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Patterns of Shell Resource Utilization by Terrestrial Hermit Crabs at Enewetak Atoll, Marshall Islands[1]

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ABSTRACT: Patterns of gastropod shell utilization by *Coenobita perlatus* and *C. rugosus* were investigated on three islets of Enewetak Atoll, Marshall Islands. Habitat, hermit crab size, and hermit crab species all influenced the utilization of shells by *Coenobita*. Small crabs (< 8 mm carapace length) used 63 shell species, while large hermit crabs (> 19 mm) used only two species. *Coenobita perlatus* occupied long, narrow shells (e.g., *Rhinoclavis*) more frequently than *C. rugosus*. By contrast, *C. rugosus* used shorter shells (e.g., *Nerita*) more frequently. Reproduction of *C. rugosus*, both the percentage of ovigerous females and fecundity, was not influenced by the shell species occupied.

GASTROPOD SHELLS ARE EXTREMELY important for the survival and fitness of hermit crabs. Shells provide protection from both predators and physical stress (Reese 1969, Vance 1972, Bertness 1981*a*). The size and species of shell occupied can influence growth (Markham 1968, Fothingham 1976*a*, Bertness 1981*b*) and reproduction (Childress 1972, Fothingham 1976*b*, Bertness 1981*b*). Shells can be a limiting resource in nature (Vance 1972, Kellogg 1976, Fothingham 1976*c*) leading to intraspecific and interspecific competition for different shell sizes and types (Bach, Hazlett, and Rittschof 1976, Abrams 1980, Bertness 1980). Interspecific competition between hermit crab species may be reduced, however, through shell resource partitioning arising from species-specific shell preferences (Reese 1962, Vance 1972, Bach, Hazlett, and Rittschof 1976, Bertness 1980). Previous studies have centered on intertidal and subtidal hermit crab assemblages. Research on patterns of shell utilization by terrestrial hermit crabs has been limited to situations where only one hermit crab species was present (Niggemann 1968, Ball 1972, Abrams 1978). The present study investigated patterns of shell utilization and the influence of shell type on reproduction of *Coenobita perlatus* and *C. rugosus* on Enewetak Atoll, Marshall Islands.

MATERIALS AND METHODS

Sampling

This study was conducted in September and October 1979 on three islets of Enewetak Atoll (11°30′ N, 162°10′ E): Ikuren and Mut located in the southwest section of the atoll and Bokandretok, a smaller islet situated in the southeast. The distribution and population structure of *Coenobita perlatus* and *C. rugosus* are given in Page and Willason (1982). *Coenobita perlatus* matures at a larger size and attains a greater maximum size, ≈ 25 mm carapace length (C.L.), than *C. rugosus*, ≈ 8 mm C.L. Small specimens of *C. perlatus* (< 8 mm C.L.), however, are very abundant and use the same shell resource as *C. rugosus*.

Crab populations and empty gastropod shells were sampled on each islet by collecting all specimens within a 20-m section of sandy beach from the water line up to and including the wrack zone. A separate collection was also taken of all specimens in a 20 × 8-m section of nearshore vegetation. Samples were taken both during the day and at night. Specimens of *Coenobita* from the interior of Ikuren were

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also sampled using "bait transects" (Page and Willason 1982).

Crabs were removed from their shells by applying heat to the shell apex. Hermit crabs were identified as to species, sexed, measured to the nearest 0.1 mm (C.L.), the presence of eggs on females was recorded, and the gastropod shell identified with the aid of the Mid-Pacific Research Laboratory reference collection. The ratio of shell length to shell width (at widest point of shell) of the eight most common shell species occupied by the crabs was determined by measuring 10 shells of each species.

Forty-one individual ovigerous *Coenobita rugosus* and their respective egg masses were dried at 60°C for 24 hr and weighed to the nearest 0.1 mg. Only females with eggs in the early stages of development (purple without eye spots) were used.

