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Land hermit crab (*Coenobita clypeatus*) densities and patterns of gastropod shell use on small Bahamian islands

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ABSTRACT

Aim To examine patterns of abundance, density, size and shell use in land hermit crabs, *Coenobita clypeatus* (Herbst), occurring on three groups of small islands, and to determine how these variables change among islands.

Location Small islands in the Central Exuma Cays and near Great Exuma, Bahamas.

Methods Land hermit crabs were captured in baited pitfall traps and were separately attracted to baits. A mark–recapture technique was used in conjunction with some pitfall traps monitored for three consecutive days. The size of each crab and the type of adopted gastropod shell were recorded, along with physical island variables such as total island area, vegetated area, island perimeter, elevation and distance to the nearest mainland island.

Results Relative abundances, densities and sizes of crabs differed significantly among the three island groups. Densities of land hermit crabs were as high as 46 m^{-2} of vegetated island area. In simple and multiple linear regressions, the only variable that was a significant predictor of the abundance of hermit crabs was the perimeter to area ratio of the island. Patterns of gastropod shell use varied significantly among the island groups, and the vast majority of adopted shells originated from gastropod species that inhabit the high intertidal and supratidal shorelines of the islands.

Main conclusions Although densities of land hermit crabs varied, they were relatively high on many islands, and land hermit crabs may play an important role in these insular food webs. Patterns of shell use may be strongly restricted by island geomorphology: irregular shorelines provide relatively more habitat for the gastropod species that account for the majority of adopted shells and the steep sides of the islands prevent the accumulation of marine gastropod shells. The size of adult hermit crabs appears to be limited by the relatively small gastropod shells available, while the abundance of hermit crabs may be limited by the number of shells available.

Keywords
Bahamas, *Coenobita clypeatus*, gastropod shell use, island biogeography, land hermit crab, periwinkles, pitfall traps.

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INTRODUCTION

Land hermit crabs are common in many insular and coastal habitats in tropical and subtropical regions worldwide (Hartnoll, 1988; Greenaway, 2003). Some species, such as *Coenobita clypeatus* (Herbst), may be found many kilometres inland (Chace & Hobbs, 1969; DeWilde, 1973; Nieves-Rivera & Williams, 2003). However, relatively few studies have addressed the densities of land hermit crabs, their ecological interactions with other types of organisms or, ultimately, the role land hermit crabs may play in food webs.

On small islands in the Bahamas, Morrison (2002a, in press) documented that interspecific competition occurred between the land hermit crab *C. clypeatus* and two ant species, representing the first direct evidence of competition between ants and crabs of any type. Land hermit crabs are generalist scavengers (Dunham & Gilchrist, 1988; Wolcott, 1988) and may also compete with other scavengers or detritivores, representing potentially important basal components in insular and coastal food webs. Land hermit crabs may feed upon resources that are derived from marine inputs (Morrison, 2005), and represent a crucial component in the marine–land interface in insular and coastal regions. Land hermit crabs may also compete with marine hermit crabs for gastropod shells (Hazlett, 1981).

The strength of such interactions, however, and the ultimate importance of land hermit crabs in terrestrial systems or the marine–land interface, will depend to a large extent on their abundance. Land hermit crabs were the most abundant crustacean in a study of very small islands in the Central Exumas, Bahamas (Morrison, 2005). Yet because land hermit crabs are primarily active at night and conceal themselves by day (Greenaway, 2003) they may not be frequently observed in cursory surveys of species diversity.

As an initial step in evaluating the importance of land hermit crabs in insular food webs we sampled populations of *C. clypeatus* on 19 small islands in three different regions of the Exumas, Bahamas. To our knowledge, this is the first study to attempt to quantify land hermit crab densities on islands. The following questions were addressed:

1. How numerous are land hermit crabs on these small islands?
2. How do the relative abundance, relative density and size of land hermit crabs vary among islands, and what physical characteristics of islands may be good predictors of these variables?
3. What patterns of gastropod shell use are evident in this region?

METHODS

Natural history and study area

All land hermit crabs in the Bahamas are *C. clypeatus*, the only species of land hermit crab in the western Atlantic (Hartnoll, 1988). Like other *Coenobita* species, *C. clypeatus* has a planktonic larval stage (Provenzano, 1962) and adopts a vacant gastropod shell when it moves to land. As the crab grows, it adopts larger shells, abandoning the old ones (Adiyodi, 1988; Greenaway, 2003).

