and Díaz, 1989).

La Mancha, on the central coast of Veracruz (Mexico) is a mosaic of vegetation associations. During the rainy season, the land crabs G. lateralis are conspicuous and ubiquitous in the tropical semi-deciduous forest, with a density of 1 ind/m² (Delfosse, 1990; Killman and Delfosse, 1993). Their main food source is leaf litter, although they can consume fruits, seeds and seedlings. It has been proposed that seedling scarcity is the result of such predation (Delfosse, 1990; García-Franco et al., 1991; Killman and Delfosse, 1993). Despite being a well-studied species, there is a lack of information on its population density and the spatial variation of its density, which may elucidate its ecological role. In this paper we addressed whether G. lateralis population density and structure vary between sites with different environmental conditions (forest type, floor topography and cover) in the tropical semi-deciduous forest at La Mancha, Mexico.

Material and Methods

Study Site

La Mancha is located on the central coast of Veracruz, Mexico (19º36’N, 96º22’W, altitude <100m). It is next to the sea and there are elevations of old littoral cordons as high as 80m at the east, parabolic dunes with an average of 40m height in the center and a surface of parabolic dunes causing the terrain slope to be very hilly (Geissert and Dubroeucq, 1995). At this site there is a tropical semi-deciduous forest (ca. 32ha) next to the Centro de Investigaciones Costeras La Mancha. The climate is warm sub-humid Aw1(w)(1)gw” (Castillo and Medina, 2002) with an average temperature of 26ºC (10-34ºC). Mean total annual rainfall is 1300mm, with a pronounced rainy season from June to October (Moreno-Casasola, 1982). A windy-cool period from November to early February overlaps with the dry
season (November-May). During the windy and cool season, trees and branches fall down and open understory gaps (Capistrán-Barradas, personal observation). These events can change microclimatic conditions such as light, temperature and humidity within the forest (Denslow et al., 1998).

The soil at the tropical semi-deciduous forest is a psamment entisol. It can be divided in two different ages that were named by Kellman (1990) as old forest (OF) with older and better formed soil, and a younger forest (YF) with more recently formed soil. Absolute age in the OF is unknown, but the appreciable clay formation and illuviation indicates considerable weathering of the sand that implies a possible Late-Glacial age (Kellman, 1990). In contrast, the YF developed on a recent dune composed by sand of identical textural characteristics than the contemporary beach; thus, its age is estimated to be no more than a few hundred years (Kellman, 1990; Kellman and Roulet, 1990). In addition, these sites have different physical and chemical conditions; the amount of organic matter, clay and moisture retention capacity are higher at OF than at YF (Kellman, 1990; Dubroeucq et al., 1992; Geissert and Dubroeucq, 1995).

In the tropical semi-deciduous forest, three vegetation strata are recognized: 1) the arboreal stratum (>20m height) represented by Brosimum alicastrum, Ehretia tinifolia, Enterolobium cyclocarpum and Ficus cotinifolia; 2) the medium stratum (6-15m) represented by Caesaria corymbosa, Coccoloba barbadensis, and Nectandra salicifolia; and 3) the shrubby stratum, represented by Crossoptilum uragoga, Hippocratea celastroides and Jaquinia macrocarpa spp. macrocarpa (Castillo and Medina, 2002). Occasionally, a herbaceous stratum is also present with species like Bromelia pinguin (García-Franco and Rico-Gray, 1995) and the forest as a whole contains very low densities of tree seedlings relative to other tropical forest (Blain and Kellman, 1991). During the surveys (rainy season of 1997-1998) few animal species were observed in the understory, such as a coyote (Canis latrans), some boas (Boa constrictor), lizards (Sceloporus variabilis, Cnemidophorus guttatus y C. deppii; Guzmán, 2000) and doves (Leptotila verreauxii).

The subject

Gecarcinus lateralis (Ferminville, 1835, Gecarcinidae) is distributed along the Atlantic Ocean from Florida to Brazil, including Mexico, the Caribbean Islands and French Guiana, and along the Pacific Ocean it is distributed from Mexico to Peru (Hartnoll, 1988). It is a land crab which, at maturity, achieves a fresh mass of approximately 45g and a carapace width of 35-60mm (Kellman and Delfosse, 1993). Females reach maturity at 30mm carapace width (Adiyodi, 1988). At La Mancha, G. lateralis is active and breeds from May through October, coinciding with the rainy season; during the rest of the year crabs remain in their burrows. Female spawning is synchronized with full moon nights. Individuals are distributed along the dunes, shrubs and the tropical semi-deciduous forest. A 24 hour study showed that their activity increases during the morning and decreases by afternoon, except at the dunes where crabs are active at night, and use most of this time to eat leaf litter and clean their burrows (Delfosse, 1990; Capistrán-Barradas, personal observation). During the rainy season the most evident species on the forest ground is G. lateralis and no other crab species are found. Small individuals of this species are very hard to see, maybe due to their cryptic coloration mimicking leaf litter.

