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UTILIZATION OF SHELL RESOURCES BY THE HERMIT CRABS *CALCINUS LATENS* AND *CALCINUS GAIMARDII* AT KENTING, SOUTHERN TAIWAN

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ABSTRACT

Shell resource utilization in two common species of hermit crabs, *Calcinus latens* (Randall) and *Calcinus gaimardii* (H. Milne Edwards), from intertidal and subtidal zones at Kenting, southern Taiwan, was studied. Field data were compared with laboratory results in shell-selection tests. Shell parameters examined included shell length, shell width, aperture length, aperture width, and weight in sea water. Crab parameters examined included carapace length, shield length, and wet weight. Most intertidal *C. latens* did not use the most abundant shell type in the field, but showed a strong preference for the most abundant shell type in shell-selection tests. The small size of the most abundant shell type in the field appeared to be responsible for this pattern. The results of shell-fit tests showed that most crabs lived in adequate shells at least in terms of internal volume. Shell-selection tests, however, proved that larger crabs (carapace length > 5 mm) are more shell-limited than smaller ones by SAI (shell adequacy index) values. Larger crabs would select much larger shells if they were available. Differences in shell utilization between the subtidal *C. latens* and *C. gaimardii* are discussed.

Hermit crabs live in empty gastropod shells and change shells frequently to allow continuous growth. Under natural conditions, they do not kill healthy snails to obtain empty shells (Scully, 1983). Therefore, their shell resource depends on natural mortality of gastropods. Because empty shells are rare on most seashores (Provenzano, 1960; Childress, 1972; Vance, 1972a; Spight, 1977), the availability of empty shells may be a limiting factor for some hermit crab populations. The advantages of owning a shell include providing space for growth, protection from predators, and preventing the abdomen from suffering mechanical abrasion. In addition, a shell prevents a crab from damage due to temperature stress, water loss, and salinity stress (reviewed by Lancaster, 1988). A suitable empty shell is important to a hermit crab; a very small shell may inhibit a crab's growth (Markham, 1968; Fotheringham, 1976a; Bertness, 1981a, b; Hazlett, 1981). In contrast, a very bulky shell also has disadvantages, e.g., more energy is expended to carry it (Elwood and Glass, 1981), resulting in inhibition of an individual's growth (Bertness, 1981a), and locomotion is more difficult (Hazlett, 1970a).

The purpose of this study is to examine shell utilization by two hermit crab species, *Calcinus latens* (Randall) and *C. gaimardii* (H. Milne Edwards), by investigating the distribution of these species and gastropods (living and dead), utilization of shell types in the field, shell-fit test in the field, and shell selection under laboratory conditions. Both species are common hermit crabs found on coral reefs of Kenting, southern Taiwan. Shell utilization by these two hermit crab species is described in terms of the relationship between crab and shell parameters, and of shell adequacy.

MATERIALS AND METHODS

Four sampling sites, located at the Kenting National Park in southern Taiwan (Fig. 1), were chosen on the basis of whether they included the possible habitats of hermit crabs and were easy to reach.

Site 1. Houwan is a large intertidal reef flat (about 100–200 m in width), where the hard bottom is covered by sand and small rocks. The bottom topography is very smooth, and almost no large rocks are present to provide refuge for intertidal animals. Most parts of the high intertidal zone at this site are sandy and inhabited by seagrasses (*Thalassia hemprichii*) and seaweeds. The low intertidal zone is a large, smooth reef flat with some depressions on the bottom. The slope of the subtidal zone is gradual.

Site 2. Maopitou is a section of reef shore in which the water is always turbulent, and the topography is diverse. The sampled area consists of a large tidepool, which can be divided into front and back pools, both measuring

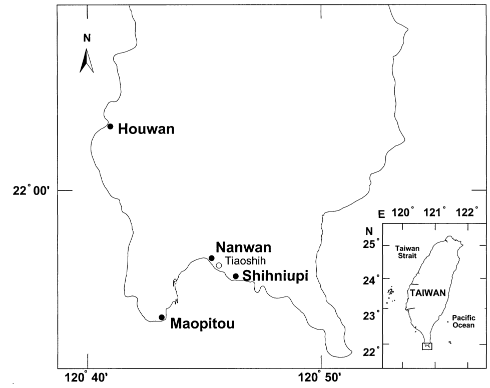

Fig. 1. Locations of four sampling sites in Kenting, southern Taiwan: Houwan, Maopitou, Nanwan, and Shihniupi.

about 10 m × 10 m. There is a very narrow path between the front and back pools, so waves barely impact the back pool, and the water there is static. Substrates in both the front and back pools are composed of sand and coral rubble. There is a barrier isolating the front pool from the open sea. Waves strike the pool, even during low tides. As a result, the habitat and fauna in the front pool is similar to those of the subtidal zone.

Site 3. Nanwan is a section of the shore located between a sandy beach, Nanwan beach, and a rugged rocky reef shore, Tiaoshih shore. The intertidal zone is a large, but not closed, tidal pool. Much of the substrate is hard bottom covered with sand, and there are some standing rocks in the high intertidal zone. There are some seagrasses (*T. hemprichii*) at the site. The intertidal width is about 10 to 20 m. The reef barrier (sometimes covered by dense seaweed) of the outer circle of the pool reduces wave impact. The subtidal zone is a coral reef shelf.

Site 4. Shihniupi is a section of the shore near the town of Kenting. Its intertidal zone is sandy mixed with small rubble and some rocks. The intertidal width is between 10 and 20 m. There are some large, flat rocks at the boundary between the intertidal and subtidal zones, and sometimes they are submerged during high tide.