This study was conducted on small islands (with a vegetated area of < 1500 m^2) in the Exumas, an archipelago of hundreds of islands in the Central Bahamas, stretching from Sail Rocks in the northwest to Little Exuma in the southeast. The small islands in this chain are composed primarily of marine limestone, and contain many cracks and cavities that provide shelter for land hermit crabs. Shorelines are often irregular, and the sides of most islands slope steeply or overhang the
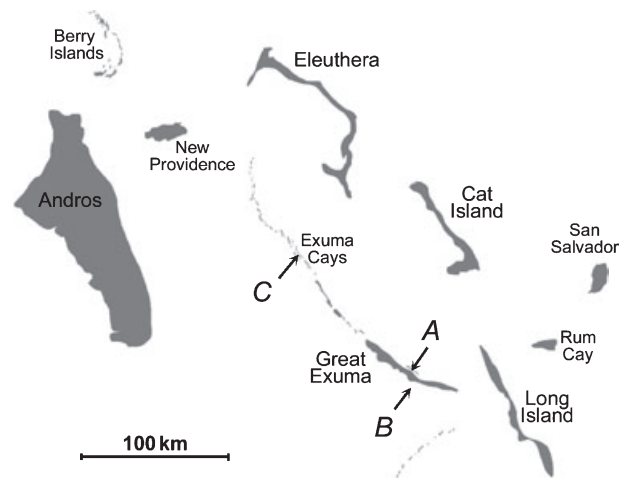

Figure 1 Map of the Bahamas showing the location of island groups studied: A, Elizabeth Harbour; B, Great Exuma Banks; C, Central Exuma Cays.

water. The mean tidal range is 0.8 m, with two daily equal high and low tides separated by *c.* 6 h.

To evaluate the patterns of the relative abundance, relative density and size of hermit crabs across different island types, we selected 19 small islands: 10 near Georgetown, Great Exuma and 9 in the Central Exuma Cays (Fig. 1). At Great Exuma, five of the islands were located on the north side of the main island in Elizabeth Harbour, a natural harbour protected from the deep ocean by a long barrier island. The other five islands were located on the southern side, on shallow water banks (see Spiller *et al.*, 1998 for a detailed map and description of the Great Exuma region). In the central Exuma Cays, four islands were located in Pipe Creek, a protected area surrounded by larger islands. The other five islands were in a channel separating larger islands of the chain (see Morrison, 1997 for a detailed map and description of the Exuma Cays region). Because no significant difference was found in the density of hermit crabs between the two island categories in the Central Exuma Cays, all nine islands were pooled together for analyses.

We attempted to select islands of a similar size range for each region, although the availability of islands limited our choices. Islands sampled ranged in size (vegetated area) from 13.75 to 790.62 m^2 in the Central Exuma Cays, from 250 to 1488 m^2 in Elizabeth Harbour and from 97 to 978 m^2 on the Great Exuma Banks. All islands sampled are near the small end of the size distribution of islands in the region (Schoener, 1991).

Sampling

We used pitfall traps, which were plastic cups [12 oz (355 mL), 8.5 cm diameter, 10 cm deep] dug into the soil and baited with tuna (in vegetable oil). These cups may have been too small to capture the largest crabs on these islands, although the difficulties associated with digging into the limestone substrate underlying the thin layer of soil precluded the use of larger

traps. Ten pitfalls were left out for 24 h on each island in December 2002. This study was conducted in December to reduce desiccation stress on captured crabs, which would be greater in the warmer months.

The number of hermit crabs in each pitfall was counted, and the size of each hermit crab was determined by measuring the length of the major chela (large claw). Chela length was the best morphological character to use for field measurements, as it was visible even when the crab retreated into its shell. To determine the correlation of chela length with body size as determined by weight, we collected 24 individuals representing the range of crab sizes observed on the islands sampled. These crabs were returned to the laboratory, dried and weighed after the animals had been removed from the shell. We performed a simple linear regression of chela length on dry body weight, after $\log_{10}$ transforming both variables.

The type of adopted shell was recorded for all crabs captured at Great Exuma, and for a subsample (about one-third of the traps) of the crabs captured in the Central Exuma Cays (where the abundance of hermit crabs was much greater). Shell type was recorded within the following six categories: knobby periwinkles, prickly periwinkles, mangrove periwinkles, top shells, nerites and others (see Table 1).

Previously (in 1998), one of us (LWM) surveyed 85 small islands in this archipelago, collecting data on bait occupancy by crabs (i.e., the proportion of baits at which land hermit crabs were present) as well as physical island variables (see below) as part of other studies (Morrison, 2002b,c). To determine whether the observed patterns for the set of 19 islands reported here were representative of the larger Exumas archipelago, we placed baits on the 19 islands where pitfall trapping was done. Baiting was conducted several days prior to pitfall trapping, and in the same manner as on the larger set of islands in 1998. Baits consisted of *c.* 1 g of tuna (in oil); the number of baits ranged from 6 to 50 and was proportional to island area (as in Morrison, 1998). The proportion of baits at which land hermit crabs were present was recorded after 45 min. This proportion was highly positively correlated with the abundance of crabs as determined by pitfall captures ($r = 0.87$). Thus, we used bait occupancy as a measure of crab abundance to evaluate predictor variables (see below) for 85 small islands in the region.

