

## Shell Selection and Utilization in a Terrestrial Hermit Crab, *Coenobita compressus* (H. Milne Edwards)

Peter Abrams\*

Institute of Animal Resource Ecology, University of British Columbia,  
Vancouver, B.C. V6T 1W5, Canada

**Summary.** Shell utilization and shell selection studied in the tropical terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). Three major shell related variables are examined; shell size, shell species, and shell condition. *Nerita scabricosta* (Lamarck) is the most commonly occupied shell, and it is also preferred over other shell species. *Coenobita* in the field are usually found in smaller than the preferred size of shell, and the difference between utilized and preferred shells is most pronounced in relatively small individuals. Shell size preference differs significantly between similarly sized crabs collected at different sites. There is also a preference for shells which have previously been used by other *Coenobita* individuals. This preference is due to shell modification by *Coenobita*, which increases the effective size of the shell. It is argued that the fitness of most sexually mature individuals is probably unaffected by the supply of new shells, since these are too small to be utilized. It is possible that the interaction of adult *Coenobita* for shells may be better described as mutualism than as competition. This illustrates the fact that a significant difference between utilized and preferred resources need not imply competition for those resources. Results indicate that the nature of intraspecific competition and population regulation in at least this terrestrial hermit crab is significantly different from these processes in marine hermit crabs.

### I. Introduction

A comparison of those resources used by an animal species with those that are preferred can often provide evidence for competition for that set of resources. It is usually reasonable to assume that preferences have been molded by natural selection. If animals are found to utilize significant amounts of nonpreferred

---

\* Present address: Department of Biological Sciences, University of California at Santa Barbara, Santa Barbara, CA 93106, USA

resources, it is often argued that preferred resources are in short supply and there is competition for those resources. This line of argument has been used in several studies which have compared the utilized and the preferred shells of several species of marine hermit crabs (e.g. Vance, 1972; Mitchell, 1975; Kellogg, 1976; Bach et al., 1976). These investigators have observed that hermit crabs often occupy shells which are smaller than the preferred size or which are of nonpreferred species. The present article describes the results of a study of shell utilization and shell selection in the tropical terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards). It seeks to determine whether significant numbers of nonpreferred shells are being used, and if so, whether this implies the existence of competition. Field observations were made on the shell utilization of this species in Panama and Costa Rica. Experiments were done to determine the preferred size, species, and condition of shells, and to study the phenomenon of shell modification which is a major determinant of shell condition.

*Coenobita compressus* is one of the most conspicuous inhabitants of the supra-littoral zone in the tropical Eastern Pacific. It seems to be found most often on or near sand or gravel beaches. It is a scavenger, and has been observed to feed on a large variety of organic matter (Ball, 1972). Large individuals are generally nocturnal, but smaller individuals were more active during the day. Oviparous females were observed at all times of the year in Panama, but were extremely uncommon during the dry season (December through April). Relatively little is known about the general ecology of *Coenobita compressus*, but some additional information on its natural history may be found in Ball (1972).

## II. Materials and Methods

This study involved both field sampling to study utilization and laboratory experiments to study preference. Most of the field sampling was carried out during the period from October 1975 until September 1976, while the author was associated with the Smithsonian Tropical Research Institute in Panama. An earlier collection was made in August 1973 at Playa Blanca, Osa Peninsula, Costa Rica. Table 1 is a complete list of field sites. Collections were made by picking up all of the crabs encountered in a given time span, or by picking up all of the individuals encountered until a certain number had been collected. Additional individuals of size classes that were poorly represented in the sample were collected in a similar manner. Although this sampling method does not allow one to determine the size structure of the population, the shells inhabited by any given size class of crabs should be representative of shells used by that size class in the population.

For each specimen collected, crab size, shell size, shell species, shell quality, and site of collection were noted. The crab size measurement was required because shell preferences are a function of size. In general, the longest linear dimension (usually length) was used as a measure of shell size. This was easy to measure, and for each shell species, it was very highly correlated with other indices of shell size such as volume or weight. Measurements were made to the nearest 0.05 mm. using a pair of dial calipers. The index of crab size was the length of the dactyl of the second left pereopod. For crabs with damaged, missing or regenerate dactyls, shield length (the anterior, calcified portion of the cephalothorax) was measured. Dactyl measurement was convenient because it could be made without extracting the crabs from their shells. It correlated well with other more commonly made measurements of hermit crab size, such as weight or shield

**Table 1.** Study sites in Panama and Costa Rica

- 
1. Boyscout Beach, Scout Island, Fort Amador, Panama Canal Zone
  2. Flamenco Island, Fort Amador, Panama Canal Zone
  3. Venado Beach, Panama (near Howard Air Force Base)
  4. Bahía Damas, Isla Coiba, Panama; prison colony beach
  5. Bahía Honda, Panama; beach on west side near entrance to bay
  6. Isla Jicaron, Panama
  7. Islas Secas, Panama
  8. Playa Blanca, Osa Peninsula, Costa Rica
- 

