Interspecific Shell Fighting in Three Sympatric Species of Hermit Crabs in Hawaii[1]

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INTERSPECIFIC COMPETITION is often difficult to measure due to the lack of a definitive limiting factor for the two (or more) species. The gastropod shell inhabited by a hermit crab represents a very discrete, definable portion of the ecological needs of every animal. A hermit crab must have protection for its soft abdomen or it will rather quickly be eaten. In addition, the ritualized shell fighting behavior patterns of hermit crabs (Hazlett, 1966*a*, 1966*b*, 1967) offer an easily observed specific behavioral parameter which reflects the extent of interspecific vs. intraspecific competition for this ecological factor.

Levins (1968) has proposed that the degree of niche overlap between two species can be calculated as the summation of interspecific competition interaction values (α) for all the factors of ecological importance to the species. In the present study, interaction coefficients for one ecological factor (gastropod shells) were obtained. Some of the ways in which a gastropod shell is important for a crab have been discussed by Reese (1968*a*, 1969).

The species studied were *Clibanarius zebra, Calcinus laevimanus,* and *Calcinus latens.* These are the most common intertidal hermits found in Kaneohe Bay, Oahu (Reese, 1968*b*). These three species are in the family Diogenidae, subfamily Diogeninae, and the shell fighting behavior patterns of the three are very similar. (They are much more similar to one another than are the patterns of the two species of *Pagurus* studied in Sweden [Hazlett, 1967]; a paper in preparation will discuss the similarity of such patterns within the genus *Calcinus* as opposed to the variability within the genus *Pagurus*). All three crabs are intertidal and overlap in microdistribution to some extent. *Calcinus latens* is generally found a foot or so deeper than *Clibanarius zebra* and *Calcinus laevimanus* (Reese, 1968*b*). All three species are found primarily in the gastropod shell *Trochus sandwichiensis* and to a lesser extent in *Turbo sandwicensis* and other shells. Preliminary searches of the study area revealed that very few empty gastropod shells of the size utilized by the crabs were present in the water, although many shells are found above the high tide level on Gravel Island. Since every crab (of all three species) must have a shell to survive and since shells seemed to be in short supply, it could be argued that shells are a limiting factor in this area.

The following experiments were designed to (1) measure the extent of interspecific competition and (2) investigate the behavioral basis of the results obtained. Using data from this and other studies, several competition coefficient values based upon shell inhabitation are obtained and compared.

MATERIALS AND METHODS

All the individuals used were collected from the same area on the windward (northeast) side of a small sandbar, Gravel Island, in Kaneohe Bay, Oahu. It is located northeast of Coconut Island. In every case, the crabs to be used in an experiment (see below) were collected on the same day they were to be used. Usually the observations were started within one hour after the crabs were collected and placed in holding containers.

Field Counts

To obtain an estimate of the distribution of the three species in the study area, series of rocks were examined. It had been noticed, during preliminary observations on the social behavior of these species in the field, that during the day the great majority of individuals of all species were under rocks or pieces of dead coral.

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The partial exception to this rule was *Calcinus laevimanus,* a number of specimens of which were sometimes seen right at the shore line—perhaps moving up and down with the tide as suggested by Reese (1969). Rather than sampling by one of the usual quadrat methods, since it was known that the distributions were patchy and the laboratory observations were to be made on animals collected in such patchy distribution patterns, the rocks under which crabs would be found were examined. A series of transects were run from the shore to the edge of a dropoff at a depth of about 6 feet. Every "rock" along the line was turned over and the individual crabs were counted. The distinct color pattern differences on the ambulatory legs and chelipeds made species identification easy.