To obtain more information on the absolute abundance of hermit crabs we conducted a mark–recapture study on three small islands in the Central Exuma Cays in December 2003. We used pitfall traps as before, although the cups used in the mark–recapture study were of a larger volume [14 oz (414 mL), 8.5 cm diameter, 11.5 cm deep] than those used in the previous study. The diameter of the opening, however, was the same. (We do not make comparisons between these two studies.) Ten pitfalls were left out for 24 h on each island. The size of all hermit crabs in each pitfall was determined by measuring the length of the major chela. A small amount of paint was applied to the shell with a UniPaint® marker (Sanford Corporation, Bellwood, IL, USA), and crabs were released in the vicinity of the pitfall. This procedure was repeated over three consecutive 24-h periods.

Application of a mark–recapture index resulted in an extremely high estimate of crab numbers, and we do not report it here because it was almost surely biased by trap-shy individuals. The use of such an index may be informative if trapping was to be conducted several weeks apart. The logistics involved in travelling to and working on these remote islands, however, prevented us from sampling over an extended period.

Statistics

The relative abundance (number of crabs/island), relative density (number of crabs m^{-2} of vegetated area) and size of hermit crabs were compared by separate one-way ANOVAs. It

Table 1 Gastropod species included within the six shell categories

Shell category	Gastropod species included in category	Shell height (cm)*	Habitat†
1. Knobby periwinkle	Knobby periwinkle *Tectarius muricatus* (L.)	2	Supratidal
2. Prickly periwinkles	Prickly periwinkle *Nodilittorina tuberculata* (Menke)	2	High intertidal
	False prickly periwinkle *Echininus nodulosus* (Pfr.)	2+	High intertidal
3. Mangrove periwinkle	Mangrove periwinkle *Littorina angulifera* (Lam.)	3+	Mangrove roots
4. Top shell	West Indian top shell *Cittarium pica* (L.)	10	Subtidal
5. Nerites	Bleeding tooth nerite *Nerita peloronta* L.	2.5–4	High intertidal
	Checkered nerite *Nerita tessellata* Gmelin	1.5–2	Intertidal
	Variegated nerite *Nerita versicolor* Gmelin	2.5	High intertidal
6. Others‡	Apple murex *Chicoreus pomum* Gmelin	5–8	Shallow water
	Hairy triton *Cymatium pileare* (L.)	7.5–13	Shallow water
	Tulip shell *Fasciolaria tulipa* (L.)	10–15	Shallow water
	Milky moon snail *Polinices lacteus* (Guild.)	2.5	Shallow water
	Chestnut latirus *Leucozonia nassa* (Gmelin)	5	Shallow water
	Deltoid rock snail *Thais deltoidea* (Lam.)	4	Intertidal

*Average, mature shells according to Morris (1973).

†According to Morris (1973).

‡Includes additional species that were not identified.

should be emphasized that, for the purposes of comparison between islands, estimates of abundance or density are all *relative* rather than absolute. Some unknown proportion of crabs (presumably a relatively small proportion) were caught in the pitfalls (see below). *Post hoc* comparisons of all factor level means were conducted by the Tukey method (Neter *et al.*, 1985). The number of crabs in the abundance and density measures was based on the cumulative number of crabs captured in all 10 pitfalls on each island. Size was measured as the length of the major chela, averaged over all crabs trapped on each island.

We conducted simple linear regressions of hermit crab abundance against three physical island variables [vegetated area, elevation and the ratio of perimeter to total area (P/A)] for the nine islands in the Central Exuma Cays. Prior to the regressions, the vegetated area was $\log_{10}$ transformed, elevation was square-root transformed and the P/A ratio was reciprocal transformed to normalize the data (see Morrison, 2002b). Separate sets of simple linear regressions were performed with hermit crab abundance, density and size as dependent variables. The sequential Bonferroni procedure (Rice, 1989) was used to correct for multiple comparisons.

Similar regression analyses were conducted at Great Exuma, except that an indicator variable was included to take into account the variation associated with the location of the islands relative to the main island of Great Exuma. We fitted a single regression with an indicator variable (Neter *et al.*, 1985), rather than use separate regressions, to increase the degrees of freedom. The same three predictor variables used in the analyses for the Central Exuma Cays were evaluated and transformed in the same way. Models with an interaction term were evaluated first, and if no interaction was present the effect of the island variable was tested.