The diversity of shell species occupied by the hermit crabs was calculated using the Shannon-Wiener diversity index:

$$\text{Diversity } (H) = \sum_{i}^{s} P_i(\ln P_i),$$

where P_i is the proportion of the ith shell species utilized by the hermit crab population and s is the number of shell species. Low values indicate the hermit crabs are using proportionally few shell species. High values indicate a proportionally greater use of many shell species. Shell species diversity was calculated for three size classes of *Coenobita perlatus* and for one size class of *C. rugosus* on all three islets. Size classes were based on behavioral and distributional criteria (Page and Willason 1982).

Shell Preference Experiment

Laboratory shell species preference was determined for small *Coenobita perlatus* and *C. rugosus*. Trials were performed using the shells of *Rhinoclavis sinensis*, *Nerita polita*, and *Nerita plicata*. The shells of the *Nerita* species were very similar to one another (identical shell length to width ratios) and were grouped together for the trials.

Ten specimens of *Coenobita perlatus* or *C. rugosus*, collected from the field while occupying either shells of *Rhinoclavis sinensis* or those of a *Nerita* species, were used in each trial. The influence of crab size on shell selection (Abrams 1978, Bertness 1980) was minimized by using only hermit crabs from 4 to 5 mm C.L. Crabs of one species, occupying the same shell type, were placed in a 0.5-m^2 arena (containing water, sand, and shelter) together with 50 empty shells of the other type. The 50 empty shells used in each trial were removed from hermit crabs ranging in size from 3 to 8 mm C.L. providing an assortment of shell sizes. After 24 hr the number of crabs that had switched to the other shell type was recorded. Two replicates were performed for each trial.

RESULTS

Shell Utilization

On the three islets 69 gastropod shell species were used by *Coenobita perlatus* and *C. rugosus* (Table 1). The smallest size class (all *C. rugosus* and *C. perlatus*, < 8 mm C.L.) used the greatest number of shell species (63). Fewer shell species were used with increasing hermit crab size. On all islets combined the shell species diversity index of *C. perlatus* decreased from 2.90 for the smallest crabs (< 8 mm C.L.) to 0.09 for the largest hermit crabs (> 19 mm C.L.). Large crabs also used different shell species than smaller crabs (Tables 2A, B, C). *Rhinoclavis sinensis* was the shell most commonly used by the smallest size class, while virtually all (98 percent) of the largest crabs were found in *Turbo argyrostomus*.

The relative proportions and the total number of shell species differed between islets. Only 16 of the 69 shell species utilized were common to all three islets. On Mut Islet *Rhinoclavis sinensis* was the most abundant shell used by the smallest size class and represented 52.0 percent of the shell total. By contrast, on Ikuren Islet *R. sinensis* represented only 3.6 percent of the shell total. An opposite pattern was found in the distribution of *Nerita plicata* on the two islets. This shell species was the numerical dominant on Ikuren (22.3

TABLE 1

Coenobita perlatus AND *C. rugosus* SHELL SPECIES DIVERSITY

	IKUREN			MUT			BOKANDRETOK			ALL ISLETS		
	C. perlatus	*C. rugosus*	BOTH	*C. perlatus*	*C. rugosus*	BOTH	*C. perlatus*	*C. rugosus*	BOTH	*C. perlatus*	*C. rugosus*	BOTH
Number of shell species	32	21	35	25	26	34	45	36	49	55	48	63
Number of hermit crabs < 8 mm	264	122	386	256	214	470	445	212	655	965	548	1513
Shell diversity	2.97	2.12	2.83	1.48	2.32	1.96	2.84	2.81	2.74	2.93	3.05	2.97
Number of shell species	6	—	6	5	—	5	10	—	10	15	—	15
Number of hermit crabs 8–19 mm	116	—	116	19	—	19	25	—	25	160	—	160
Shell diversity	0.36	—	0.36	0.55	—	0.55	1.34	—	1.34	1.01	—	1.01
Number of shell species	2	—	2	1	—	1	2	—	2	2	—	2
Number of hermit crabs > 19 mm	111	—	111	45	—	45	7	—	7	163	—	163
Shell diversity	0.05	—	0.05	0	—	0	0.60	—	0.60	0.09	—	0.09
Total shell species	34	21	37	28	26	37	46	36	50	61	48	69
Total hermit crabs	491	122	613	320	214	534	477	212	687	1288	548	1836

NOTE: Shell diversity was calculated using the Shannon-Wiener diversity index (see Materials and Methods).