Experiment 1

To measure the frequency of interspecific shell fighting, 10 specimens of each species were placed in an opaque plastic container (32 × 25 × 12 cm deep), filled with seawater and the bottom covered with sand. The 30 animals were allowed to move about and interact without intentional observer interference. All shell fights were recorded as to: (1) whether or not the attacking animal won (defender came out of its shell after a series of raps); (2) the species of the attacker and defender; and (3) the size (cephalothorax length, c.l.), sex, and exoskeleton condition of each crab. Fights were recorded only if the attacking animal executed rapping behavior. This is the rapid movement by the attacking animal of its shell against the shell of the defending crab. In these species the pattern of movement is very similar to that described for *Calcinus tibicen* and *Clibanarius tricolor* (Hazlett, 1966*a*). Interactions which involved only shell investigation or "positioning" behavior (Hazlett, 1966*a*) were not counted. As soon as a fight was decided (loser comes out of shell or attacker gives up), the two crabs were removed and replaced by two crabs of the same species as those removed. The crabs were all of similar size, but an effort was made to have a size range in all three species such that for each species pair there would be some individuals of the first species larger and some smaller than some of the second species. Since the *Calcinus* species crabs inhabit shell of a slightly different size for a given size crab than individuals of *Clibanarius zebra,* this size range was necessary to ensure the possibility of interspecific interactions. These observations were carried out between 1100 and 1900 hours.

Experiment 2

The differences in shell fighting frequency between the three species obtained in experiment 1 could have been a result of several factors, including differential shell-changing drives in the individuals brought in from the field. To obtain an independent measure of the drive levels for shell changing, individual crabs fresh from the field were placed, along with five empty shells, in 10-cm culture dishes containing sand on the bottom. In each replication, one crab of each species which inhabited a *Trochus sandwichiensis* shell when collected was placed (in that shell) with five empty *Trochus* shells, and one crab of each species inhabiting a *Turbo sandwicensis* shell when collected was placed with five empty *Turbo* shells. It was necessary to put *Turbo*-inhabiting crabs with empty *Turbo* shells, since shell preferences (Reese, 1962, 1963, and unpublished data) could result in increased shell changing that would obscure possible differences between species in shell-changing drive level. For each crab, the size range of the empty shells was chosen to include at least one shell smaller than, and at least one shell larger than, the shell inhabited by the crab when collected. All six crabs were placed in individual dishes at the same time and then observed for 30 minutes. Every shell change was recorded. Twenty-two replications were run, between 1300 and 1800 hours.

Experiment 3

The apparent differences in shell-changing drive level seen in experiment 2, could be due to several factors, one of which could be species differences in closeness of shell fit "required" by a crab of a given size. For this ecological factor (shell of a correct size), the individuals of a species could vary in their niche breadth (Levins, 1968). To measure relative closeness of fit between a crab and its shell, 60 crabs of a species, all inhabiting *Trochus sandwichiensis* shells, were placed in a 10-gallon aquarium with 180 empty *T. sandwichiensis* shells. These

TABLE 1

DISTRIBUTION OF THREE CRAB SPECIES UNDER ROCKS IN THE STUDY AREA

ROCK SIZE (cm)	*Calcinus laevimanus*	*Calcinus latens*	*Clibanarius zebra*
27 × 17	2	0	23
16 × 6	5	0	25
10 × 20	1	2	1
36 × 20	10	0	75
14 × 21	0	7	0
20 × 30	15	0	80
10 × 20	10	0	30
10 × 17	0	0	40
15 × 30	8	0	65
20 × 22	4	3	10
10 × 21	12	0	15
10 × 20	0	4	0
15 × 15	0	0	25
16 × 30	2	0	105
10 × 10	1	0	25
11 × 14	1	0	110
10 × 10	3	0	25
14 × 24	4	2	12
31 × 25	4	0	80
30 × 20	0	3	0

empty shells were chosen to provide a size range greater than that of the shells inhabited by the 60 crabs when collected. The aquarium was supplied with a sub-sand filter-aeration system. The crabs were left in the aquarium with the empty shells for 48 hours. They were then separated, each crab's cephalothorax length was measured, and the shell was weighed after it had been air-dried at room temperature for over 48 hours.

RESULTS

A total of 40 rocks from six transect lines were examined in the study area. The distribution of crabs under 20 of these is shown in Table 1, and it represents the approximate range of species composition found. Occasionally a specimen of *Calcinus elegans* was found in the study area, but these were rare even in comparison with *Calcinus latens*. A total of 86 *Calcinus laevimanus*, 24 *Calcinus latens*, and 1,062 specimens of *Clibanarius zebra* were found under the 40 rocks. Thus *Cal. laevimanus* constituted 7.3 percent of the specimens, *Cal. latens* 2.0 percent and *Cli. zebra* 90.7 percent of the total. Obviously all three species were not present under most of the rocks examined, but some overlap did occur. The microgeographical separation of the species in this area is not complete during the day and the degree of mixing at night was not estimated.