**Table 2.** Description of crab extension-withdrawal categories, and associated numerical values (low values represent shells which allow the crabs to withdraw the farthest into the shell). Angles were estimated visually

- 
1. The angle from the plane of the shell aperture to the plane of the manus of the major cheliped is greater than or equal to 90 degrees
  2. The angle from the plane of the shell aperture to the plane of the manus of the major cheliped is greater than or equal to 60 degrees, but less than 90 degrees
  3. The angle from the plane of the shell aperture to the plane of the major cheliped is greater than or equal to 30 degrees, but less than 60
  4. The angle between the plane of the aperture and the plane of the major cheliped is less than 30 degrees, and the crab does not extend beyond the aperture
  5. The crab extends slightly beyond the aperture of the shell, but not more than one left side ambulatory leg projects beyond the aperture
  6. More than one, but not more than two ambulatory legs (left side) project beyond the aperture
  7. Both left ambulatory legs extend beyond the aperture, and the manus of the major cheliped extends beyond the aperture. Not more than half of the merus of the major cheliped extends beyond the aperture
  8. At least half the merus of the major cheliped extends beyond the aperture, but the eyestalks do not
  9. Some, but less than half of the eyestalk projects beyond the aperture
  10. More than half of the eyestalk, but no other part of the cephalothorax projects beyond the aperture
  11. Part of the hard portion of the cephalothorax extends beyond the aperture
  12. Part of the soft portion of the cephalothorax extends beyond the aperture
- 

length. Weight is related to dactyl length by the following equation, with  $r^2 = 0.96$ :

$$\ln(\text{crab weight}) = -6.15 + 3.03 \ln(\text{dactyl length}). \quad (1)$$

The relationship between shield length and dactyl length is

$$\text{Shield length} = 0.01 + 0.75 (\text{dactyl length}) \quad (r^2 = 0.92). \quad (2)$$

A final observation which was recorded for each crab was the degree to which the crab extended beyond the plane of the aperture of the shell when the crab was withdrawn into the shell as far as it would go. This was an additional index of the relative size of the shell and the crab. When withdrawn into a shell within the preferred size range, many *Coenobita* form a "pseudo-operculum" with the dactyl of the second left pereopod and the manus of the major cheliped. Although this structure often is close to an imaginary plane passing through the aperture of

the shell, many crabs cannot withdraw this far, and some of the limbs and/or cephalothorax will project out of the shell. In other cases, the "pseudo-operculum" may lie well within the shell. Table 2 lists the categories used to classify crab extension.

The above measurements were made on a total of 1344 individuals from eight different collections.

To investigate shell preference, a number of shell selection experiments were performed. The basic design of all of the experiments was similar. A number of recently (within 24 h) collected *Coenobita* was placed in a large container (a plastic children's wading pool) in the lab along with a much larger number of empty shells of an appropriate range of sizes (including shells both larger and smaller than those occupied by the crabs). The bottom of the container was covered with sand, and the crabs were provided with food, fresh water, and debris for hiding places. The empty shells were marked using Brady micro wire markers. Experiments were generally run for at least 24 h. One experiment was continued for 5 days, and even at the end of this period, shell changes were still occurring. In this experiment 50% of the crabs changed shells in the final 24 h. Average shell size, species, and condition did not change significantly after the first 24 h, however, and any individual should have been able to encounter a large proportion, if not all of the shells during that time period. All experiments were carried out at the Naos Marine Laboratory of the Smithsonian Tropical Research Institute. Details on the procedure followed in specific experiments are given in the next sections.

### III. Shell Utilization: Results and Discussion

At least three major factors are important in determining whether a given shell will be suitable for or preferred by a hermit crab. These are shell species, shell size, and shell condition. Therefore, each of these variables was considered in describing the shell utilization pattern of *Coenobita*.

*Coenobita* was observed to inhabit the shells of at least 30 species of gastropod. Table 3 summarizes shell utilization for all sites pooled in terms of shell species. The proportions of crabs inhabiting different shell species are similar to those reported by Ball (1972), who collected over the entire range of the species. The most commonly used shells for moderate to large sized crabs were *Nerita scabricosta*, *Turbo saxosus*, and *Natica* sp. *Nerita scabricosta* was used approximately three times as often as the next most commonly used species. Smaller individuals (less than 10 mm dactyl length) also used *Nerita scabricosta* more often than any other species, but *Nerita funiculata* and *Strombus gracilior* were also commonly used. The smallest individuals (dactyl length less than 5 mm) were usually found to occupy *Planaxis planicostatus*, *Nerita funiculata*, and small *Nerita scabricosta*.

Most sites were similar in having larger numbers of crabs inhabiting *Nerita scabricosta* than any other shell, but *Turbo saxosus* was the predominant shell at one site (Jicarón). Empty shells of the species commonly used by *Coenobita* were rare. Although a systematic search for empty shells was not carried out at most sites, there was only one location where empty shells were readily visible. This was Playa Blanca, Costa Rica. Here, empty *Strombus gracilior* shells were very common, but this shell was among the least preferred shell species, and could only be used by a very limited size range of crabs. A scarcity of empty shells in hermit crab habitat has been noted by most other individuals who have worked on this group (e.g. Vance, 1972; Bach et al., 1976; Kellogg, 1976).