For the larger Exumas archipelago we conducted stepwise multiple regression analyses on data from the 85 small islands. The abundance of hermit crabs (as determined by bait occupancy) was regressed on six predictor variables: vegetated area, total area, distance to nearest mainland island, the ratio of vegetated area to total area (VA/A), the ratio of perimeter to total area (P/A) and elevation. To normalize the distributions of the variables, the following transformations were performed: Total area, vegetated area and distance were all $\log_{10}$ transformed. Elevation was square-root transformed. The P/A ratio was reciprocal transformed; the VA/A ratio and proportion of baits occupied by hermit crabs were arcsine square-root transformed (see Morrison, 2002b for a description of the variables and rationale for the transformations). Both forward and backward stepwise procedures were used.

In the mark–recapture experiment we used a two-way ANOVA to evaluate the effects of island and trapping day on hermit crab size. Only unique captures were considered. (A repeated measures design was not employed because the same subjects were never measured more than once.)

A two-way ANOVA was performed to elucidate the effects of adopted shell type and island location on hermit crab size. Only the three most common shell categories were included in the analysis (i.e. knobby periwinkles, prickly periwinkles and top shells; the nerite category was not included as it contained three different species of gastropods of varying sizes.) StatView 5.0.1 (SAS Institute 1999) was used for all statistical analyses.

RESULTS

Patterns of relative abundance, relative density and size

Overall, 6124 hermit crabs were captured in pitfalls on the 19 islands (919 on 10 islands at Great Exuma; 5205 on 9 islands in the Central Exuma Cays) sampled in December 2002. At Great Exuma, shell type was identified for all 919 hermit crabs captured. In the Central Exuma Cays, shell type was identified for a subset of 1501 crabs (29%). Chela length was strongly positively correlated with dry body weight (Fig. 2). Thus, 'hermit crab size' as used in this paper is based on chela length.

The mean number of crabs captured per island varied significantly, ranging from 11 on the islands of the Great Exuma Banks to 578 in the Central Exuma Cays (Table 2; $F = 10.52$, $P = 0.0012$, d.f. = 2, 16). Hermit crab density varied over three orders of magnitude, with the greatest densities found in the Central Exuma Cays and the lowest densities on the islands of the Great Exuma Banks (Table 2; $F = 3.96$, $P = 0.040$, d.f. = 2, 16). Hermit crab size revealed the opposite pattern, with the largest average size on the islands of the Great Exuma Banks, and the smallest in the Central Exuma Cays (Table 2; $F = 49.85$, $P = 0.0001$, d.f. = 2, 16). The ranges for abundance and density among the three island groups often encompassed an order of magnitude or more and did not overlap, with the exception of the abundance category which contains a small degree of overlap (Table 2).

In simple linear regressions for the Central Exuma Cays, only P/A was a significant predictor of hermit crab abundance (Table 3). Hermit crab abundance was positively associated
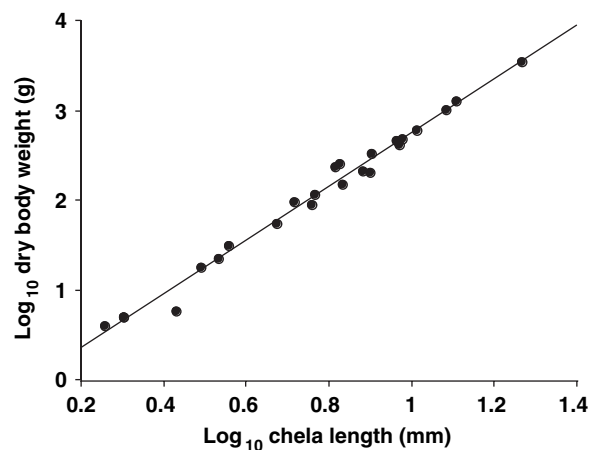

Figure 2 Relationship between hermit crab chela length and dry body weight ($y = -0.231 + 2.995x$; $r = 0.99$; $n = 24$).