Eighty-three shell fights were observed in experiment 1. The distribution of attacking and defending species is shown in Table 2. *Cli. zebra* attackers had seven intra- and one interspecific fights (12 percent interspecific), *Cal. latens* attackers had 28 intra- and 19 interspecific (40 percent interspecific), and *Cal. laevimanus* attackers had seven intra- and 21 interspecific fights (75 percent interspecific). In interspecific fights, attacking crabs of *Cal. latens* won 21 percent of the interactions they initiated, *Cal. laevimanus* 70 percent, and *Cli. zebra* none. In addition, defending crabs of *Cal. latens* did not

TABLE 2

SHELL FIGHTS WHEN 10 INDIVIDUALS OF EACH SPECIES WERE PLACED TOGETHER

ATTACKING ANIMAL	DEFENDING ANIMAL			
	Cal. laevimanus	*Cal. latens*	*Cli. zebra*	TOTAL FIGHTS
Cal. laevimanus				
Unsuccessful	3	3	4	28
Successful	4	1	13	
Cal. latens				
Unsuccessful		16	15	47
Successful	1	12	3	
Cli. zebra				
Unsuccessful		1	7	8
Total fights	8	33	42	83

come out of their shells in 80 percent of their interspecific fights, *Cal. laevimanus* in 100 percent, and *Cli. zebra* in 54 percent. It should be noted that the number of shell fights started by individuals of a species was inversely proportional to its relative density in the field (Fig. 1).

The size differences between attacking and defending crabs in successful and unsuccessful fights are summarized in Table 3. Although a successful *Cal. laevimanus* attacker was, on the average, 0.2 mm larger in cephalothorax length than a losing *Cli. zebra* in interspecific fights between those species, in seven of the 13 pairs the *Cli. zebra* was larger than the *Cal. laevimanus* which won the fight—in one case by 1.1 mm c.l. On the other hand, all three successful *Cal. latens* were larger than the defending *Cli. zebra.* However, t test values indicated that the difference between the average size difference in successful *Cal. laevimanus–Cli. zebra* and *Cal. latens–Cli. zebra* fights (+0.2 mm vs. +1.2 mm) was not significant ($t = 2.0$, $p > 0.05$). Also the difference between the *Calcinus* species in unsuccessful fights against individuals of *Cli. zebra* (—0.5 mm for *Cal. laevimanus* vs. 0.0 mm for *Cal. latens*) was not significant ($t = 1.0$, $p > 0.10$). However, the proportion of interspecific fights won is very significantly different, 13 out of 17 for *Cal. laevimanus* compared with 3 out of 19 for *Cal. latens* (chi-square = 13.9, $p < 0.005$).

The results of experiment 2 are shown in Tables 4, 5, and 6. There was no statistical difference in the number of changes into *Trochus* and *Turbo* shells (38 vs. 33). Counting all changes, the distribution of changes by species is significantly different from chance (chi-square = 8.9, $p < 0.02$), indicating a higher drive level for shell changing for *Cal. laevimanus* than for *Cli. zebra.* However, as shown in Table 5, proportionally more *Cal. laevimanus* individuals changed more than once. If the number of individuals making one or more changes is tabulated (Table 5, last column), no differences are found

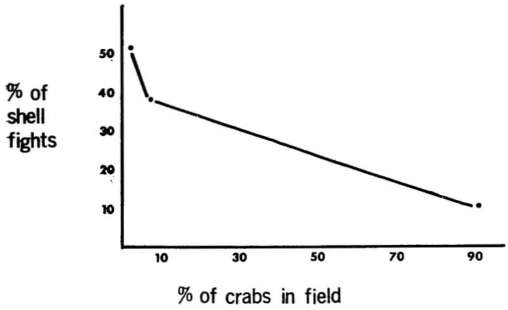

FIG. 1. Relationship between relative field density and relative tendency to start shell fights.