**Table 3.** Shell species utilization by *Coenobita compressus* (species identified using Keen, 1971)

Shell species	% of crabs in shell	% of crabs under 10 mm dactyl length in shell	% of crabs over 10 mm dactyl length in shell
<i>Nerita scabricosta</i>	40.55	28.57	48.00
<i>Nerita funiculata</i>	6.25	14.12	0
<i>Turbo saxosus</i>	13.32	8.91	16.09
<i>Polinices</i> sp.	2.53	1.34	3.77
<i>Thais melones</i>	3.65	2.86	4.15
<i>Thais biserialis</i>	3.72	4.70	2.77
<i>Leucozonia cerata</i>	0.15	0.16	0.13
<i>Planaxis planicostatus</i>	1.11	2.52	0
<i>Muricanthus</i> sp.	1.34	1.00	1.88
<i>Latirus mediamericanus</i>	0.89	0.17	0.51
<i>Cantharus ringens</i>	1.19	2.52	0.12
<i>Bursa</i> sp.	0.45	0.50	0.37
<i>Natica</i> sp.	6.47	5.04	8.41
<i>Solenosteira fusiformis</i>	2.31	1.34	3.27
<i>Bulla punctulata</i>	2.38	3.03	2.00
<i>Nassarius versicolor</i>	0.67	1.51	0
<i>Cerithidea valida</i>	0.37	0.84	0
<i>Modulus catenulatus</i>	0.07	0.17	0
<i>Littorina zebra</i>	4.09	3.70	5.27
<i>Cerithium stercumscarum</i>	0.37	0.84	0
<i>Opeatostoma pseudodon</i>	0.37	0.50	0.37
<i>Purpura</i> sp.	0.15	0	0.24
<i>Neritina</i> sp.	1.04	2.35	0
<i>Murex</i> sp.	0.52	1.00	0.12
<i>Cerithium adustum</i>	0.67	1.51	0
<i>Astraea</i> sp.	0.15	0.34	0
<i>Acanthina brevidentata</i>	0.22	0.50	0
<i>Strombus gracilior</i>	4.09	8.24	1.38

The second important variable in describing shell utilization is shell size. The size of shell occupied is to a large extent dependent upon crab size, so shell size utilization for each species of shell may be described by plotting a regression equation of shell length vs. crab dactyl length. For *Coenobita* in *Nerita scabricosta*, the regression equation is Shell length = 6.89 + 1.59 (dactyl length);  $N=545$ ,  $r^2=0.83$ . Such an equation could have been calculated for each shell species. This did not seem necessary in the present case, since the main purpose was to compare the sizes of occupied shells with those of the preferred shells, and this could be done using the crab extension measurements. This method has some advantages over plotting a regression of shell size vs. crab size. A problem with indexing shell size by any single measurement is that there is considerable variation in shell morphology. Thus, two shells of identical length (or width) may represent very different sizes to a hermit crab. This problem may be lessened by taking several measurements on each shell and using multivariate statistical methods to define a shell size measurement (e.g. Kuris and Brody, 1976). This is at best a partial solution, however,

**Table 4.** Regression of crab extension vs. crab size for all crabs and for those in *Nerita scabricosta* only

---

I. For all shells: Extension = 2.093 + 0.334 (dactyl)
significant at 0.0001 level
$r^2 = 0.269$
Standard error of regression coefficient = 0.015
Standard error of regression constant = 0.1664
II. For <i>Nerita scabricosta</i> only: Extension = 1.165 + 0.4028 (dactyl)
significant at 0.0001 level
$r^2 = 0.3085$
Standard error of regression coefficient = 0.0259
Standard error of regression constant = 0.3052

---

**Table 5.** Average extension of *Coenobita* beyond the aperture of the shell for different sites

---

Site	Sample size	Average extension	Standard error
Boyscout Beach	59	5.458	0.2527
Venado Beach	88	5.405	0.1936
Bahia Damas	60	7.167	0.3217
Jicaron	355	4.82	0.1947
Secas	181	6.657	0.2097
Osa Peninsula	278	6.748	0.2602

---

obtained at the expense of the requirement for much larger amounts of data. In the case of *Coenobita compressus*, relative shell size may be measured directly by determining how far a crab extends from its shell or how far it can withdraw into the shell. For most marine species, the crab can withdraw so far into the shell that it is physically very difficult to measure the distance from the aperture of the shell to any given part of the crab's anatomy. In *Coenobita compressus*, this is almost never the case. This is what made possible the measurement of extension described in the previous section.