The hermit crabs studied were *Calcinus latens* (Randall) and *C. gaimardii* (H. Milne Edwards). The former is abundant in intertidal habitat and the latter is dominant in subtidal habitat. *Calcinus latens* is always found in the high, median intertidal and shallow subtidal zones. In the high and median intertidal habitats, it is found in high densities under rocks and in depressions of the reef but is seldom exposed to the air. It is frequently sympatric with *Calcinus laevimanus* (Randall), *Clibanarius virescens* (Krauss), and *Clibanarius humilis* Dana. In the subtidal habitat, *C. latens* can be found on coral branches and rock surfaces (with dense epiphytic algae) on the reef front, and it is commonly sympatric with *C. gaimardii*, *C. minutus* Buitendijk, *C. guamensis* Wooster, and *C. vachoni* Forest (see Shih and Yu, 1995; Shih and Lee, 1997). Most *C. gaimardii* live on the reef front to a depth of approximately 3 m in the shallow subtidal zone, where the moving water is clear. In the low intertidal zone, a few individuals of *C. gaimardii* can occasionally be found, whereas the density of its subtidal population is high. Its habitat is the same as that of *C. latens* in the subtidal zone.

From December 1988 to February 1990, sampling by skin diving was conducted at the four sites. At low tide, several transect lines were set up from the high intertidal line to the intertidal and subtidal boundary. All hermit crabs, live snails, and empty shells were collected within arm's reach from the transect line. The sampling at Nanwan was extended to the shallow subtidal zone (about 1 to 3 m in depth). The Maopitou site was divided into front and back pool sampling areas. Two transect lines were randomly set perpendicularly to each other with intersection of the lines at the center of each pool. All above-mentioned benthos within a 50-cm-wide range of the middle lines were collected. The intertidal samples were those collected from the intertidal habitat of Nanwan, Houwan, and Shihniupi, and the back pool of Maopitou. Subtidal samples were from the subtidal zone of Nanwan and the front pool of Maopitou. Additional crab samples were collected at the four sites by the method mentioned above, but only the crab species and shell types were determined. The results were incorporated into the result of shell types used.

Crabs were removed from shells by heating the shell apexes or by crushing the shells with a clamp. Species name, sex, brooding status, carapace length, shield length, and wet weight of the crabs were recorded. All length parameters were measured to the nearest 0.1 mm with a vernier caliper. Each crab was weighed to the nearest 0.01 g by a triple-beam balance after being blotted dry.

Shell identification is based on Lai (1986, 1987, 1988). The ability of hermit crabs to discriminate between different species of shells seems to be based more on relative weight and shell morphology than actual species recognition (Scully, 1983). Bertness (1982) considered shells that belong to the same genus (e.g., *Cerithium* and *Nerita*) to have similar morphology and did not classify them to species level. Besides, shape of some shells is always obscured by thick epiphytic algae that encrust the shell surface (Reese, 1969; Abrams, 1981a, b). Shells belonging to the same genus have similar shape and structure, so use of shells by hermit crabs is assumed to be based on generic characteristics or types of shells. Therefore, shells are identified to genus level in this study (the abbreviations and full names of shell types in this study are given in Appendix 1). If shells belonged to the same genus, but the shape and structure obviously differed, then these shells were divided into different types. For example, the aperture of the rare *Thais tuberosa* Roeding is wider and larger than that of the common *Thais aculeata* Deshayes. Those species are divided into "TTU" and "TH" shell types, respectively. *Morula* shells, e.g., *Morula granulata* (Duclos) and *M.* (*Cronia*) *margariticola* (Broderip), have a spindle shape of small size (average shell length = 16.1 mm, *n* = 404). Larger crabs cannot live in them. Other groups of shells, however, in which structure and aperture shape are similar to those of *Morula*, such as *Drupella cornus* (Roeding) (average shell length = 28.5 mm, *n* = 80) and *Ergalatax contractus* (Reeve) (average shell length = 21.9 mm, *n* = 9), were combined into the *Morula* shell type (MOT). For the same reason, shells of *Cerithium*, *Batillaria*, *Rhinoclavis*, and *Clypeomorus,* found in the high intertidal zone and long cone-shaped, were all combined into the *Cerithium* shell type (CET).

The records of a shell that a crab occupied include species name, shell length, shell width, aperture length, aperture width, weight in sea water, and shell conditions.

The linear dimensions measured of a shell followed after Kuris and Brody (1976). The actual effective aperture length, i.e., the longest distance of the aperture that a crab can use as a "pigeonhole", was measured by vernier calipers. Therefore, the siphonal canal, inner margin, and outer margin of a shell were excluded because a crab cannot actually use them. Aperture width is the longest distance perpendicular to aperture length. Sometimes debris (e.g., small stones, shell pieces, or wood pieces) may have partially blocked this entrance, and so the actual space that crabs can use was measured as the aperture length and aperture width.

Shell weight was measured in sea water. Using a triple-beam balance, the shell was clamped and hung from the pan-end of the balance (after removing the balance pan) by a fine line; then the shell was immersed in sea water. The weight obtained minus the weight of the clamp in sea water was defined as the shell weight in sea water. Before weighing, the air of the empty shell was expelled by turning the aperture upside down and shaking it in sea water. If the shell was broken in order to remove the crab inside, the fragments were collected and weighed in the same way. Shell weight in sea water is used throughout this paper.

Shell-fit Tests in the Field

The degree to which a crab exceeds the plane of the shell aperture after it has withdrawn inside as far as possible is a direct and effective representation of protection (Abrams, 1978; McClintock, 1985). If a crab cannot withdraw deeply into its shell, it may be more easily eaten by a predator or may be pulled out by a larger hermit crab. If the crab body is too exposed from the shell, body water may evaporate more quickly. A stick was inserted into the aperture to force the crab to withdraw as deeply as possible, and the exposed body parts were observed. Five scores (1–5) were given according to the following criteria. A lower score represents a shell that allows a crab to withdraw more deeply, and the crab is considered to live in a better shell at least by internal volume (modified from the method of McClintock (1985)). Score 1: The crab body cannot be seen from any angle, i.e., the crab can completely withdraw into the shell. Score 2: Part of the chela or walking legs can be seen. Score 3: All surfaces of the chela can be seen, and the surface of the chela almost parallels the plane of the aperture. Score 4: The surface of the chela is almost vertical to the plane of the aperture, but the chela remains below the plane of the aperture. Score 5: The chela penetrates the plane of the aperture. Category "others": Some crabs lived in broken shells in which the apexes were seriously broken or with a large broken hole in the shell wall. Consequently, the tail emerged from the "backdoor opening" under the shell-fit test.