Table 2 Comparison of abundance, density, and size of land hermit crabs among three island groups. Different letters denote significantly different treatment means

Island group	Abundance (*n* per island)		Density (*n* m^{-2} vegetated area)		Size (length of claw in mm)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Great Exuma Banks	11 ± 17 A	0–40	0.013 ± 0.021 A	0.00–0.05	8.38 ± 1.20 A	6.9–9.7
Elizabeth Harbour	172 ± 127 A	34–352	0.224 ± 0.142 A	0.06–0.37	5.74 ± 0.64 B	5.1–6.5
Central Exuma Cays	578 ± 324 B	170–1133	13.201 ± 14.308 B	0.60–46.17	3.72 ± 0.64 C	3.14–5.07

Table 3 Results of simple linear regressions of three hermit crab variables on three physical island variables

Variable	Abundance (*n* per island)			Density (n m^{-2} vegetated area)			Size (length of claw)		
	Corr.*	*r*	*P*	Corr.	*r*	*P*	Corr.	*r*	*P*
Vegetated area	+	0.13	0.73	–	0.67	0.05	–	0.46	0.21
Elevation	–	0.54	0.13	–	0.51	0.17	–	0.74	0.023
Perimeter/total area	+	0.77	0.0162†	+	0.21	0.59	+	0.31	0.43

*Corr. = correlation; indicates the relationship (positive or negative) between the hermit crab variables and the untransformed island variables.

†Significant by the sequential Bonferroni procedure; three comparisons were made for each dependent variable (Rice, 1989).

with *P/A*. No variables were significant predictors of hermit crab density or size after correction for multiple comparisons. In the regressions for Great Exuma, no island variables were significant predictors of hermit crab abundance, density or size after taking into account the effect of island location relative to the mainland (all *P* > 0.05).

In the stepwise multiple regression analysis conducted over 85 islands in the Central Exuma Cays, only *P/A* was selected as significant by the model (*P* = 0.0012), in both the forward and backward procedures. *P/A* was positively correlated with hermit crab abundance, although variation in *P/A* explained a relatively small amount of variation in the dependent variable (r^2 = 0.12).

Mark–recapture study

A cumulative total of 2710 unique (non-marked) hermit crabs were captured over 3 days on all three islands sampled in December 2003 (Table 4). Recaptures were uncommon, accounting for < 3% of all crabs captured. Unique captures on the third day represented 72%, 47% and 27% of the first day's total captures, suggesting that a relatively large number of hermit crabs were not captured in pitfalls over the 3-day period.

Sampled densities ranged from two to four individuals m^{-2} of total island area, or 11 to 33 individuals m^{-2} of vegetated island area. True densities are unknown, but are presumably much higher. The size of land hermit crabs captured in the pitfalls declined over the 3 days of trapping (Fig. 3). The effect of island and trapping day were both significant (*F* = 12.14, *P* < 0.0001, d.f. = 2, 2701 and *F* = 54.26 *P* < 0.0001, d.f. = 2,

Table 4 Numbers of land hermit crabs captured on three small islands, over 3 days of pitfall trapping

	Island designation		
	206	208	211
Total island area (m^2)	321	394	204
Vegetated area (m^2)	112	49	19
New captures (recaptures in parenthesis)			
Day 1	562	299	387
Day 2	486 (7)	258 (1)	134 (3)
Day 3	263 (24*)	216 (21†)	105 (14‡)
Total unique captures	1311	773	626
Density (*n* m^{-2} total area)	4.1	2.0	3.1
Density (*n* m^{-2} vegetated area)	11.7	15.8	32.9

*21 from day 1; 3 from day 2.

†17 from day 1; 4 from day 2.

‡12 from day 1; 1 from day 2; 1 captured on both preceding days.

2701, respectively). All *post hoc* pairwise comparisons of factor level means were different by the Bonferroni method (α = 0.05), for both island and trapping day.