By assigning numerical values to the descriptive categories of crab extension, it is possible to calculate an average extension for crabs at a given site, of a given size, or in a given species of shell. Two major features emerge from this sort of analysis. In the first place, the average extension measure increases with crab size. Table 4 gives the results of regression analyses of extension vs. crab size for all crabs and for those occupying *Nerita scabricosta* shells only. Both regressions have significant positive coefficients. Large *Coenobita* are not able to withdraw as far into their shells as small *Coenobita*. A second feature is that there is a significant difference in the average extension at different sites. Table 5 shows average extension values for different samples. Average crab size was similar at most sites, so the difference between sites is not a result of different crab sizes. It reflects the fact that at some sites, crabs are in relatively smaller shells than at other sites.

**Table 6.** Comparison of used and unused *Nerita scabricosta* shells [regression equations of shell weight (g) vs. shell length (mm)]

I. Unused shells: $\ln(\text{weight}) = -9.248 + 3.291(\ln(\text{length}))$ $n = 84$ Standard error of regression coefficient = 0.0037 Standard error of regression constant = 0.09137 $r^2 = 0.968$			
II. Used shells: $\ln(\text{weight}) = -8.022 + 2.863(\ln(\text{length}))$ $n = 51$ Standard error of regression coefficient = 0.1646 Standard error of regression constant = 0.5569 $r^2 = 0.861$			
III. Weights of used and unused shells for selected lengths, calculated from the regression lines			
Shell length	Unused weight	Used weight	% reduction in weight
20	0.611 g	0.555 g	9.13
24	1.211 g	1.077 g	11.06
28	1.718 g	1.518 g	11.65
32	2.158 g	1.901 g	11.91
36	2.545 g	2.233 g	12.26

For marine hermit crabs, shell condition is often an important variable in determining shell suitability (Kellog, 1971). Some factors which make shells less suitable (or unsuitable) are such things as the presence of holes in the shell or the settlement of encrusting organisms inside or on the shell. Occasional *Coenobita* individuals were found occupying shells with one or more holes, but this was true for only 1–2% of the crabs collected. There were no encrusting organisms. The inside of many shells had a coating of a bright green alga (Ball, 1972, also observed this) but this did not appear to affect shell suitability.

Several previous workers had noted that the shells occupied by crabs of the genus *Coenobita* often lack a columella (Ball, 1972; Kinoshita and Okajima, 1968; Kuris and Brody, 1976). Kinoshita and Okajima attribute this to mechanical and chemical abrasion, but do not report any experimental analysis of the phenomenon. Other modifications noted on shells occupied by *Coenobita compressus* were enlargement of the aperture of the shell, and in the case of *Nerita scabricosta*, wearing away of the ridge on the inner margin of the shell's aperture. The majority of shells occupied by *Coenobita* showed some sort of modification. All shells obtained from individuals with a dactyl length greater than 12 mm were modified. One of the major results of modification which could be measured quantitatively was the decrease in the weight of shells of a given length. Table 6 compares regression lines for used and unused shells from Boy Scout Beach. The proportional loss of weight which can be attributed to shell use is greater for larger shells, reflecting a greater average degree of modification for these shells.

An attempt was made to determine how long it took for these modifications to occur. Fifteen crabs were collected and removed from the shells which they

had been occupying. They were then allowed to select from an array of 60 previously unused *Nerita scabricosta* shells. The crabs were kept in a large container in the lab and were fed ad libitum. Ten individuals survived for two months, at which time the experiment was terminated. At that time, none of the shells occupied showed any signs of wear that could be perceived with the unaided eye. This suggests that the process of shell modification is quite slow. The fact that most shells occupied in the field show a large amount of modification may indicate that those shells have been occupied by *Coenobita* for a number of years. Ball (1972) also speculates that shells may remain in the population for several years. Many of the *Nerita scabricosta* shells occupied on Boy Scout Beach were significantly larger than any of the living *Nerita* which could be found in the area. This again suggests that the shells may have been several years old. The laboratory results must, however, be interpreted with some caution, since laboratory conditions may have adversely affected the crabs' growth or shell modification abilities.

One feature of the hermit crab-shell interaction that is not discussed here is shell fighting (e.g. Hazlett, 1966). In a shell fight, one crab "forces" another to give up its shell by a series of ritualized behaviors. The loser will then usually enter the shell abandoned by the winner. This has a potential impact on shell utilization. I did not observe this kind of shell exchange in *Coenobita compressus* either in the field or in the laboratory. Although Ball (1972) reports having observed shell fights, the behavior he describes is not a shell fight in the sense of Hazlett (1966), and it did not result in a shell exchange.

#### IV. Shell Selection: Results and Discussion

Several different shell selection experiments were performed to help explain the utilization patterns observed and to determine the degree of difference between preferred shells and shells available in the field.