TABLE 3

AVERAGE SIZE DIFFERENCES IN MILLIMETERS OF CEPHALOTHORAX LENGTH (ATTACKER OVER DEFENDER) IN THE FIGHTS OF THREE SPECIES PAIRS

	SUCCESSFUL FIGHTS	UNSUCCESSFUL FIGHTS
Attacker *Cal. laevimanus* Defender *Cli. zebra*	+0.2 (13)*	—0.5 (4)
Attacker *Cal. latens* Defender *Cli. zebra*	+1.2 (3)	0.0 (20)
Attacker *Cal. latens* Defender *Cal. latens*	+0.5 (11)	—0.2 (16)

* Number of pairs given in parentheses.

TABLE 4

NUMBER OF SHELL CHANGES WHEN CRABS WERE PLACED WITH 5 EMPTY SHELLS FOR 30 MINUTES

	GENUS OF EMPTY SHELL		
CRAB SPECIES	*Trochus*	*Turbo*	SUM
Calcinus laevimanus	18	17	35
Calcinus latens	10	11	21
Clibanarius zebra	10	5	15
Sum	38	33	71

TABLE 5

NUMBER OF CRABS CHANGING SHELLS DURING 30-MINUTE PERIOD

	NUMBER OF INDIVIDUALS WHICH CHANGED SHELLS		
CRAB SPECIES	ONCE	MORE THAN ONCE	TOTAL
Calcinus laevimanus	12	11	23
Calcinus latens	10	4	14
Clibanarius zebra	8	3	11

TABLE 6

NUMBER OF SHELL CHANGES DURING DIFFERENT TIME INTERVALS

CRAB SPECIES	NUMBER OF SHELL CHANGES IN FIRST 10 MINUTES	IN SECOND 10 MINUTES	IN THIRD 10 MINUTES
Calcinus laevimanus	24	6	5
Calcinus latens	13	4	4
Clibanarius zebra	6	4	5

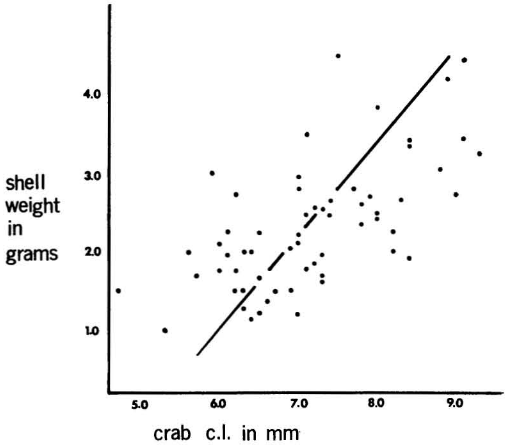

FIG. 3. Relationship between crab size and shell size in *Calcinus latens*.

between species (chi-square = 4.8, $p > 0.05$). The temporal distribution of changes (Table 6) shows that *Cli. zebra* is a more "timid" species; *Cal. laevimanus* made 69 percent of its changes in the first 10 minutes and *Cal. latens* 62 percent, but individuals of *Cli. zebra* made only 40 percent of its changes in the first 10 minutes.

The results of experiment 3 are shown in Figures 2, 3, and 4. In all three species, animal size is significantly correlated ($p < 0.001$) with shell weight. However, the correlation for *Cal. laevimanus* ($r = +0.758$) is significantly different from that for *Cli. zebra* ($r = +0.589$) (t value for Z transformation = 1.6, p = 0.05). The value for *Cal. latens* ($r = +0.633$) is not significantly different from that for *Cal. laevimanus* or *Cli. zebra*. It is interesting to note that the species with the closest fit to (the weight of) a shell, *Cal. laevimanus*, is also the species which changed shells most frequently when given the opportunity in experiment 2. And the species with the less close fit, *Cli. zebra*, changed shells least frequently in experiment 2 and started the smallest number of shell fights in experiment 1.

DISCUSSION

These observations may be discussed in regard to two aspects: (a) strictly behavioral factors and (b) ecological competition.