TABLE 2A

PROPORTION OF SHELL SPECIES OCCUPIED BY *Coenobita perlatus* (< 8 MM C.L.) AND *C. rugosus*

	IKUREN		MUT		BOKANDRETOK		
SHELL SPECIES	*C. perlatus*	*C. rugosus*	*C. perlatus*	*C. rugosus*	*C. perlatus*	*C. rugosus*	TOTAL *n*
Rhinoclavis sinensis	.049 (13)	.008 (1)	.652 (167)	.364 (78)	.216 (96)	.146 (31)	386
Cerithium columna	.099 (26)	.065 (8)	.129 (33)	.173 (37)	.126 (56)	.186 (39)	199
Nerita plicata	.122 (32)	.447 (55)	.008 (2)	.028 (6)	—	.005 (1)	96
Cymatium nicobarium	.030 (8)	.008 (1)	.027 (7)	.037 (8)	.104 (46)	.033 (7)	77
Cerithium nodulosum	.008 (2)	—	.023 (6)	.023 (5)	.108 (48)	.028 (6)	67
Nerita polita	.034 (9)	.089 (11)	.004 (1)	.019 (4)	.038 (17)	.066 (14)	56
Cymatium muricinum	—	—	—	.005 (1)	.065 (30)	.099 (21)	52
Cantharos undosus	.095 (25)	.057 (7)	.016 (4)	.051 (11)	.002 (1)	.005 (1)	49
Peristernia nassatula	.091 (24)	.089 (11)	.004 (1)	.047 (10)	.002 (1)	—	47
Rhinoclavis articulatus	—	—	.023 (6)	.079 (17)	.036 (16)	.028 (6)	45
Turbo setosus	.061 (16)	.041 (5)	.016 (4)	.019 (4)	.007 (3)	.028 (6)	38
Turbo argyrostomus	.068 (18)	—	.020 (5)	.014 (3)	.009 (4)	.009 (2)	32
Nassarius graniferus	—	—	—	—	.016 (7)	.108 (23)	30
Strombus gibberulus	.049 (13)	.016 (2)	.004 (1)	—	.023 (10)	.014 (3)	29
Nassarius sp.	.004 (1)	.008 (1)	—	—	.041 (18)	.009 (2)	22
Cerithium brevis	.030 (8)	.033 (4)	.012 (3)	.019 (4)	—	.009 (2)	21
Peristernia columbarium	.053 (14)	—	.008 (2)	—	.004 (2)	.009 (2)	20
Vasum armigera	.057 (15)	.008 (1)	.004 (1)	—	.002 (1)	—	18
Morula fiscella	.004 (1)	.016 (2)	.008 (2)	.037 (8)	.002 (1)	.005 (1)	15
Terebra maculata	.004 (1)	—	.004 (1)	—	.020 (9)	.014 (3)	14
Others—43 species	.146 (38)	.113 (13)	.040 (10)	.086 (18)	.170 (79)	.205 (42)	200
TOTAL	1.000 (264)	1.000 (122)	1.000 (256)	1.000 (214)	1.000 (445)	1.000 (212)	1513

NOTE: The numbers in parentheses are the numbers of crabs in each shell type.

percent) but represented only 1.7 percent of the shell total on Mut.

Empty shells were extremely rare on Mut and Ikuren (less than 0.3 percent of the shell total) but comprised 5.5 percent of all shells found on Bokandretok. The empty shells (most were small and in good condition) on Bokandretok were all found during one sampling period which followed a series of small storms. Several shells with the gastropod still inside were also found on the beach after the storms.