Shell use

Patterns of shell use differed significantly among the three island groups (Fig. 4; χ^2 = 519.0, *P* = 0.0001; χ^2 test of homogeneity; Daniel, 1990). Most hermit crabs (89.3% in the Central Exuma Cays, 88.4% at Elizabeth Harbour and 63.0% on the Great Exuma Banks) occupied the shells of periwinkles that were common in the high intertidal or supratidal region of
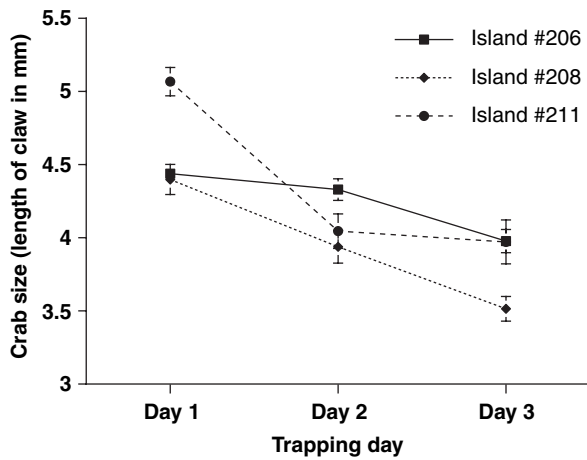
Figure 3 Size of land hermit crabs in the mark–recapture experiment as a function of island and trapping day. Error bars indicate 1 SE.
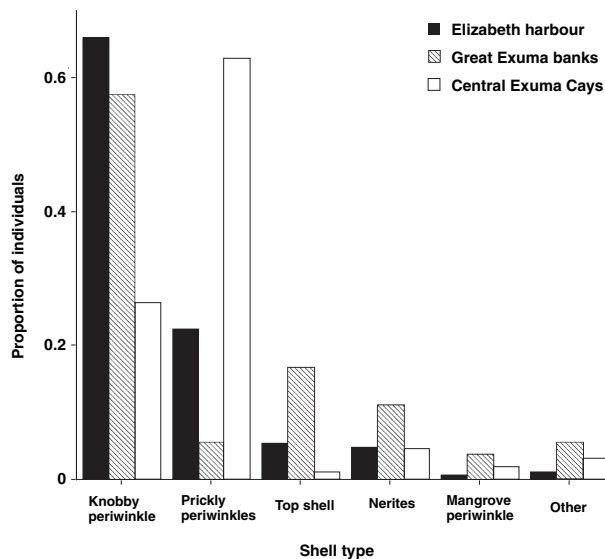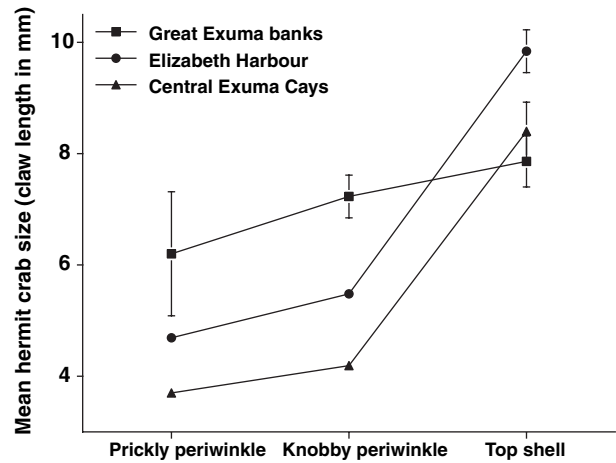

Figure 5 Size of land hermit crabs as a function of shell type and island group. Error bars indicate 1 SE. (Some SEs are so narrow, they are obscured by the symbols on the graph.)

Figure 4 Frequency distribution of six adopted shell types for the three island groups.

the islands (Fig. 4, Table 1). Top shells and nerites were usually present on the islands sampled. These islands did not contain intertidal mangroves, and mangrove periwinkles probably originated on other islands in the region. Most of the gastropods in the 'others' category inhabit shallow water rather than the intertidal zone of rocky islands, and shells of these species probably originated in the surrounding waters (Table 1). The proportions of adopted shells that could have originated on the islands sampled were 94.9% for the Central Exuma Cays, 91.0% for the Great Exuma Banks and 98.4% for Elizabeth Harbour (Table 1, Fig. 4).

Of the most common shell types, the prickly periwinkles housed the smallest individuals, the knobby periwinkles housed somewhat larger crabs and the top shells housed the

largest. Interestingly, the size of crab occupying these three shell types varied among island groups (Fig. 5). In the two-way ANOVAs, the effect of shell type was significant ($F = 106.205$, $P = 0.0001$, d.f. = 2, 2195), as was the effect of location ($F = 43.9$, $P = 0.0001$, d.f. = 2, 2195). The shell type × location interaction was also significant ($F = 11.6$, $P = 0.0001$, d.f. = 4, 2195). All *post hoc* pairwise comparisons of factor level means were different by the Bonferroni method ($\alpha = 0.05$), for both shell type and location.

The overall size distribution of crabs varied according to shell type [$\chi^2 = 296$, $P < 0.0001$, d.f. = 39, χ^2 test of homogeneity (Daniel, 1990), all three island groups considered together; Fig. 6]. The nerites, composed of three gastropod species of varying sizes, housed a wide range of crab sizes, excluding the largest size classes. Land hermit crabs that reach a relatively large size on these small islands probably use the shells of two or three different gastropod species as they grow.

DISCUSSION

Densities of land hermit crabs

On islands where pitfalls were left out for a single 24-h period, average densities of land hermit crabs varied over three orders of magnitude in the three island groups sampled, with the highest average densities reaching 13 crabs m^{-2} of vegetated area. Much variation in crab density was observed among islands, and the highest density observed on an island was 46 crabs m^{-2} of vegetated area. In the mark–recapture experiment, crab densities ranged from 11 to 33 crabs m^{-2} of vegetated area. These high densities are even more amazing in light of the fact that our sampling procedure caught some unknown fraction of the total number of crabs actually present.