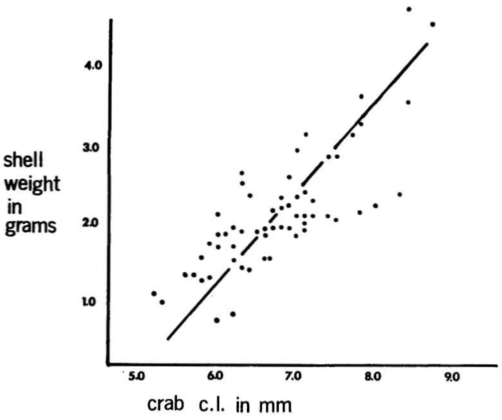

FIG. 2. Relationship between crab size (cephalothorax length in mm) and shell size (dry weight in grams) in *Calcinus laevimanus*.

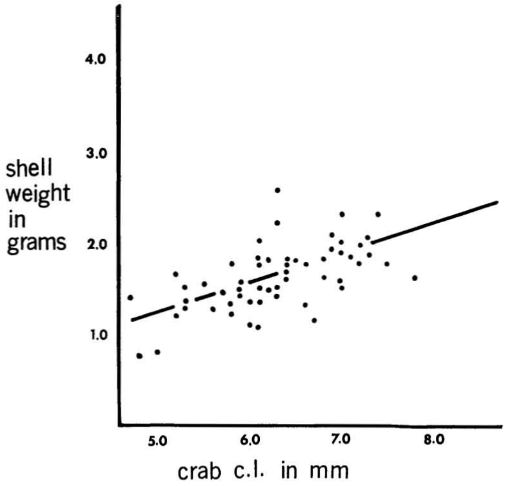

FIG. 4. Relationship between crab size and shell size in *Clibanarius zebra*.

Behavioral Aspects

In an earlier paper on interspecific shell fighting (Hazlett, 1967), it was suggested that species differences in behavioral repertoires resulted in an advantage for one species (*Pagurus cuanensis*) and that the other species (*P. bernhardus*) utilized chemotactic stimuli in avoiding interspecific fights. Neither of these phenomena was observed in this study. The behavioral patterns followed during shell fighting appear to be very similar qualitatively in these diogenid crabs. However, the intensity of the raps did markedly differ. Rapping movements by the attacking animal are the most important part of the behavioral pattern in shell fighting, and attacking individuals of *Calcinus laevimanus* rapped (brought their own shells into contact with those of the defending crabs) noticeably harder than did those of *Cal. latens.* And the latter rapped harder than individuals of *Clibanarius zebra.* Thus it is not surprising that individuals of *Cal. laevimanus* could win fights over the other species, and that *Cal. laevimanus* of a given size could, in a number of cases, win fights over *Cli. zebra* individuals that were larger than the attacker. And it would seem likely that individuals of *Cli. zebra,* since their rapping movements were relatively weak, would have little chance of winning a fight against an individual of *Cal. laevimanus.* In intraspecific shell fights in a number of species (Hazlett, 1966*a*, 1966*b*, 1970), it is very, very unlikely that an attacker could win a fight against a defender that was larger, unless the defender was soft from a recent molt. Exceptions to this rule occurred in experiments using *Cli. vittatus,* where the attacker was inhabiting a shell which had been made much heavier than is normal for that size crab. When these attackers rapped, the resulting sudden contact between shells seemed harder, and defending crabs came out rather rapidly. The naturally harder raps of attacking *Cal. laevimanus* may have produced similar results in their interspecific fights with individuals of *Cli. zebra.*

The frequency with which the other species attacked individuals of *Cli. zebra* may be related to both the behavior and morphology of *Cli. zebra.* While crabs of all three species were active during observation periods, individuals of *Cli. zebra* tended to duck into their shells more readily and to remain withdrawn longer than those of the *Calcinus* species. An empty-looking shell is more readily investigated than a shell with a crab visible in the aperture, and investigation always precedes shell fighting (although in many cases investigation is not followed by a shell fight). Even when an individual of *Cli. zebra* is up in the aperture of its shell, it may present fewer inhibiting (aggressive) stimuli to an attacking *Calcinus* since the chelipeds of a *Cli. zebra* are relatively smaller than those of *Calcinus* species and are rather uniformly dark colored. The *Calcinus* species used in study, as well as a number of other species of the genus, have marked white tips on the cheliped mani. Experiments with other hermits have shown that cheliped size is important in agonistic interactions (Hazlett, 1969) and that the white tips on appendages have important stimulus value (Hazlett, 1966*a;* in prep.).