The microhabitat influenced the shell utilization of *Coenobita perlatus* but not that of *C. rugosus*. Specimens of *C. perlatus* collected on sandy beaches occupied both *Rhinoclavis sinensis* and *Cerithium columna* more frequently than did crabs under the nearshore vegetation ($p < 0.001$, chi-square test, all islets combined). Conversely, *Nerita* shells (both species) were occupied more frequently by *C. perlatus* located under nearshore vegetation ($p < 0.01$, chi-square test). For *C. rugosus* there were no differences in the utilization of these same shell types between the sandy beach habitat and the nearshore vegetation habitat ($p > 0.1$, chi-square test, for all comparisons).

Coenobita perlatus (< 8 mm) and *C. rugosus* had different patterns of shell utilization (Table 2A). Of the eight most abundant shell species, *C. rugosus* occupied *Nerita plicata* and *N. polita* more frequently than did *C. perlatus* ($p < 0.005$, chi-square test). Both *Nerita* species were short and rounded with shell length to width ratios of 1.3. *Coenobita perlatus* on the other hand, occupied *Rhinoclavis sinensis*, *Cerithium nodulosum*, and *Cymatium nicobarium* more frequently than did *C. rugosus* ($p < 0.005$, chi-square test). These shells were longer and had mean shell length to width ratios of 2.5, 2.6, and 1.7, respectively. There was no significant difference in the utilization of the shells of *Cymatium muricinum*, *Cantharus undosus*, and *Cerithium columna* between the two her-

TABLE 2B

PROPORTION OF SHELL SPECIES OCCUPIED BY *Coenobita perlatus* (8–19 MM C.L.)

SHELL SPECIES	IKUREN	MUT	BOKANDRETOK	TOTAL *n*
Turbo argyrostomus	.914 (107)	.737 (14)	.240 (6)	127
Turbo setosus	.026 (3)	.105 (2)	.040 (1)	6
Cerithium nodulosum			.240 (6)	6
Terebra maculata			.160 (4)	4
Vasum armigera	.017 (2)		.040 (1)	3
Trochus niloticus			.120 (3)	3
Tonna perdix	.017 (2)			2
Bursa bufonia	.009 (1)		.040 (1)	2
Others—7 species	.009 (1)	.159 (3)	.120 (3)	7
TOTAL	1.000 (116)	1.000 (19)	1.000 (25)	160

NOTE: The numbers in parentheses are the numbers of crabs in each shell type on each islet.

TABLE 2C

PROPORTION OF SHELL SPECIES OCCUPIED BY *Coenobita perlatus* (> 19 MM C.L.)

SHELL SPECIES	IKUREN	MUT	BOKANDRETOK	TOTAL *n*
Turbo argyrostomus	.991 (110)	1.000 (45)	.714 (5)	160
Tonna perdix	.009 (1)	—	.286 (2)	3
TOTAL	1.000 (111)	1.000 (45)	1.000 (7)	163

NOTE: The numbers in parentheses are the numbers of crabs in each shell type on each islet.

mit crab species. These last three shell types had shell length to width ratios of 1.5, 1.7, and 2.0, respectively.

The difference in shell utilization between the two *Coenobita* species is reflected in the shell species diversity indices (Table 1). The most abundant shell on Mut Islet, *Rhinoclavis sinensis*, was used primarily by *Coenobita perlatus*. This resulted in a lower shell diversity index for this species on Mut. On Ikuren Islet, *C. rugosus* used the most abundant shell, *Nerita plicata*, more frequently and had the lower shell diversity index.