Shell-selection Tests and Shell Adequacy

Shell-selection tests were conducted in the laboratory to see which shell types and shell parameters were preferred by hermit crabs under ideal conditions. In these tests, only the intertidal *C. latens* was used.

Hermit crabs were collected in the field and tested within 1 to 4 d. The crabs were removed from their shells by crushing or heating methods. Then the naked crab was placed into a plastic container (45 × 60 × 30 cm) in which the bottom was embedded with small coral rubble (about 4 to 5 cm high). The tests were made in a pairwise fashion (Bertness, 1982), i.e., two shell types were plentifully supplied in the same number. If crabs preferred type A to B and preferred type B to C, then the preference order of shell types was A > B > C. The shell types offered included those of *Conus*, MOT, *Cypraea*, *Mitra*, and *Drupa,* which were commonly occupied by hermit crabs in their natural habitats. The size range of shells supplied included the size range of shells that could be collected in the field. The ratio of the number of crabs to the number of shells provided for the tests was approximately 1:2 to 1:5. The time given for the naked crabs to select their shells was 24 to 48 h. At the end of the tests, the parameters of crabs and their shells were measured. Some individuals may live in very small shells or never enter shells because of injuries or other unknown factors. Therefore, only individuals with a score of 1 in shell-fit tests (see above) and with no apparent injury were used for the tests.

To see whether hermit crabs live in suitable shells in the field, Vance (1972a) devised a shell adequacy index (SAI). This SAI is defined as the crab size for which a shell is of the preferred size in shell selection tests divided by the actual crab size in the field. A value larger, equal to, or smaller than 1 means the shell occupied by the crab is larger, equal to, or smaller than the shell preferred by that crab. This method has been followed by many investigators (Vance, 1972b; Fotheringham, 1976b; Bertness, 1980, 1981a–d). Similarly, the SAI of Kellogg (1976) is the size of a shell occupied by a crab of a given size in the field divided by the size of the preferred shell in shell-selection tests, and the meaning of the value is the same as that of Vance. In the present study, we follow the calculation of SAI by Vance (1972a) to estimate the adequacy of shells occupied by field hermit crabs. The carapace and shell lengths were used as crab and shell sizes, respectively, because the correlation between carapace length and shell length is higher (0.780, $n = 504$) than the other combinations (e.g., carapace length vs. shell width: 0.753; carapace length vs. shell weight in sea water: 0.696).

RESULTS

Distribution of Gastropods

No empty shells were found at the study sites. A total of 673 livng gastropod specimens were collected, of which MOT was the most abundant shell type (44.43% of the total number of gastropod specimens). The remaining shell types were *Conus* (19.76%), *Thais* (13.08%), *Mitra* (6.39%), *Cypraea* (5.65%), and *Drupa* (2.53%) (Table 1). These six gastropod types made up 91.84% of the total shell specimens. In the intertidal habitat, 424 gastropod specimens were collected, of which MOT was the dominant shell type (49.53%). The remaining types were *Conus* (17.92%), *Thais* (8.49%), *Mitra* (8.25%), *Cypraea* (3.54%), *Engina* (3.07%), and *Nerita* (2.12%) (Table 1, the lower part of Fig. 2). These seven shell types made up 92.92% of the intertidal shell specimens. In the subtidal habitat, 249 specimens were collected.

Table 1. Distribution of gastropods sampled in Kenting, southern Taiwan. The gastropods are represented by shell types and the complete names of shell types are shown in Appendix 1. In each column, the number of living snails collected is shown, and the figure in parentheses is the percent of the total number of each column.

Shell type	Intertidal no. of snails (%)	Subtidal no. of snails (%)	Total no. of snails (%)
MOT	210 (49.53)	89 (35.74)	299 (44.43)
CN	76 (17.92)	57 (22.89)	133 (19.76)
TH	36 (8.49)	52 (20.88)	88 (13.08)
MI	35 (8.25)	8 (3.21)	43 (6.39)
CP	15 (3.54)	23 (9.24)	38 (5.65)
DP	8 (1.89)	9 (3.61)	17 (2.53)
EN	13 (3.07)	1 (0.40)	14 (2.08)
NE	9 (2.12)	0	9 (1.34)
CET	7 (1.65)	0	7 (1.04)
BU	3 (0.71)	1 (0.40)	4 (0.59)
PE	1 (0.24)	3 (1.20)	4 (0.59)
PY	3 (0.71)	0	3 (0.45)
ST	3 (0.71)	0	3 (0.45)
TTU	2 (0.47)	1 (0.40)	3 (0.45)
CH	1 (0.24)	1 (0.40)	2 (0.30)
TR	1 (0.24)	1 (0.40)	2 (0.30)
LA	0	2 (0.80)	2 (0.30)
PL	1 (0.24)	0	1 (0.15)
TU	0	1 (0.40)	1 (0.15)
Total	424	249	673

The dominant shell type was MOT (35.74%), and the remaining types were *Conus* (22.89%), *Thais* (20.88%), *Cypraea* (9.24%), *Drupa* (3.61%), and *Mitra* (3.21%) (Table 1, the lower part of Fig. 3). These six types made up 95.56% of the subtidal samples.