Conversely the general behavior and cheliped morphology of the *Calcinus* species may have inhibited attack by potential *Cli. zebra* attackers. Retreat by an individual of *Cli. zebra* which had been investigating the aperture of a *Calcinus*-inhabited shell, very often seemed to occur when the chelipeds of the defending crab came into view as it moved up in its shell aperture. There was no indication that one particular species was more likely to retreat from another when physical contact was made.

In addition to these (proposed) behavioral differences, the shell-changing drive levels of the crabs when brought in from the field contributed to the different amounts of shell fighting seen. An individual of *Cli. zebra* was less likely to start a shell fight, in part because the probability of a crab changing shells by any means was lower for this species. The results of experiment 2 also showed that individuals of *Cli. zebra* were slower to execute any type of shell changing—most of the changes into empty shells by *Cli. zebra* were made after the crabs had been in the observation dishes for more than 20 minutes.

The fact that there was no difference in the number of changes into *Turbo* and *Trochus* shells indicates that the closeness of fit of animal to shell in the field is similar for the two shell species. This was somewhat unexpected since *Turbo* shells are not as common in the study area and there are indications (Reese, unpublished data) that of the two species, *Turbo* shells are preferred by crabs in some size ranges. The lack of a difference in number of shell changes into *Turbo* and *Trochus* shells also means that the measurements in experiment 3, on *Trochus* inhabitation only, may be extendable to *Turbo* shells. The great majority of crabs of all three species (of the size range used) in the study area inhabited either *Trochus* or *Turbo* shells.

It was noted in the results that if "number of crabs making a change" in experiment 2 is used as a measure of shell-changing drive (rather than "total number of changes"), the differences between the crab species in this particular were not significant. It could be argued that, since crabs were removed once they had had a shell fight in experiment 1, the "number of crabs" is the more appropriate measure (to partially explain the results of experiment 1). However, relative drive level for shell changing is the factor of importance, and it is felt that total number of changes is the better measure of that variable since each change reflects the presence of such a drive.

It could be argued that individuals of *Cli. zebra* were less likely to change shells (lower shell-changing drive) because they were most likely to have changed shells recently in the field. The latter could be the case since the field population density of *Cli. zebra* was markedly higher than that of the other species. Particularly in the case of *Cal. latens*, the population density in experiment 1 (30 crabs in 800 cm^2) was much higher than the density of crabs (of all species) which individuals of *Cal. latens* would experience in the field. The field and laboratory densities for *Cal. laevimanus* and *Cli. zebra* were not markedly different. For individuals of *Cal. laevimanus* this is due in large part to the presence of numbers of *Cli. zebra* in the same microhabitat.

While this field density factor may be partially responsible for the observed differences in shell fighting-changing, the selectivity of the crab species with regard to shell weight also seems to be important. An individual of *Cli. zebra* was likely to have a lower shell-changing drive partially because it is less selective in the size shell it will inhabit. Thus the deviation from the crab size–shell size regression could be greater for a *Cli. zebra* than for a *Cal. laevimanus* before the crab was stimulated to change shells. Therefore crabs of *Cli. zebra* were less likely to start a fight partly because of a lower shell-changing drive.

An important consideration, which these observations cannot resolve, is that shell weight might not be equally important for all three species. Reese (1962, 1963) showed that for a number of crab species, including *Cal. laevimanus,* shell weight is correlated with animal size, and that if shell volume is held constant, the crabs are able to choose the "proper" weight. However, as Völker (1967) showed for *Coenobita scaevola* and Hazlett (1970) for *Pagurus bernhardus,* internal shell volume is more closely related to crab size than is shell weight. Data on individuals of *P. bernhardus* starting shell fights indicated that for a crab in a shell that was too small internal volume was the important parameter, while for crabs in shells that were too large shell weight was the more important parameter (Hazlett, 1970). Thus, in the present study, shell weight may not be the criterion which the crabs utilized most frequently in shell selection. However, until the necessary measurements have been made for all three species, shell weight would seem to be a satisfactory, and easy to make, measure for interspecific comparisons.