Figure 1. Crab density (mean ±SE) of Gecarcinus lateralis at different sites of the tropical semi-deciduous forest at La Mancha, Mexico. Pooled data for 1997 and 1998.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>X²</th>
<th>Variation (%)</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year (Y)</td>
<td>1</td>
<td>1.198</td>
<td>1.46</td>
<td>0.274</td>
</tr>
<tr>
<td>Forest (F)</td>
<td>1</td>
<td>2.529</td>
<td>3.08</td>
<td>0.112</td>
</tr>
<tr>
<td>Topography (T)</td>
<td>2</td>
<td>3.752</td>
<td>4.58</td>
<td>0.153</td>
</tr>
<tr>
<td>Cover (C)</td>
<td>1</td>
<td>4.489</td>
<td>5.48</td>
<td>0.034</td>
</tr>
<tr>
<td>Y x F</td>
<td>1</td>
<td>7.258</td>
<td>8.86</td>
<td>0.007</td>
</tr>
<tr>
<td>Y x T</td>
<td>2</td>
<td>0.708</td>
<td>0.86</td>
<td>0.702</td>
</tr>
<tr>
<td>F x T</td>
<td>2</td>
<td>4.267</td>
<td>5.20</td>
<td>0.118</td>
</tr>
<tr>
<td>Y x C</td>
<td>1</td>
<td>5.483</td>
<td>6.69</td>
<td>0.019</td>
</tr>
<tr>
<td>F x C</td>
<td>1</td>
<td>1.298</td>
<td>1.58</td>
<td>0.255</td>
</tr>
<tr>
<td>T x C</td>
<td>2</td>
<td>12.878</td>
<td>15.72</td>
<td>0.002</td>
</tr>
<tr>
<td>Y x F x T</td>
<td>2</td>
<td>0.844</td>
<td>1.03</td>
<td>0.656</td>
</tr>
<tr>
<td>Y x F x C</td>
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<td>3.559</td>
<td>4.34</td>
<td>0.059</td>
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<tr>
<td>Y x T x C</td>
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<td>1.189</td>
<td>1.45</td>
<td>0.552</td>
</tr>
<tr>
<td>F x T x C</td>
<td>2</td>
<td>2.689</td>
<td>3.28</td>
<td>0.261</td>
</tr>
<tr>
<td>Y x F x T x C</td>
<td>1</td>
<td>1.788</td>
<td>2.18</td>
<td>0.409</td>
</tr>
<tr>
<td>Error</td>
<td></td>
<td>27.984</td>
<td>34.16</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>81.913</td>
<td>100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
In the tropical semi-deciduous forest, 36 plots of 25m² each were randomly selected. Plots were representative of the following conditions: two kinds of forest based on soil age (OF and YF), three kinds of topographies (valleys, 0-4%; slopes, 5-17%; and peaks, 18-27%), and two forest covers (understorey, >80%; and gaps, <15%). For each combination there were three replicates, making a total of 36 plots. Once per month from June to September of 1997 and 1998, the temperature in two burrows randomly assigned within plots was recorded. Every month, the soil humidity was measured (at surface, 20cm and 40cm depth) in the center of each plot and the leaf litter present in three subplots of 1m² selected at random was collected by hand. The samples were weighed, then dried in an oven at 75°C during 24h and weighed again. In addition, soil compaction was determined using a penetrometer (Proctor) in five points selected at random within plots during 1997.

In order to estimate crab density, a 24-hour preliminary study was done in the forest (OF and YF), showing that the activity of *G. lateralis* mainly occurs between 07:00 and 11:00h. Based on this, we counted once per month all active crabs every hour between 07:00 and 11:00 during the wet season (June-September of 1997 and 1998). We did not sample during the dry season because the crabs are inactive. A crab was considered as active when it was outside its burrow and performing an action (cleaning its burrow, eating or interacting with other crab).

In *Cardisoma guanhumi*, *Ocypode quadrata* and *Ocypode gaudichaudii* there is a positive significant correlation between burrow diameter and carapace size (Feliciano, 1962; Taissoum, 1974; ODowd and Lake, 1989; Green, 1997; Alberto and Fontoura, 1999; Quijón et al., 2001). To assess this correlation for *G. lateralis*, 30 burrows were chosen haphazardly and its diameter measured; the inhabiting crabs were collected by hand and the carapace length measured. The resulting correlation was significant (r² = 0.68, n= 30, P <0.05). Thus, we used burrow diameter as predictor of crab size. One crab per burrow was systematically found, so burrow abundance was associated with crab abundance (Green, 1997). To determine the population structure of *G. lateralis*, all the active burrows (opened and without leaf litter in the entrance) were measured and counted in every plot. Using the data of burrow size and abundance, frequency plots were constructed and the corresponding population structure of *G. lateralis* under different sites was determined.