Preferred shell sizes could be determined by allowing crabs to select from a wide variety of shells, and then calculating a regression equation for shell size as a function of crab size. In the first experiment in this series, 55 *Coenobita compressus* from Boy Scout Beach were allowed to select from an array of approximately 500 *Nerita scabricosta* shells. The shells used had been obtained from hermit crabs in the field, so most exhibited a large degree of modification, as did the shells initially occupied by the experimental crabs. The hermit crabs used in the experiment ranged in size from 4.5 to 20.0 mm dactyl length. By only using *Nerita scabricosta* shells, it was possible to examine size preference without the complication of different shell species. After 72 h, crabs were resampled. Regression lines were calculated for *Nerita* length vs. crab size for those shells occupied at the beginning and those occupied at the conclusion of the experiment. The results are shown in Table 7. There is a significant difference in the regression constants, but not in the coefficients. Selected shells are larger than initially occupied shells by approximately 3 mm for all crab sizes. This represents a greater proportional increase for small crabs. Vance (1972) com-



**Table 7.** Regression equations relating shell length and crab size for *Coenobita* occupying *Nerita scabricosta* before and after shell selection. Crabs were collected on Boy Scout Beach ( $n=55$ ) (lengths in mm)

I. At beginning of selection experiment		
Shell length = 1.782 (dactyl length) + 5.148		
Standard error of regression coefficient = 0.0882		
Standard error of regression constant = 1.053		
$r^2 = 0.8851$		
II. At end of selection experiment		
Shell length = 1.697 (dactyl length) + 8.479		
Standard error of regression coefficient = 0.0718		
Standard error of regression constant = 0.8917		
$r^2 = 0.9144$		
III. Average shell sizes for several crab sizes before and after shell selection calculated from regression lines		
Crab dactyl length	Shell size before selection	Shell size after selection
6 mm	15.84 mm	18.66 mm
8 mm	19.40 mm	22.05 mm
10 mm	22.97 mm	25.45 mm
12 mm	26.53 mm	28.84 mm
14 mm	30.10 mm	32.24 mm
16 mm	33.66 mm	35.63 mm
18 mm	37.22 mm	39.03 mm
20 mm	40.79 mm	42.42 mm

pared the sizes of preferred and occupied shells using a quantity he defined as the shell adequacy index. This is a ratio whose denominator is the weight of a crab in a given shell, and whose numerator is the weight of a crab for which the shell is of the preferred size. Using my data, it is possible to calculate the average shell adequacy index as a function of crab size. Since I measured dactyl lengths rather than weights, it is necessary to use the weight vs. dactyl regression equation [Eq. (1)] to convert dactyl length to weight. Thus, the weight of a crab of a given dactyl length (denoted  $D_1$ ) is given by

$$\text{Crab Weight} = \exp(-6.15 + 3.03 \ln(D_1)). \quad (3)$$

The average sized *Nerita* shell occupied in the field by a crab of this dactyl length is found using the crab size-shell size regression in Table 7, part I:

$$\text{Shell Length} = 5.15 + 1.78(D_1). \quad (4)$$

The crab size for which this shell size is preferred may be found by performing a regression of dactyl length vs. shell size using the data from the experiment described in Table 7, part II. The regression equation is given below where  $D_2$  is the dactyl length of this second crab.

$$D_2 = 0.54(\text{Shell length}) - 3.57. \quad (5)$$

Substituting the right hand side of Equation (4) for shell length in Equation (5) relates the two crab sizes:

$$D_2 = 0.54 (5.15 + 1.78 (D_1)) - 3.57. \quad (6)$$

To obtain the numerator of the expression for the shell adequacy index,  $D_2$  must be converted to weight by substituting the right hand side of Equation (6) in Equation (1). The shell adequacy index is the ratio of this weight to the weight given by Equation (3).

Shell Adequacy Index

$$= \frac{\exp(-6.15 + 3.03 \ln(0.54 (5.15 + 1.78 (D_1)) - 3.57))}{\exp(-6.15 + 3.03 \ln(D_1))} \quad (7)$$

The shell adequacy index increases from a value of 0.678 for crabs of dactyl length 10 mm to a value of 0.775 for crabs with a dactyl length of 20 mm. This result contrasts with that of Vance (1972), who found that the shell adequacy index decreased with crab size for two marine hermit crabs.

It is also possible to analyze the results of the selection experiment from the standpoint of crab extension rather than shell size. Extension was recorded for each individual at the beginning and the end of the selection experiment, and these data were analyzed in two ways. Average extension at the beginning of the selection experiment was 4.53 (standard error 0.116) and average extension at the end of the experiment was 3.48 (standard error 0.183). This difference is significant at the 0.001 level. Since the field observations had indicated a higher average extension for large crabs, it was of interest to determine whether this was also true of crabs which had selected shells of the preferred size. Regression equations of crab extension vs. crab dactyl length at the beginning and at the end of the shell selection experiment are given in Table 8. Average extension does in fact increase with dactyl length. In addition, the ratio of average extension before selection to average extension after selection decreases with increasing crab size, again suggesting that larger crabs are using shells which are closer to the preferred size than small crabs. Thus, the fact that large crabs occupy shells which are smaller relative to their body size than the shells occupied by small crabs reflects a preference for such shells, rather than a more severe shortage of preferred shells for larger crabs.