Shell Preference

The results of a laboratory shell species preference experiment suggested that specimens of *Coenobita rugosus* preferred the rounded *Nerita*-type shells over the elongated *Rhinoclavis sinensis* (Table 3). Almost all *C. rugosus* (85 percent) collected from the field in *R. sinensis* switch shell types in the presence of empty *Nerita* shells. Only 20 percent of the *C. rugosus* individuals collected in *Nerita* shells switched to *R. sinensis*. Small specimens of *C. perlatus* exhibited the opposite behavior,

TABLE 3

SHELL PREFERENCE EXPERIMENT: SUMMATION OF TWO TRIALS FOR EACH COENOBITA SPECIES AND SHELL-TYPE COMBINATION

	C. rugosus	*C. perlatus*
A. In *Rhinoclavis sinensis*—given *Nerita* species		
Switched	17	2
Did not switch	3	18
B. In *Nerita* species—given *Rhinoclavis sinensis*		
Switched	4	12
Did not switch	16	8

NOTE: $p < 0.05$, chi-square test for both treatments.

TABLE 4

PERCENT OVIGEROUS FEMALES OF *Coenobita rugosus*

SHELL SPECIES	TOTAL FEMALES	PERCENT OVIGEROUS
Rhinoclavis sinensis	88	20.5
Cerithium columna	43	20.9
Nerita plicata	20	20.0
Peristernia nassatula	16	31.3
Nerita polita	14	14.3
Rhinoclavis articulatus	13	15.4
Cymatium muricinum	12	50.0
Cantharos undosus	12	58.3
Cymatium nicobarium	10	40.0
Others—32 species	86	18.6
TOTAL	314	23.3

NOTE: All hermit crabs were 3–8 MM C.L. ($0.1 < p < 0.25$, chi-square test).

switching shell types more frequently when they were collected in *Nerita* shells.

TABLE 5

FECUNDITY OF *Coenobita rugosus*

SHELL SPECIES	FECUNDITY	*n*
Rhinoclavis sinensis	0.141 ± 0.053	9
Cerithium columna	0.141 ± 0.029	3
Nerita plicata	0.121 ± 0.020	5
Cymatium muricinum	0.113 ± 0.029	5
Cantharos undosus	0.112 ± 0.034	4
Others—12 species	0.105 ± 0.027	13

NOTE: Fecundity is expressed as dry weight egg mass/dry weight crab and egg mass. Mean and standard deviation are given for each shell species ($P > 0.2$, ANOVA).

Reproduction

With the exception of three small ovigerous females found on Bokandretok, all ovigerous specimens of *Coenobita perlatus* were greater than 20 mm C.L. and all were found in *Turbo argyrostomus* shells. Ovigerous specimens of *C. rugosus* were found in 22 different shell species on all three islets. The species of shell did not significantly influence the percentage of females carrying eggs (Table 4). The three most abundant shell species in which female *C. rugosus* were found were remarkably similar in the percentage of crabs with eggs (≈ 20 percent).

Clutch size (dry weight of the egg mass) of *Coenobita rugosus* was highly dependent on the dry weight of the female crab (Figure 1). There were no differences in the fecundity (dry weight egg mass/dry weight crab and egg mass) of *C. rugosus* in different shell types (Table 5).

DISCUSSION

The large number of shell species (69) used by the land hermit crabs of Enewetak Atoll greatly exceeds that reported for other hermit crab assemblages (subtidal, Orians and King 1964; intertidal, Bach, Hazlett, and Rittschof 1976, Abrams 1980, Fothingham 1980; terrestrial, Abrams 1978). Shells become available for use by *Coenobita* when marine gastropods die and the empty shells wash ashore or when gastropods wash ashore and then die. A storm enhanced this process on Bokandretok. Empty shells on beaches bordering the Red Sea (Niggemann 1968) and on beaches along the west coast of the United States (J. J. Alio, in prep.) were also more numerous following storms. Differences in shell species between islets of Enewetak probably reflect local intertidal and subtidal gastropod communities.