The distribution of shell types in the intertidal zone differed from that in the subtidal zone ($P < 0.001$, chi-square test, shell types compared were MOT, *Conus*, *Thais*, *Mitra*, *Cypraea*, *Drupa*, and CET). *Conus*, MOT, and *Thais* were abundant shell types in both the intertidal and subtidal zones; fewer *Drupa* shells were found in the intertidal zone; and *Mitra*, *Engina*, and *Nerita* were scarce in the subtidal zone (Table 1, the lower parts of Figs. 2, 3).

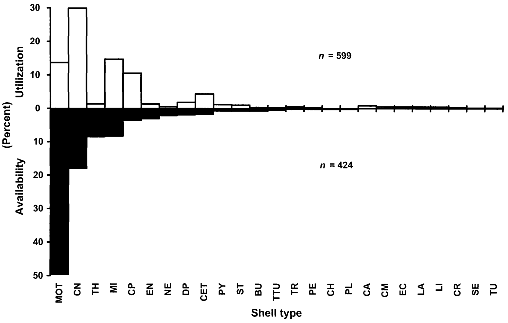

Fig. 2. Shell utilization by the intertidal *Calcinus latens* and the distribution of shell types in the intertidal habitat from the study sites of Kenting, southern Taiwan: shell utilization by crabs is indicated by open bars; shell-type distribution is indicated by solid bars. Shell types are indicated by abbreviations on the horizontal axis. The complete names of shell types are shown in Appendix 1.

Distribution of Hermit Crabs

Of the 1,088 hermit crab specimens collected, 809 were from the intertidal zone, and 279 were taken from the subtidal zone. The dominant species was *C. latens* (62.41% of total number of specimens, 679/1,088). In the intertidal zone, *C. latens* was dominant in number (74.04% of the intertidal sample, 599/809), whereas *C. latens* was the secondary species in the subtidal zone (28.67% of the subtidal sample, 80/279). *Calcinus gaimardii* was dominant in the subtidal zone (41.58%, 116/279) but scarce in the intertidal zone (5.32%, 43/809). The other species collected in this study included: *Calcinus elegans* (H. Milne Edwards), *C. laevimanus*, *C. minutus*, *C. guamensis*, *C. vachoni* (Shih and Yu, 1995; Shih and Lee, 1997), *Clibanarius virescens*, *C. corallinus* (H. Milne Edwards), *C. humilis*, *C. eurysternus* Hilgendorf, *Dardanus pedunculatus* (Herbst), and *D. guttatus* (Olivier).

Shell Types Used by Hermit Crabs

In the intertidal *C. latens* sample, the most common shell type used was *Conus*. The re-

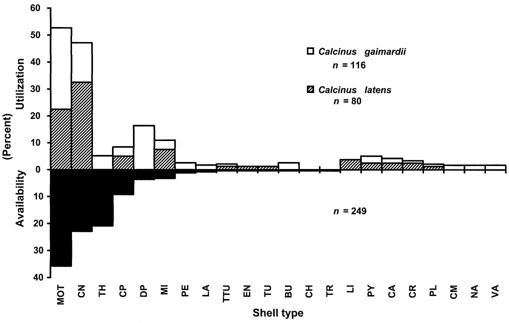

Fig. 3. Shell utilization by subtidal hermit crab species and the distribution of shell types in the subtidal zone from the study sites of Kenting, southern Taiwan. Shell utilization by crabs is indicated by open bars for the subtidal *Calcinus gaimardii* and gray bars for the subtidal *C. latens*; shell-type distribution is indicated by solid bars. Shell types are indicated by abbreviations on the horizontal axis. The complete names of shell types are shown in Appendix 1.

Table 2. Comparison of shell types used by the intertidal *Calcinus latens*, subtidal *C. latens,* and subtidal *C. gaimardii* by chi-square test, and means of parameters of shells used and of crabs by Hotelling's T^2 statistic (the items in parentheses are the parameters contributing to the total difference in Hotelling's T^2 statistic).

	Shell types used		Mean of shell parameters	Mean of crab parameters
Groups compared	Chi-square test	Shell types compared	Hotelling's T^2 statistic	Hotelling's T^2 statistic
Intertidal and subtidal *C. latens* (n = 457 and 54 in chi-square test; n = 282 and 37 in Hotelling's T^2)	$P < 0.02$*	MOT, CN, TH, MI, CP, DP, CET	n.s.	n.s.
Subtidal *C. latens* and *C. gaimardii* (n = 50 and 81 in chi-square test; n = 37 and 37 in Hotelling's T^2)	$P < 0.001$***	MOT, CN, DP, MI	$P < 0.01$** (shell length, shell width, shell weight)	$P < 0.01$** (carapace length, shield length, crab weight)

maining occupied shell types listed in decreasing order were *Mitra*, MOT, *Cypraea*, and CET. The above shell types made up 73.12% of the intertidal *C. latens* sample (the upper part of Fig. 2). In the subtidal zone, *C. latens* also used *Conus* most often, and the others included MOT, *Mitra*, and *Cypraea* (gray bars in the upper part of Fig. 3). These shell types made up 67.50% of the subtidal *C. latens* sample. Shell types commonly used by the subtidal *C. gaimardii* listed in decreasing order were MOT, *Drupa*, *Conus*, and *Thais* (open bars in the upper part of Fig. 3). These shell types made up 66.38% of the subtidal *C. gaimardii* sample.

To test the difference of the means of morphological parameters of crabs and their shells between two groups, Hotelling's T^2 statistic was applied. The three crab parameters compared were carapace length, shield length, and wet weight. If there was any missing value in the data of a crab's parameters, the missing value was predicted according to another known parameter (e.g., carapace length, shield length, or logarithmic weight) through regression equations between these parameters. The five shell parameters were shell length, shell width, aperture length, aperture width, and shell weight in sea water. The means of the crab morphological parameters and the parameters of their shells between the intertidal and subtidal *C. latens* are both identical (Table 2). In the subtidal *C. latens* and *C. gaimardii*, the means of crab parameters differ in carapace length, shield length, and crab weight, and the means of shell parameters differ in shell length, shell width, and shell weight in sea water. Most shell types that these two species used did not overlap and differed significantly ($P < 0.001$, chi-square test; Table 2, upper part of Fig. 3). Intertidal and subtidal *C. latens* also differed significantly in the utilization of shell types ($P < 0.02$, chi-square test; Table 2).