The factors responsible for the observed variability in abundance and density of crabs are not clear, and may involve
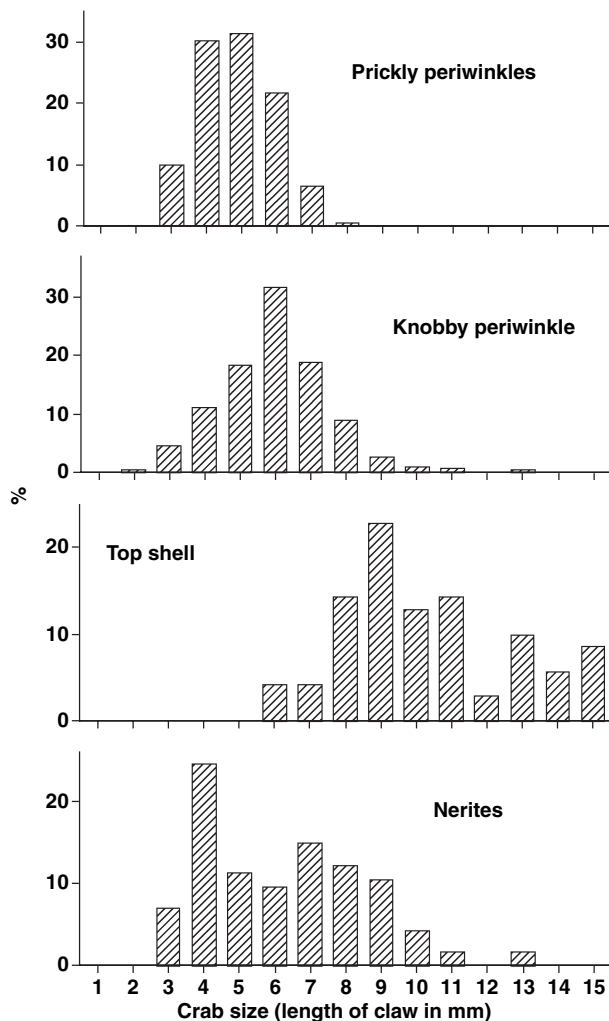
Figure 6 Frequency distributions of land hermit crab size by shell type, summed over all island groups.

differences in shell availability (see below), dispersal of larvae, food resources, etc. Marine currents could play an important role both in recruitment of crab larvae and allochthonous food sources. It is also not obvious why crab size is inversely related to abundance or density among the island groups. Lower crab abundances may translate into reduced intraspecific competition for food or shelter. This suggests that hermit crabs on these islands may be limited by food or by shell availability, with the relatively more important of the two factors varying among islands. For example, if food resources are similar among a set of islands, then crabs on islands with fewer shells may reach larger sizes. Shell availability would be the more limiting resource, and once a shell was acquired less competition for food would exist, allowing crabs to reach a larger size.

In the mark–recapture experiment, relatively few crabs were recaptured. Once captured, crabs may have avoided recapture due to stress resulting from up to 24 h in the pitfalls (often interacting with many other crabs), or stress from the handling and marking procedure. Additionally, hermit crabs are known to avoid recently eaten foods (Thacker, 1996, 1998). We

offered the same food in each 24-h period, because different types of food may have been differentially attractive and represented another source of sampling error.

Coenobita are attracted to congregations of conspecifics (Kurta, 1982), yet negative interspecific interactions were evident at small food sources. Because more than 100 individuals were frequently captured in a single pitfall, aggregations of crabs did not preclude the capture of additional crabs, at least to a degree. The number that could be captured was effectively limited, however, as once a certain number was present it was possible for crabs to reach the lip of the cup and pull themselves out (personal observations). Crabs did decrease in size over time, suggesting that larger crabs were more successful at obtaining food early but became trap-shy after being captured. This success could be due to greater aggressiveness or speed in locating resources relative to smaller crabs.

In the mark–recapture study relative densities varied over an order of magnitude depending upon whether vegetated or total island area is used. The perimeter of the islands is characterized by a swash zone – an area regularly disturbed by high tides and waves – that is usually barren of vegetation. Vegetated area is a better indicator of 'habitable area' for most organisms, and is usually a superior predictor in many island analyses (Morrison, 2002b). Land hermit crabs may, at times, utilize much of the swash zone, however, so both measures of island size are included for comparison.