Four-way ANOVA was performed to determine the effect of environmental variables (year, forest type, floor topography, and cover) on the dependent variables (burrow temperature, soil compaction and leaf litter). A logarithmic transformation was used to fulfill the normality assumption. ANCOVA was used to test differences in soil humidity, using depth as covariate. Crab densities were analyzed using a four-factor ANCOVA (with year, forest, topography and cover as main factors) and the number of burrows as covariate. As “count data” were used, the data were adjusted to a log-normal linear model with Poisson error and the goodness-of-fit was evaluated with a X² test. With Poisson error distribution, the change in the deviance can be directly compared with X² tables to assess its significance (Crawley, 1993; Francis et al. 1993). The mean, mode, range and percentiles were estimated to describe the population structure in different environmental conditions defined by forest type, topography and cover. Data analysis was done using the Statistica software package (Statsoft, 2000).

**Results**

**Physical conditions**

Significant differences were found for several physical factors, mainly between forest and cover types. Burrow temperature did not vary between years (*F*<sub>1,48</sub> = 3.9, *P* = 0.08), and was higher in OF as compared to YF (*F*<sub>1,254.29</sub> = 254.29, *P* <0.0001). In YF burrow temperature was similar in valleys and peaks, but in slopes it was higher in gaps than in the understorey (*F*<sub>1,63</sub> = 6.63, *P* = 0.0001). No significant differences were found between years in soil humidity (*F*<sub>1,42.5</sub> = 4.25, *P* = 0.093); however, OF presented higher humidity levels than YF, caused by higher humidity in the understorey than in gaps (*F*<sub>1,46.4</sub> = 4.46, *P* = 0.006). The soil humidity of valleys (both forests) and slopes in OF were higher than slopes and peaks in YF (*F*<sub>1,3.84</sub> = 3.84, *P* = 0.028). Soil compaction in OF was higher than in YF due to higher values recorded on peaks and slopes at OF, while in YF it was higher in valleys as compared with slopes and peaks (*F*<sub>1,111.1</sub> = 1.111, *P* <0.0001). No differences were found between gap and understorey in either forest (*F*<sub>1,27</sub> = 1.27, *P* = 0.590). The average amount of leaf litter was three times higher at OF than at YF (*F*<sub>1,12.42</sub> = 12.42, *P* <0.0009). In both forests, either at valleys and peaks, there was more leaf litter in the understorey as compared with gaps; however, at slopes the opposite was found (*F*<sub>1,42.4</sub> = 12.42, *P* <0.0001).

**Crab density**

The crab density (Figure 1) varied significantly for forest and cover conditions but it did not differ between years. In 1997, density (mean ±SD) did not change between OF (0.46 ±0.15 ind/m²) and YF (0.45 ±0.14 ind/m²). In contrast, in 1998 significantly more crabs were found at OF than at YF (0.54 ±0.20 ind/m² vs. 0.42 ±0.15 ind/m², Table I) and, in the same way, a higher density in the understorey than in gaps was found only in 1998 (0.52 ±0.18 ind/m² vs. 0.43 ±0.13 ind/m²). Independently of year and forest, in valleys and peaks a higher density in the understorey was recorded (0.54 ±0.17 ind/m² and 0.49 ±0.17 ind/m², respectively) than in gaps (0.45 ±0.12 and 0.40 ±0.11 ind/m²), while in slopes no significant differences were found (Figure 1, Table I).

**Population structure**

The population structure of *G. lateralis* (Figure 2 and 3) was affected mainly by forest and cover conditions. Crabs were bigger (mean ±SD) in YF (4.27 ±1.08cm) than in OF (3.47 ±1.41cm), in the valleys (4.13 ±1.34cm) than in slopes (3.68 ±1.27cm) and peaks (3.52 ±1.12cm), and in the understorey (3.94 ±1.36cm) when compared to gaps (3.58 ±1.12cm). In the OF minimum and maximum sizes were 0.99 and 7.52cm, respectively, with a unimodal distribution of 3.6cm and 75% of the individual size being <4.2 (Figure 3). In the valleys, crabs were larger (3.77 ±1.22cm) compared with those present in slopes (3.35 ±0.92cm) and peaks (3.28 ±0.12cm; Figure 2). In this forest, the size of the crabs was higher in the understorey (3.50 ±1.06cm) than in gaps (3.42 ±1.11cm). In the YF minimum and maximum sizes were 1.65 and 9.65cm, respectively (Figure 3) with a multimodal distribution and 75% of the individual size being ≤5.07cm. In the valleys (4.54 ±1.37cm) and slopes (4.31 ±1.55) crabs were larger in comparison to peaks (3.83 ±1.18cm; Figure 3). Crab size was larger in the understorey (4.60 ±1.49cm) than in gaps (3.77 ±1.10cm; Figure 2).