Large specimens of *Coenobita perlatus* were restricted primarily to *Turbo argyrostomus*

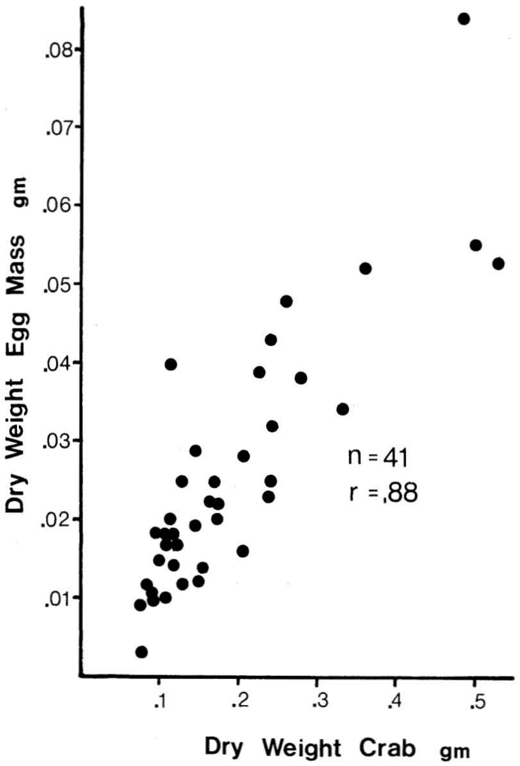

FIGURE 1. Female *Coenobita rugosus*. Crab weight versus egg mass weight ($y = 0.001 + 0.13x$, $r = .88$, $p < 0.001$).

shells. This large shell was very abundant on subtidal reefs surrounding the islets (per. obs.). The other shell species occupied by large *C. perlatus*, *Tonna perdix*, was much more fragile than *Turbo argyrostomus* and was not seen subtidally. Large specimens of *C. scaevola* (Niggemann 1968) and *C. compressus* (Abrams 1978) also occupied fewer shell species than smaller hermit crabs.

Species specific shell preferences, found also in intertidal hermit crab assemblages (Reese 1962, Bach, Hazlett, and Rittschof 1976, Fothingham 1976*b*, Bertness 1980), probably contributed to the different shell utilization patterns of small *Coenobita perlatus* and *C. rugosus* in the field. Bertness (1981*c*) postulated that some shell types are better suited than others for occupying certain habitats. For example, intertidal hermit crabs in Panama, which occupied *Nerita* shells, had poor resistance to thermal stress (loss of water) during exposure at low tide (Bertness 1981*a*). *Cerithium* shells, which are longer with a much higher spire than *Nerita* shells, retained water much better during exposure. At Enewetak, *C. perlatus* (which may prefer narrow shells, e.g., *Rhinoclavis*) was much more abundant on sand beaches, especially when exposed to direct sun, than *C. rugosus* (Page and Willason 1982). By contrast, *C. rugosus* (which may prefer shorter shells, e.g., *Nerita*) was much more numerous in the shade under the nearshore vegetation. The shell types at Enewetak may convey similar advantages (*Rhinoclavis* and *Cerithium*) and disadvantages (*Nerita*) as those in Panama in withstanding thermal stress. Thus, the different patterns of shell utilization of the two *Coenobita* species may be related to their preferred habitats. A significantly higher proportion of *C. perlatus* in *Nerita* shells were found under nearshore vegetation than on the beach, also supporting this hypothesis.

No obvious influence of shell type on the reproduction of *Coenobita rugosus* was found, in contrast to the effects reported for some intertidal species (Bach, Hazlett, and Rittschof 1976, Bertness 1981*b*). Shell type, however, may influence interspecific aggression, predation, and growth (Bertness 1981*c*). These factors, which also contribute to species-specific patterns of shell utilization, were not investigated in this study.

In summary, hermit crab size, hermit crab species, and habitat influenced patterns of gastropod shell utilization by *Coenobita perlatus* and *C. rugosus* at Enewetak Atoll. This terrestrial hermit crab assemblage thus has many of the same characteristics as do subtidal hermit crab assemblages.

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