The only physical island variable that was selected as a significant predictor (after multiple comparisons) of any hermit crab variable was the perimeter to area ratio P/A, which was positively correlated with hermit crab abundance in two regression analyses. Variation in P/A explained 59% of the variation in hermit crab abundance (determined by pitfall traps) for the nine islands in the Central Exuma Cays. Variation in P/A explained only 12% of the variation, however, in relative abundance of hermit crabs (determined by baits) for the larger set of 85 islands in that region.

Pitfall trapping, however, is likely to be a better index for assessing the abundance of land hermit crabs than baiting: Baits were left out for only 45 min, whereas pitfall traps were left out for 24 h. The activity of land hermit crabs on these islands is known to be affected by temperature and relative humidity (Morrison, 2002a), and variability in climatic conditions is likely to account for some of the unexplained variability in the larger data set (which was collected over 1 month, compared with the pitfalls that were run in a 2-week period). Additionally, land hermit crabs are known to compete with ants for food on these islands, and variability in the abundance of ants may account for some of the unexplained variation in the relative abundance of hermit crabs at baits. In stepwise multiple linear regressions of hermit crab bait occupancy as a function of environmental variables and competing ants, ant occupancy of baits was selected as a significant predictor in two of four years (Morrison, 2002a).

It is of interest that elevation was negatively correlated with crab size and, although not significant after correction for

multiple comparisons, elevation did explain 55% of the variability in crab size. Higher islands in this archipelago tend to have steeper sides. Gastropod species found in subtidal areas or surrounding shallow water tend to be larger than those found in the intertidal or supratidal zones (Table 1). It is likely these larger, heavier shells are not as frequently washed up on the higher, steeper islands, and hermit crabs on these islands have access to relatively fewer large gastropod shells.

Shell use

Coenobita clypeatus primarily utilized shells that most likely originated along the rocky shores of these islands (91–98%). Thus, the *P/A* ratio may be important because a more irregular shoreline would have relatively more gastropod habitat, all else being equal. Additionally, if marine subsidies are an important food source for hermit crabs (see below), more irregular shorelines would provide relatively more contact with the marine environment.

Only 1.6–9% of the shells identified would have originated in surrounding areas. The islands with the highest proportion of shells (9%) that would have originated off the island – in the Great Exuma Banks – are subject to the greatest amount of wave action, which could deposit shells from the sea on the islands. The steep, often overhanging, sides of the islands would appear to be a barrier to acquisition of marine gastropod shells without such a mechanism. In contrast, the islands of Elizabeth Harbour are the most sheltered, and had the lowest proportion of shells (1.6%) that would have originated in the surrounding area. Thus, factors such as exposure to wave action may be important in determining patterns of shell use on these small islands.

Hermit crabs may adopt shells from a great diversity of gastropod species, and the type and size of shell used are likely functions of shell availability (Ball, 1972). In general, most hermit crab populations are thought to be limited by shell availability (Greenaway, 2003; see Barnes, 1999 for an exception). Shell exchange is common (Hazlett, 1981); crabs appear to prefer shells with higher internal volume/weight ratios and attempt to increase this ratio with each exchange (Osorno *et al.*, 1998). Qualitatively, we noticed few vacant gastropod shells on the islands sampled. Because the majority of gastropod shells on these islands are relatively small, crabs also appear to be limited in size by the availability of larger shells. Ultimately, the question of why shell type and size varied among the island groups sampled becomes a question of why the various gastropod species were present in varying abundances or sizes, which is largely beyond the scope of this study. It does not appear that competition between land and marine hermit crabs for gastropod shells (Hazlett, 1981) is important in most areas of this archipelago, as few shells of marine origin were used by land hermit crabs.

One interesting finding is that the West Indian top shell, *Cittarium pica* (L.), was relatively much more abundant in the Great Exuma Banks than the other two areas (Fig. 3). The likely reason for this is that this species is commonly consumed by residents, and lower human population densities in the area of the Great Exuma Banks result in less harvesting of marine resources relative to the other two regions. This species reaches the largest size of any of the commonly encountered species (Table 1, Fig. 6), indicating that harvesting this gastropod may limit the size hermit crabs may reach on these islands. In Puerto Rico, for example, *C. clypeatus* individuals no longer attain normal adult size, in part because of the removal of large shells by humans (Nieves-Rivera & Williams, 2003).

Implications

On some islands of our study, land hermit crabs may account for the greatest biomass of any animal taxa (see also Morrison, 2005). Given their great abundance, it is possible that food webs on such islands may be strongly influenced from the bottom up. The ultimate importance of crabs is likely to depend upon their density, which will be determined by the availability of gastropod shells. This in turn will depend upon the factors that affect patterns of abundance of intertidal or supratidal gastropod shells on the islands, the forces that result in marine shells being deposited upon the islands and the impact of human harvesting of gastropod shells.

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