The shell-fit scores of most (> 87%) intertidal *C. latens*, subtidal *C. latens*, and subtidal *C. gaimardii* individuals were 1 (Table 3). This score implies that an individual can withdraw deeply enough inside the shell that it cannot be seen from the outside. That is, these individuals lived in suitable shells in

Table 3. Results of shell-fit tests for the intertidal *Calcinus latens*, subtidal *C. latens*, and subtidal *C. gaimardii* expressed as the percentage of crabs with each score.

Score of shell-fit tests	Intertidal *C. latens* (n = 538)	Subtidal *C. latens* (n = 20)[a]	Subtidal *C. gaimardii* (n = 46)[a]
1	88.9	90.0	87.0
2	5.6	5.0	8.7
3	3.4	5.0	4.3
4	0.7	0	0
Others[b]	1.5	0	0

[a] Samples of the front pool of Maopitou were not included in the subtidal samples, because some individuals died before the shell-fit tests, and the sample size was too small.

[b] Broken shells in which the apexes were seriously broken or those with a large broken hole in the shell wall.

Table 4. Results of shell-selection tests of the intertidal *Calcinus latens*; numbers in parentheses represent the number of replications. The total number of crabs tested is 149.

Choice 1	Choice 2	Results of Choice 1 : Choice 2 (replication no.)	Significance of preference by chi-square test
MOT	CN	52: 3 (2)	$P < 0.001$***
CN	CP	21: 3 (1)	$P < 0.01$**
CP	MI	19: 17 (2)	n.s.
MI	DP	15: 19 (1)	n.s.

terms of shell volume. A small percentage of individuals had scores of 2 and 3; individuals with a score of 4 only occurred in the intertidal *C. latens* (0.7%). No individuals had a score of 5, but a few individuals of the intertidal *C. latens* (1.5%) lived in seriously broken shells (Table 3).

Shell-selection Tests in the Laboratory

There was a strong tendency for intertidal *C. latens* to prefer certain shell types. The preference is listed in decreasing order (Table 4) as follows: MOT > *Conus* > *Cypraea* = *Mitra* = *Drupa*. The carapace lengths of crabs in the five shell types did not differ significantly ($P = 0.154$, ANOVA).

Comparison Between Size of Shells Occupied in the Field and in Shell Selection

Lengths of shells occupied in the field and in the shell-selection tests were plotted against carapace lengths of the crabs (Fig. 4). An ANCOVA was used to determine whether or not the four regression lines differ. The results show that the regression lines of the subtidal *C. gaimardii* and *C. latens* are the same ($P = 0.08$, *d.f.* = 70, ANCOVA) and those of the intertidal and subtidal *C. latens* are the same ($P = 0.54$, *d.f.* = 315, ANCOVA). That is, the same-sized crabs of the three groups use shells of similar sizes. However, there is a significant difference between the intertidal *C. latens* and the *C. latens* used in shell-selection tests ($P < 0.001$, *d.f.* = 427, ANCOVA).

In the field, larger individuals of intertidal *C. latens* (with carapace length > 5 mm) showed a tendency to use *Conus* more often than *Morula* shells (22.92% vs. 10.53% of the total number of crabs living in *Conus* and *Morula*, respectively; $n = 96$ and 38), although smaller intertidal *C. latens* (with carapace length ≤ 5 mm) used *Morula* more often than *Conus* (89.47% vs. 77.08%; $n = 38$ and 96). Intertidal *C. latens* with carapace length exceeding 6 mm rarely lived in MOT shells (none in *Morula*, one in *Drupella*, and one in *Ergalatax*), but they could be found in *Conus* ($n = 7$).

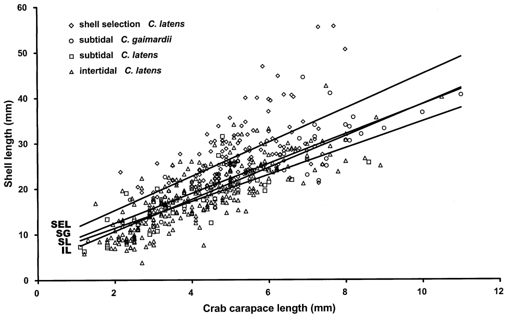

Fig. 4. Shell length plotted as a function of crab carapace length. The four regression lines are (SEL) *Calcinus latens* used in shell-selection tests: $Y = 3.746X + 7.767$ ($r^2 = 0.369$, $n = 149$); (SG) subtidal *C. gaimardii*: $Y = 3.268X + 5.921$ ($r^2 = 0.729$, $n = 37$); (SL) subtidal *C. latens*: $Y = 2.935X + 5.484$ ($r^2 = 0.624$, $n = 37$); and (IL) intertidal *C. latens*: $Y = 3.497X + 3.672$ ($r^2 = 0.669$, $n = 282$). The lines SG and SL do not differ; lines SL and IL also do not differ, but lines SEL and IL differ significantly (ANCOVA).

From the results of the shell-selection test that supplied MOT and *Conus* shells (the total number of crabs that selected each shell type was 52 and 3, respectively; Table 4), the size of crabs that selected either shell type was the same (average carapace length of crabs was 5.05 and 4.66 mm, respectively; $P = 0.56$, *t*-test). Some crabs with carapace length exceeding 6 mm selected MOT shells, and most of those MOT shells were of *Drupella cornus* (85.71%, 12/14).