The data from the experiment just described were reanalyzed to determine if there was a difference in the shell size preferences of male and female crabs. Since females have to carry eggs within the shell (on the pleopods), it seemed possible that they might prefer relatively larger shells than males. The separate regression equations for male and female crabs are shown in Table 9. The lines do not differ significantly, indicating that crab sex does not greatly affect shell size preference.

A further question regarding shell size preference was whether there was an effect of location on preference. In order to examine this question, two groups of *Coenobita* which had greater average extension than the crabs from Boy Scout Beach were allowed to select from the same array of shells. The other sites

**Table 8.** Regression equations relating crab extension and crab size for *Coenobita* occupying *Nerita scabricosta* before and after shell selection. Crabs were collected on Boyscout Beach. The data are from the same experiment as those in Table 7 (lengths are in mm)

I. Before shell selection			
Crab extension = $2.913 + 0.14$ (dactyl length)			
Standard error of regression constant = 0.3875			
Standard error of regression coefficient = 0.0324			
$r^2 = 0.260$			
II. After shell selection			
Crab extension = $0.5938 + 0.2468$ (dactyl length)			
Standard error of regression constant = 0.6735			
Standard error of regression coefficient = 0.0560			
$r^2 = 0.284$			
III. Average extension before and after shell selection calculated using regression equations for several crab sizes			
Crab dactyl length	Extension before selection	Extension after selection	$\frac{\text{Extension before}}{\text{Extension after}}$
6	3.75	2.07	1.81
8	4.03	2.57	1.57
10	4.31	3.06	1.41
12	4.59	3.56	1.29
14	4.87	4.05	1.20
16	5.15	4.54	1.13
18	5.43	5.03	1.08
20	5.71	5.53	1.03

**Table 9.** Regression equations for male and female *Coenobita* which have selected *Nerita scabricosta* shells. Data obtained from the same experiment as that in Tables 7 and 8

I. Male crabs ( $n = 26$ )	
Shell length = $1.727$ (dactyl length) + 7.815	
Standard error of regression coefficient = 0.1152	
Standard error of regression constant = 1.339	
$r^2 = 0.911$	
II. Female crabs ( $n = 29$ )	
Shell length = $1.707$ (dactyl length) + 8.709	
Standard error of regression coefficient = 0.092	
Standard error of regression constant = 1.139	
$r^2 = 0.927$	

were Flamenco Island and the Secas Islands. The range of crab sizes used in the experiment was similar to that for Boyscout Beach. Regression lines for the crabs from Secas and Flamenco are shown in Table 10. Both of these lines differ significantly from the regression line for *Coenobita* from Boyscout Beach. Small crabs from these two sites select slightly larger shells than comparably sized *Coenobita* from Boyscout Beach, but large individuals select smaller shells than crabs from Boyscout. This result indicates that the observed difference

**Table 10.** Regression equations for crabs from the Secas Islands and Flamenco Island which have selected *Nerita scabricosta* shells (lengths in mm)

I. <i>Coenobita</i> from Secas ( $n=13$ )			
Shell length = $13.80 + 1.112$ (dactyl length)			
Standard error of regression coefficient = 0.1699			
Standard error of regression constant = 1.827			
$r^2 = 0.796$			
II. <i>Coenobita</i> from Flamenco ( $n=17$ )			
Shell length = $11.26 + 1.487$ (dactyl length)			
Standard error of regression coefficient = 0.1704			
Standard error of regression constant = 2.156			
$r^2 = 0.8355$			
III. Comparison of shell sizes calculated from regressions for different crab sizes at three locations			
Crab dactyl length	Boyscout Beach	Secas I	Flamenco I
6	18.66	20.47	20.18
8	22.05	22.70	23.16
10	25.45	24.92	26.13
12	28.84	27.14	29.10
14	32.24	29.37	32.08
16	35.63	31.59	35.05
18	39.03	33.80	38.03
20	42.42	36.04	41.00

in shell utilization between locations is at least in part due to different shell size preferences. This in turn suggests that if preferred shell size is to be compared with utilized shell size in hermit crabs, this comparison should be done separately for each study site. There is no reason to believe that the phenomenon of different preferences at different sites should be restricted to *Coenobita compressus*. This provides an explanation for an anomalous set of observations made by Vance (1972) in a study of shell selection in several marine hermit crabs. He found that the hermit crab *Pagurus hirsutiunculus* from one site (Buoy Rock) was in shells which were on the average significantly larger than the preferred size. The most likely explanation for this is that crabs at that site preferred larger shells than the crabs (from a different site) which were used to determine size preference.

Many studies of shell preference in hermit crabs have been concerned with the question of shell species preference (e.g. Reese, 1962; Mitchell, 1975), and several investigators have shown for several crab species that there is a preference for some shell species over others. Reese's approach, which was used by several subsequent workers (Volker, 1967; Childress, 1972), was to present crabs with shells of different species, all of the same weight, and then to repeat the experiment for several different weights of shells. Since weight does not appear to be the most important variable in shell selection, however, this approach can confound species preference and size preference. Species preference can be examined independently of size preference only by presenting crabs with shells which are of the preferred size for each species. In practice, this was done by presenting the crabs with a sufficiently large number of each species of shell so that it was likely that there were several shells of the preferred size for each species.