Ecological Considerations

Several data of ecological interest can be examined. Niche breadth in terms of shell inhabitation can be measured in several ways for hermit crabs. The degree to which animal size is correlated with shell size can be used as one measure of niche breadth, just as Levins (1968) has used ecological tolerance for other parameters. Thus *Calcinus laevimanus* would have a more narrow "shell size" niche than *Cal. latens,* and *Clibanarius zebra* would have a broader "shell size" niche. Using $1/r^2$ where r is the correlation coefficient between animal size and shell size, as a measure of niche breadth for this factor, *Cal. laevimanus* has a breadth of 1.78, *Cal. latens* 2.51, and *Cli. zebra* 3.03.

A second shell-related niche breadth measure for hermit crabs can be obtained by tabulating the variety of gastropod shell species inhabited. The breadth can then be calculated from the

TABLE 7

DISTRIBUTION OF HERMIT CRABS IN VARIOUS SPECIES OF GASTROPOD SHELLS ARRANGED ACCORDING TO DECREASING FREQUENCY OF INHABITATION BY EACH CRAB SPECIES

HOST SHELL INHABITED BY EACH SPECIES	CRAB SPECIES *Pagurus hirsutiusculus* %	*Pagurus samuelis* %	*Pagurus granosimanus* %	*Diogenes gardineri* %	*Dardanus scutellatus* %	*Calcinus latens* %
Most commonly	50.9	59.0	28.9	58.0	41.5	64.2
Second most commonly	13.5	24.0	24.0	9.4	30.4	17.9
Third most commonly	12.2	9.5	21.6	8.1	14.1	8.0
Fourth most commonly	10.0	3.9	18.1	5.8	7.3	1.8
Fifth most commonly	10.0	1.8	6.4	4.1	1.7	1.8
All other species	3.4	1.5	1.0	14.6	5.0	6.3
Niche breadth	3.32	2.40	4.50	2.65	3.44	2.20

SOURCE: Data from Orians and King (1964).

formula $B = 1/\Sigma p_i^2$, where p_i is the proportion of crabs found in shells of species i. Unfortunately, the necessary data are not available for the determination of this value for the crab species studied in this paper. Reese (1962, 1969) gives data for two species of hermits along the California coast. *Pagurus hirsutiusculus* in northern Santa Monica Bay were found in *Acanthina* shells 50.3 percent of the time, in *Olivella* shells 44.8 percent, and 4.9 percent of the time in other species; this would give an approximate B of 2.22. *Pagurus samuelis* from the same area were found in *Acanthina* shells 61.9 percent of the time and the rest distributed in eight other species of shells ($B = 2.46$). Those data would suggest a broader niche for *Pagurus samuelis*. Reese also gives data for San Nicolas Island, where 72.3 percent of the *P. samuelis* were in *Tegula* shells ($B = 1.87$); and 95.4 percent of the *Pagurus hirsutiusculus* were in *Olivella* shells and the remaining 4.6 percent in *Tegula* shells ($B = 11.1$). This value of 1.11 is close to the limit (1.00) in narrowness of niche breadth for this factor.

Orians and King (1964) give data for six species of hermits from several Pacific locations (*Pagurus* species from California, other genera from Eniwetok). Their data, rearranged, are given in Table 7, along with the niche breadth values calculated from these distributions. *P. granosimanus* had the broadest niche with respect to shell species inhabited ($B = 4.50$), while *Calcinus latens* had the most narrow. The value for *Pagurus hirsutiusculus* calculated from Orians and King's data on a population from Horseshoe Cove, California ($B = 3.32$), would seem to be much higher than either of the values from Reese's data (1.11 and 2.22). Of particular interest is the similarity in niche breadth for shell factors for *Calcinus latens*: $B = 2.20$ from shell species inhabited, and $B = 2.51$ from shell weight measures.