The mean of SAI values of the intertidal *C. latens* was 1.13 ± 0.33 SD. This value implies that the individuals of intertidal *C. latens* always occupied suitable shells as reflected by shell length. However, if the SAI value is plotted against crab carapace length (Fig. 5), there is an apparent tendency for values to be larger than 1 for most small crabs (carapace length ≤ 5 mm, mean SAI value of 1.24 ± 0.31 SD, $n = 208$) but less than 1 in most large crabs (carapace length > 5 mm, mean SAI of 0.81 ± 0.11 SD, $n = 74$).

DISCUSSION

Shell Types Used by Intertidal *C. latens*

In the intertidal and subtidal zones of the Kenting area, MOT shells are the most abun-

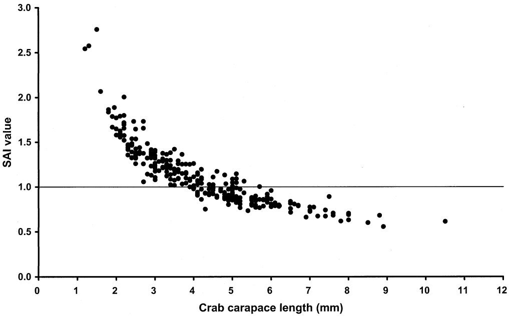

Fig. 5. The SAI value of the intertidal *Calcinus latens* ($n = 282$) plotted against crab carapace length. This shows that values are larger than 1 in most smaller crabs (carapace length ≤ 5 mm) and smaller than 1 in most larger crabs (carapace length > 5 mm).

dant shell type, with the next abundant being *Conus* (Table 1, the lower parts of Figs. 2, 3). The results show that the dominant hermit crab species, *C. latens*, in the intertidal zone most often uses *Conus* instead of the most common shell type, i.e., MOT. Utilization of MOT by *C. latens* is even lower than that of *Mitra*. That is, intertidal *C. latens* seems to shun the most common shell type in the field. However, the results of shell selection tests of intertidal *C. latens* conducted in the laboratory showed that individuals have a very strong tendency to select MOT, not *Conus* (Table 4). Other studies also reported that individuals of *C. latens* rarely use *Conus* shells (Reese, 1968, 1969; Hazlett, 1970b; Miyake and Imafuku, 1980; Abrams, 1981a, b; Wooster, 1984; Asakura, 1987). From the field-survey results, more large-sized intertidal *C. latens* were found in *Conus* than in *Morula*; in contrast, more small-sized ones lived in *Morula* than in *Conus*. However, in the shell-selection test offering MOT and *Conus* (with MOT shells including large-size species, e.g., *Drupella cornus,* which inhabits the subtidal zone and is not very abundant) the results showed that most large crabs would choose shells of *Drupella cornus*. Different size classes of hermit crabs would select different shell species because of the available size ranges of each shell species (Mitchell, 1975; Asakura and Kikuchi, 1984a; Wilber, 1990; Reddy and Biseswar, 1993). Therefore, we suggest that the larger intertidal *C. latens* does not utilize the most abundant shell type because large-sized shells of this shell type are rare. Larger individuals will select *Conus* instead, because of the large size range of this genus.

Shell Types Used by Subtidal *C. latens* and *C. gaimardii*

Utilization of the main shell types by intertidal and subtidal *C. latens* differs (Table 2), which may be explained by the different distribution of shell types in these areas ($P < 0.001$, chi-square test), despite the means of the parameters of crab and shell being the same. Many hermit crab species migrate to subtidal habitats in winter (Rebach, 1974; Fotheringham, 1975; Asakura and Kikuchi, 1984b). It is reasonable to suggest that the intertidal and subtidal *C. latens* come from the same population. Abrams (1981a) states that the subtidal *C. latens* reaches larger sizes than the intertidal *C. latens*, but our survey result does not show such a tendency.

The subtidal *C. latens* and *C. gaimardii* differ in the means of parameters of crab and of shell used and of the main shell types used (Table 2). The means of shell length, shell width, and shell weight in sea water of *C. gaimardii* (26.32 mm, 16.96 mm, 3.01 g, $n = 37$) are larger than those of *C. latens* (17.09 mm, 11.49 mm, 1.32 g, $n = 37$), which may be explained by the larger body size of *C. gaimardii* (mean carapace length: *C. gaimardii*: 6.24 mm, $n = 37$; *C. latens*: 3.95 mm, $n = 37$). The MOT is the most abundant shell type both in the intertidal and subtidal zones (Table 1, Figs. 2, 3), and larger MOT shells (e.g., of *Drupella*) are more abundant in the subtidal zone. The limiting factors in the intertidal habitat (i.e., MOT are smaller and the large shells are rare) do not exist in the subtidal habitat. However, the second-most abundant shell type, *Conus*, is still the type most used by the subtidal *C. latens*, and MOT is the shell type most often used by *C. gaimardii* (Fig. 3). Shell utilization of the two subtidal species has a tendency to compensate each other. *Drupa* is commonly used (second order) by *C. gaimardii*, but scarcely by *C. latens*. *Mitra*, *Cypraea*, and *Thais* also show such a tendency. The overlap between these two species in Enewetak Atoll and Guam is also low (Table 6 in Abrams, 1981b). Thus, it is reasonable to hypothesize that these two sympatric species in the subtidal zones use different shell types to minimize competition (Vance, 1972a; Grant and Ulmer, 1974; Bach *et al.*, 1976; Bertness, 1980, 1981b, c, d, 1982; Imazu and Asakura, 1994).