Since *Coenobita compressus* occupies at least thirty different shell species, it would take an inordinate amount of effort to determine the relative preferences for all of the shell species. The approach that I took was to compare the preference of *Coenobita* for *Nerita scabricosta* shells and non-*Nerita* shells considered as a single group. Another experiment was run to compare the relative preferences for the two most commonly occupied shells—*Nerita scabricosta* and *Turbo saxosus*.

In the first shell species selection experiment, a group of 20 *Coenobita* occupying *Nerita scabricosta* was collected at Boy Scout Beach. The crabs were allowed to select from an array of approximately 200 *Nerita scabricosta* shells and 200 shells of other species (*Turbo saxosus*, *Natica chemnitzii*, *Littorina zebra*, *Polinices* sp., *Thais melones*, and *Thais biserialis* were the most common shell species in this second group of shells). The experiment was allowed to run for 72 h. Simultaneously, a group of 20 *Coenobita* occupying non-*Nerita* shells (7 in *Turbo saxosus*, 2 in *Opeatostoma pseudodon*, 5 in *Thais melones*, 3 in *Polinices* sp., 1 in *Thais biserialis*, 1 in *Acanthina brevidentata*, and 1 in *Cantharus ringens*) was allowed to select from a similar array of *Nerita* and non-*Nerita* shells. After selection, 19 of the 20 crabs originally in *Nerita* shells were still in *Nerita*, although not more than 4 individuals occupied shells which they had initially inhabited. The result for crabs which were collected in shells other than *Nerita* was similar; only one crab out of 20 occupied a shell other than *Nerita* at the end of the experiment, and none of the crabs stayed in their original shells. This strongly suggests that the preference for *Nerita* is independent of prior shell occupancy. Although it is possible that the crabs collected in non-*Nerita* shells had occupied *Nerita* at some point in their life, the fact that most individuals were significantly larger than 12 mm dactyl length suggests that they had occupied the shells in which they were collected for a considerable time (the reasons for this assertion are given in the following discussion of shell modification). Since 52% of the crabs over 10 mm in dactyl length which were collected in the field occupied non-*Nerita* shells, it is clear that a significant number of crabs were in non-preferred shell species.

The preference for *Nerita* over *Turbo* was examined in more detail, because *Turbo* was the second most commonly used shell. Twenty *Coenobita* from Boy Scout Beach which were mainly in *Nerita* shells (one individual was in a *Natica* shell and one in a *Polinices*) were offered 200 empty but previously used *Turbo* shells. At the conclusion of the experiment (after 72 h), 17 crabs occupied their original shells, and 3 occupied *Turbo* shells. This 15% rate of shell changing should be compared with the 100% shell change frequency observed when crabs collected in non-*Nerita* shells were allowed to select *Nerita* as well as non-*Nerita* shells. Thus, the preference for *Nerita* over *Turbo* appears to be much stronger than the preference for larger shells, since a large proportion of the *Turbo* which were offered were significantly larger than the shells which the crabs originally inhabited. This suggests that in general shell species preference is stronger than shell size preference for *Coenobita compressus*. This correlates with the fact that size preference, but not species preference, seems to be sensitive to previous experience. It would be interesting to determine whether this was also the case for marine hermit crabs, many of which seem to have rather poorly defined shell species preferences (unpublished data).

The third variable considered in the shell selection experiments was shell condition—whether or not the shell had been modified by previous occupancy by *Coenobita*. Two experiments were done to examine the effect of modification on preference. In the first, 20 crabs from Boy Scout Beach were offered approximately 200 empty *Thais melones*, *Nerita scabricosta*, *Leucozonia cerata*, and *Opeatostoma pseudodon*, all of which were unused. Only two individuals had changed shells when the experiment was terminated at the end of 48 h. An individual with a dactyl length of 9.5 moved into a *Nerita scabricosta* shell of 28.4 mm, and an individual of dactyl length 9.6 moved into a *Thais melones* shell 30.9 mm in length.

In a second experiment the shell species variable was removed by using only *Nerita scabricosta* shells. Twenty six crabs from Boy Scout Beach were offered a choice of 100 unused *Nerita* and 100 previously used *Nerita* shells with similar external dimensions. At the termination of the experiment, 23 crabs were in used shells, and only three had entered new unused shells. The average size of crabs which moved into unused shells was 6.55 mm dactyl length, compared to an average dactyl length of 8.70 mm for all crabs used in the experiment. Thus, there is a strong selection against unused shells, which is especially pronounced in larger individuals. Even when only those individuals with a dactyl length of less than 7 mm are considered, the majority (71%) did not move into unused shells. The apparent advantage of shell modification is that it provides additional living space and a larger entrance to that space, allowing the crab to grow larger without completely outgrowing its shell. As a consequence, however, the crab may become too large to occupy most unused shells, and this appears to account for the selection against unused shells.