**Discussion**

Population density and structure of the red land crab *Gecarcinus lateralis* significantly varied according to environmental conditions. Heterogeneous physical conditions could be playing a role in the ecology of crabs. For example, crabs are more abundant in OF than in YF, as well as leaf litter (three times higher in OF vs. YF), being the latter basic in the diet of *G. lateralis*. In the forest, this species can
consume from 75 to 97% of the leaf litter biomass available for decomposition (Kellman and Delfosse, 1993). Kellman and Delfosse (1993) similarly found higher crab density in two plots (one in OF and the other in YF). In concordance, crab density in valleys and peaks was higher in the understorey than in gaps. Again, a higher abundance of leaf litter was detected in the understorey in relation to gaps, and O’Dowd and Lake (1989) and Green et al. (1999) found a significant correlation between crab density and leaf litter quantity consumed by *G. natalis*. Additionally, leaf litter could reduce visibility of *G. lateralis* predators, and the possibility of being captured or killed.

Even though it is very difficult to consider that one condition may limit crab distribution, it is also hard to deny that humidity plays an important role affecting their behavior (Bliss et al., 1978; Wolcott, 1988, Green, 1997). The species under study seems to rely on water conservation rather than having a specialized mechanism for water uptake (Wolcott, 1988). The capacity of humidity retention in OF is higher than in YF (Kellman, 1990) and we found a higher soil humidity in OF than in YF, and in understorey than in gaps, which could also affect the occurrence of crabs. The crab shell is permeable and they can die due to dehydration (Bliss et al., 1978) if they are exposed to direct solar radiation, as it happens in the gaps. These authors suggested that several strategies prevent this from happening (e.g., hiding into their burrows or foraging at night), but this could negatively affect foraging time and, thus, food acquisition. But shade in the understorey can maintain high humidity levels and protect crabs from dehydration. In Central America, Britton et al. (1982) found that crab density increased in plots under the understorey and Green (1997) found that the activity of *Gecarcinocidea natalis* diminished at relative humidity below 77%, while Jiménez et al. (1994) suggested that the density of *G. planatus* is affected by vegetation structure and soil moisture (higher in understorey). Another possibility that has to be considered in gaps is crab predation by *Buteogallus anthracinus*, the common black hawk.

The heterogeneity of the forest seems to exert effects in the population structure of *G. lateralis* (Figure 2). Differences between forest type and cover were detected. Larger sizes were registered in YF than in OF, as well as in valleys than slopes and peaks, and at the understorey compared with gaps. This could be due to two sources of variation. Again, leaf litter quantity in OF is greater and it is the main food for crabs. Small and medium crabs have a faster metabolism (Mattson, 1980; Herreid and Full, 1988) and “should” preferentially inhabit those places that can more easily meet their metabolic needs. In other words, larger animals need to extract less energy per ingestion unit than smaller ones, since they have higher respiration losses (Mattson, 1980). On the other hand, in YF larger crabs can tolerate abiotic stress (higher temperatures and less leaf fall and soil humidity) better than smaller ones (Wolcott and Wolcott, 1984) and, in some species an adult can survive eating daily only 0.7g of leaf litter (Green, 1997). This result is contrary to that obtained in mangroves where larger individuals of *Aratus pisonii* live in more productive places (Conde and Díaz, 1989).
The effect of soil compaction has to be considered, since in softer sandier soils the problem is not constructing but supporting the burrow. In those places where soil compaction was very low (e.g., slopes and peaks at YF), crabs spent more than half an hour of their activity period excavating their burrows (Capistrán-Barradas, personal observation) using up energy and time needed for foraging. Probably, the younger crabs in OF, where soil is more compact than in YF, do not waste time in these activities. It has also been suggested that in places with poor food quality (as the YF) cannibalism may occur (Wolcott, 1988); thus, it is to be expected that small individuals may be displaced towards YF, even though cannibalism was not observed.

In summary, distribution and population structure of the red land crab Gecarcinus lateralis at La Mancha is probably affected by physical and biological conditions of the tropical semi-deciduous forest. Further work is necessary on the ecology of land crabs in the field (Wolcott, 1988), but leaf litter, humidity and soil compaction might be the most significant conditions affecting the density and population structure of G. lateralis in the tropical semi-deciduous forest of La Mancha, Mexico.

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