Results of Shell Selection

The results of shell-fit estimation of hermit crabs in the field show that most crabs have a score of 1, i.e., if crabs completely withdraw, they are not visible externally. In terms of shell volume, this means that the shells used are large enough to protect them from predators (Vance, 1972a; Conover, 1978; Scully, 1983). Also from the result of shell selection tests, the average SAI value of the intertidal *C. latens* is 1.13 implying that their shells are adequate in terms of shell length. However, from Fig. 5, the SAI values are smaller than 1 in most larger crabs, i.e., the shells occupied by larger crabs in the field are suboptimal to those in the shell-selection test (Vance, 1972a). In most small crabs, the occupied shells were suitable (mean SAI value = 1.24). From the regression lines (Fig. 4), intertidal *C. latens* select much larger shells under laboratory conditions than they do in the field. Childress (1972) considered that because empty shells are rare in the field, the time from when a crab obtains a shell to when it changes to a new shell may be very long. If it has the opportunity, it would be more beneficial to choose a larger shell in order to prevent it from suffering space limitations. Furthermore, risks are high when entering a new shell or during the process of shell fighting (Dowds and Elwood, 1983; Elwood and Stewart, 1985; Elwood and Neil, 1986). A larger shell increases the weight to the crab living in it, and the inhabitant may encounter many disadvantages (Hazlett, 1970a; Bertness, 1981a; Elwood and Glass, 1981), but the disadvantages may not be very serious because the buoyancy of sea water will reduce a portion of the shell weight (Elwood and Neil, 1992). It is suggested that selection of a much larger shell would increase a hermit crab's fitness because it will not need to change shells frequently. In the field, smaller crabs tend to live in larger shells than the preferred ones, while in contrast, larger crabs live in smaller shells than the preferred ones (Fig. 5). It is not easy for a larger crab to find a shell of suitable size, and it is more shell-limited than a smaller crab (Scully, 1983). Thus, the opportunity for a smaller crab to find a larger shell is high, and it is likely to change into a shell larger than it needs (Hazlett, 1981).

Severely Damaged Shells Used by Intertidal *C. latens*

A small portion of the intertidal *C. latens* lived in severely damaged shells (Table 3) during the shell-fit tests. Some crabs carried bulky and heavy shells but used a large hole on the wall as the "pigeonhole", and some crabs' shells retained only the apex. The inhabitants of those damaged shells were always very small crabs. Asakura (1987) reported that some individuals of *C. latens* of the intertidal reef-flat of Guam utilized highly damaged shells as homes. Imafuku (1983) also reported that two *Pagurus geminus* McLaughlin individuals lived in a single shell, with the smaller one living in a large hole in the wall. Those phenomena indicate that high-quality shells are in short supply in those areas.

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LITERATURE CITED

Abrams, P. 1978. Shell selection and utilization in a terrestrial hermit crab, *Coenobita compressus* (H. Milne Edwards).—Oecologia 34: 239–253.

———. 1981a. Alternative methods of measuring competition applied to two Australian hermit crabs.—Oecologia 51: 233–239.

———. 1981b. Competition in an Indo-Pacific hermit crab community.—Oecologia 51: 240–249.

Asakura, A. 1987. Unique shell utilization by reef-flat hermit crabs in Guam, Micronesia.—Researches on Crustacea 16: 25–31.

———, and T. Kikuchi. 1984a. Population ecology of the sand dwelling hermit crabs, *Diogenes nitidimanus* Terao. 1. Shell utilization.—Publications from the Amakusa Marine Biological Laboratory 7: 95–108.

———, and ———. 1984b. Population ecology of the sand dwelling hermit crabs, *Diogenes nitidimanus* Terao. 2. Migration and life history.—Publications from the Amakusa Marine Biological Laboratory 7: 109–123.

Bach, C., B. A. Hazlett, and D. Rittschof. 1976. Effects of interspecific competition on fitness of the hermit crabs *Clibanarius tricolor*.—Ecology 57: 579–586.

Bertness, M. D. 1980. Shell preference and utilization patterns in littoral hermit crabs of the Bay of Panama.—Journal of Experimental Marine Biology and Ecology 48: 1–16.

———. 1981a. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura).—Crustaceana 40: 197–205.

———. 1981b. Pattern and plasticity in tropical hermit crab growth and reproduction.—American Zoologist 117: 754-773.

———. 1981c. Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage.—Journal of Experimental Marine Biology and Ecology 49: 189–202.

———. 1981d. Competitive dynamics of a tropical hermit crab assemblage.—Ecology 62: 751–761.

———. 1982. Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison.—Journal of Experimental Marine Biology and Ecology 64: 159–187.

Childress, J. R. 1972. Behavioral ecology and fitness theory in a tropical hermit crab.—Ecology 53: 960–964.

Conover, M. R. 1978. The importance of various shell characteristics to the shell-selection behavior of hermit crabs.—Journal of Experimental Marine Biology and Ecology 32: 131–142.

Dowds, B. M., and R. W. Elwood. 1983. Shell wars: assessment strategies and the timing of decisions in hermit crab shell fights.—Behaviour 85: 1–24.

Elwood, R. W., and C. W. Glass. 1981. Negotiation or aggression during shell fights of the hermit crab *Pagurus bernhardus*?—Animal Behaviour 29: 1239–1244.

———, and S. J. Neil. 1986. Asymmetric contests involving two resources.—Journal of Theoretical Biology 120: 237–249.

———, and ———. 1992. Assessments and decisions: a study of information gathering by hermit crabs. Chapman & Hall, London. 192 pp.

———, and A. Stewart. 1985. The timing of decisions during shell investigation by hermit crabs *Pagurus bernhardus*.—Animal Behaviour 33: 620-627.

Fotheringham, N. 1975. Structure of seasonal migrations of the littoral hermit crab *Clibanarius vittatus* (Bosc).—Journal of Experimental Marine Biology and Ecology 18: 47–53.

———. 1976a. Effects of shell stress on the growth of hermit crabs.—Journal of Experimental Marine Biology and Ecology 23: 299–305.

———. 1976b. Population consequences of shell utilization by hermit crabs.—Ecology 57: 570–578.

Grant, W. C., Jr., and K. M. Ulmer. 1974. Shell selection and aggressive behavior in two sympatric species of hermit crabs.—Biological Bulletin, Woods Hole 146: 32–43.