I attempted to determine the maximum sized crab which would fit (i.e. could withdraw all of the cephalothorax) into *Nerita scabricosta* shells which were as large as the largest living *Nerita* in the area (for Boy Scout Beach, this meant *Nerita* shells 31 to 33 mm in length.) No crabs with a dactyl length greater than 12 mm were able to fit into these *Nerita* shells, and many crabs with dactyls 10 to 12 mm in length were unable to do so. 48% of all individuals collected at all localities were larger than 11 mm in dactyl length. Virtually all ovigerous females were larger than this size. Three individuals of the 287 ovigerous females examined had dactyl lengths between 10 and 11 mm. There are some other shell species which reach larger sizes than *Nerita scabricosta*, but they are relatively rare. Unmodified *Muricanthus* shells were large enough to accommodate a *Coenobita* of 15 mm dactyl length, but only approximately 1% of the crabs collected occupied *Muricanthus* shells, and no *Muricanthus* (*M. ambiguus* and *M. princeps*) shells were chosen in any of the shell selection experiments. It thus appears that a large fraction of the population (most sexually mature individuals) would be unable to move into an unused shell, should one be encountered. These individuals can only change shells if a used shell becomes available through the death of another *Coenobita* which does not entail the destruction of its shell.

Thus, for sexually mature individuals, the fact that many utilized shells are smaller than the preferred size or of non-preferred species does not imply that there is competition for shells. The only shell large enough to be used

by an adult *Coenobita* is one that has been used previously by another *Coenobita*. Therefore, it is possible that the supply of usable shells is an increasing function of adult *Coenobita* population density, suggesting facilitation rather than competition. Total population density in this species may be regulated either by the rate at which new shells become available to the small (non-reproductive) size classes, or by a different factor which may operate on adult crabs, such as food supply or predation. This system illustrates the need to study the mechanism by which preferred resources become available when making inferences about the existence of competition based on resource quality. Marine hermit crabs do not appear to modify their shells, so that inferring competition from use of nonpreferred resources is probably valid for these species.

It would be of interest to determine whether the phenomenon of shell modification plays as great a role in the shell utilization patterns of other species of the genus *Coenobita*. The only previous published study of shell selection in this genus was a study of *Coenobita scaevola* by Volker (1967). He only examined shell species preference, however, and his use of Reese's (1962) weight ratios method makes comparison with the present study difficult.

*Acknowledgements.* This work was carried out while I held a Smithsonian Institution Postdoctoral Fellowship. I am grateful to D. Diener, D. West, and G. Hendler for assistance in collecting *Coenobita* and to Kathy Durham for helping mark *Nerita* shells. Data from Costa Rica was collected while I was a participant in the summer 1973 Organization for Tropical Studies Fundamentals of Tropical Biology course. Paul Hertz assisted with crab measurement in Costa Rica. Armand Kuris and Mary Ann Scott made helpful comments on an earlier draft of the manuscript.

## References

- Bach, C., Hazlett, B., Rittschof, D.: Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. *Ecology* **57**, 579–586 (1976)
- Ball, E.E.: Observations on the biology of the hermit crab *Coenobita compressus* H. Milne Edwards (Decapoda; Anomura) on the west coast of the Americas. *Rev. Biol. Trop.* **20**, 265–273 (1972)
- Childress, J.R.: Behavioral ecology and fitness theory in a tropical hermit crab. *Ecology* **53**, 960–964 (1972)
- Hazlett, B.A.: Social behavior of the Paguridae and Diogenidae of Curacao. *Stud. Fauna Curacao Caribb. Isl.* **23**, 1–143 (1966)
- Keen, A.M.: Sea shells of tropical Western America, 2nd ed. Palo Alto: Stanford University Press 1971
- Kellogg, C.W.: The role of gastropod shells in determining the pattern of distribution and abundance in hermit crabs. Ph.D. thesis, Duke University (1971)
- Kellogg, C.W.: Gastropod shells: A potentially limiting resource for hermit crabs. *J. Exptl. Mar. Biol. Ecol.* **22**, 101–111 (1976)
- Kuris, A.M., Brody, M.S.: Use of principal components analysis to describe the snail shell resource for hermit crabs. *J. Exptl. Mar. Biol. Ecol.* **22**, 69–77 (1976)
- Mitchell, K.A.: An analysis of shell occupation by two sympatric species of hermit crab. I. Ecological factors. *Biol. Bull.* **149**, 205–213 (1975)
- Vance, R.R.: Competition and the mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology* **53**, 1062–1074 (1972)
- Volker, L.: Zur Gehäusewahl der Land-Einsiedlerkrebse *Coenobita scaevola* Forskal vom Roten Meer. *J. Exptl. Mar. Biol. Ecol.* **1**, 168–190 (1967)