Hazlett, B. A. 1970a. The effect of shell size and weight on the agonistic behavior of a hermit crab.—Zeitschrift für Tierpsychologie 27: 369–374.

———. 1970b. Interspecific shell fighting in three sympatric species of hermit crabs in Hawaii.—Pacific Science 24: 472–482.

———. 1981. The behavioral ecology of hermit crabs.—Annual Review of Ecology and Systematics 12: 1–22.

Imafuku, M. 1983. Two hermit crabs inhabiting a single gastropod shell.—Journal of Ethology 1: 113, 114.

Imazu, M., and A. Asakura. 1994. Distribution, reproduction and shell utilization patterns in three species of intertidal hermit crabs on a rocky shore on the Pacific coast of Japan.—Journal of Experimental Marine Biology and Ecology 184: 41–65.

Kellogg, C. W. 1976. Gastropod shells: a potentially limiting resource for hermit crabs.—Journal of Experimental Marine Biology and Ecology 22: 101–111.

Kuris, A. M., and M. S. Brody. 1976. Use of principal components analysis to describe the snail shell resource for hermit crabs.—Journal of Experimental Marine Biology and Ecology 22: 69–77.

Lai, K.-Y. 1986. Marine gastropods of Taiwan (1). Taiwan Museum, Taipei, Taiwan. 49 pp. [In Chinese.]

———. 1987. Marine gastropods of Taiwan (2). Taiwan Museum, Taipei, Taiwan. 116 pp. [In Chinese.]

———. 1988. Gastropods. Tuchia Publishing, Taipei, Taiwan. 197 pp. [In Chinese.]

Lancaster, I. 1988. *Pagurus bernhardus* (L.)–an introduction to the natural history of hermit crabs.—Field Studies 7: 189–238.

McClintock, T. S. 1985. Effects of shell condition and size upon the shell choice behavior of a hermit crab.—Journal of Experimental Marine Biology and Ecology 88: 271–285.

Markham, J. C. 1968. Notes on growth-patterns and shell-utilization of the hermit crab *Pagurus bernhardus* (L.).—Ophelia 5: 189–205.

Mitchell, K. A. 1975. An analysis of shell occupation by two sympatric species of hermit crab. I. Ecological factors.—Biological Bulletin, Woods Hole 149: 205–213.

———. 1976. Shell selection in the hermit crab *Pagurus bernhardus*.—Marine Biology 35: 335–343.

Miyake, S., and M. Imafuku. 1980. Hermit crabs from Kii Peninsula I.—Nankiseibutu 22: 1–7. [In Japanese.]

Provenzano, A. J., Jr. 1960. Notes on Bermuda hermit crabs (Crustacea; Anomura).—Bulletin of Marine Science 10: 117–124.

Rebach, S. 1974. Burying behavior in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*.—Ecology 55: 195–198.

Reddy, T., and R. Biseswar. 1993. Patterns of shell utilization in two sympatric species of hermit crabs from the Natal coast (Decapoda, Anomura, Diogenidae).—Crustaceana 65: 13–24.

Reese, E. S. 1968. Annual breeding seasons of three sympatric species of tropical intertidal hermit crabs, with a discussion of factors controlling breeding.—Journal of Experimental Marine Biology and Ecology 2: 308–318.

———. 1969. Behavioral adaptations of intertidal hermit crabs.—American Zoologist 9: 343–355.

Scully, E. P. 1983. The behavioral ecology of competition and resource utilization among hermit crabs. Pp. 23–55 *in* S. Rebach and D. W. Dunham, eds. Studies in adaptation: the behavior of higher Crustacea. Wiley-Interscience, New York.

Shih, H.-T., and S.-C. Lee. 1997. Identity of two hermit crabs, *Calcinus vachoni* Forest, 1958, and *Calcinus seurati* Forest, 1951, from the coral reefs of Taiwan (Crustacea: Decapoda: Anomura).—Journal of Taiwan Museum 50: 21–31.

———, and H.-P. Yu. 1995. New records of *Calcinus* hermit crabs (Decapoda: Anomura: Diogenidae) from Taiwan.—Zoological Studies 34: 241–247.

Spight, T. M. 1977. Availability and use of shells by intertidal hermit crabs.—Biological Bulletin, Woods Hole 152: 120–133.

Vance, R. R. 1972a. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs.—Ecology 53: 1062–1074.

———. 1972b. The role of shell adequacy in behavioral interactions involving hermit crabs.—Ecology 53: 1075–1083.

Wilber, T. P., Jr. 1990. Influence of size, species and damage on shell selection by the hermit crab *Pagurus longicarpus*.—Marine Biology 104: 31–39.

Wooster, D. S. 1984. The genus *Calcinus* (Paguridea, Diogenidae) from the Mariana Islands including three new species.—Micronesica 18: 121–162. [Dated 1982.]

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APPENDIX 1

Abbreviations of the names of shell types used in this study

Abbreviation	Shell-type names
BU	*Bursa*
CA	*Cantharus*
CET	*Cerithium* type (*Cerithium*, *Rhinoclavis*, *Batillaria*, *Clypeomorus*)
CH	*Chicoreus*
CM	*Cymatium*
CN	*Conus*
CP	*Cypraea*
CR	*Coraliophila*
DP	*Drupa*
EC	*Echininus*
EN	*Engina*
LA	*Latirus*
LI	*Littorina*
MI	*Mitra*
MOT	*Morula* type (*Morula*, *Drupella*, *Ergalatax*)
NA	*Nassa*
NE	*Nerita*
PE	*Peristernia*
PL	*Pleuroploca*
PY	*Pyrene*
SE	*Serpulorbis*
ST	*Strombus*
TH	*Thais*
TR	*Trochus*
TTU	*Thais tuberosa*
TU	*Turbo*
VA	*Vasum*