Preliminary data for two species of Caribbean hermit crab are given in Table 8. These crabs were collected in the vicinity of Big Pine Key, Florida. The niche breadth values with respect to species of shell inhabited were 3.70 for *Calcinus tibicen* and 2.17 for *Clibanarius tricolor*. For *Cli. tricolor* 65 percent were found in *Cerethium* shells, while 42 percent of *Cal. tibicen* were in *Thais* shells and 29 percent in

TABLE 8

DISTRIBUTION OF 249 SPECIMENS OF *Calcinus tibicen* AND 202 SPECIMENS OF *Clibanarius tricolor* IN VARIOUS GASTROPOD SHELLS

HOST SHELL INHABITED	CRAB SPECIES *Cal. tibicen* %	*Cli. tricolor* %
Most commonly	0.42	0.65
Second most commonly	0.29	0.17
Third most commonly	0.10	0.12
Fourth most commonly	0.08	0.03
Fifth most commonly	0.06	0.02
Other species	0.05	0.01
Niche breadth	3.70	2.17

Nerita shells. Measurements on temperature and salinity tolerances (Hazlett, unpublished data) indicate that *Cli. tricolor* may have an overall wider niche than *Cal. tibicen*. This brings up the question of how to combine niche breadth values for various ecological parameters to obtain the best overall measure of a species' degree of ecological specialization. Since measures may be either of proportions of specimens in discrete, meristic categories or of correlations between continually varying features, it may not be possible to ". . . divide by the maximum number, which is the number of classes, to give comparable measures of niche breadth" (Levins, 1968, p. 44). The simplest method of combining different measures would use the formula

$$B' = \frac{\sum\limits_{m} Bm}{m}$$

where m is the number of individual B values obtained. For *Cal. latens*, $B' = (2.20 + 2.5)/2 = 2.35$.

Interspecific competition between hermit crabs can be measured in two ways with the data available—by overlap of shell inhabitation and by amount of interspecific shell fighting.

Orians and King (1964) present the most complete data on overlap of shell inhabitation. Figure 3 (p. 303) of their article gives the percentages of overlap among three species of crabs for all species of shells at four different locations around Eniwetok. Levins's (1968) formula $d_{ij} = \sum\limits_{h} (p_{ih} - p_{jh})^2$ and $O_{ij} = \frac{1}{d_{ij}}$ seems appropriate in that when a crab of one species inhabits a gastropod shell, that shell cannot be occupied (at the same time) by a member of a second species. For the three species studied by Orians and King at Eniwetok, the shell niche overlap values would be 1.84 between *Diogenes gardineri* and *Dardanus scutellatus*, 27.03 between *Diogenes gardineri* and *Cal. latens*, and 1.88 between *Dardanus scutellatus* and *Cal. latens*. Orians and King's data for three species of *Pagurus* in Horseshoe Cove, California, give overlap values of 2.05 between *P. hirsutiusculus* and *P. samuelis*, 6.66 between *P. hirsutiusculus* and *P. granosimanus*, and 3.94 between *P. samuelis* and *P. granosimanus*. For the two species collected in Florida (this paper), overlap of shell species inhabited gave an O_{ij} value of 2.28 between *Cal. tibicen* and *Cli. tricolor*.

The data on shell fighting obtained in the present study are perhaps the most direct measures of interspecific competition. In almost all other measures relating to niche overlap, the existence of competition rests on one or more cause-effect assumptions, the exception being growth experiments with unicellular organisms (see Vandermeer, 1969). When two crabs are directly fighting over an item of ecological importance (executing behavior patterns that are used only when crabs are fighting over that type of item), no assumptions are needed. While the loser in a shell fight almost always gets the shell discarded by the winning crab, it is probably safe to conclude that, on the average, this shell will not be as satisfactory for the losing crab as was its former shell. How detrimental the exchange of shells will be to the defending crab will depend in part on empty shell availability in the area. If shells are in very short supply (i.e., limiting), as in Bermuda (Haas, 1950; Provenzano, 1960), a shell of appropriate size may not be available. If a hermit is kept in a shell that is too small, its growth is inhibited (Markham, 1968), and within a species, crab size is positively correlated with number of larvae released.

Since the competition is direct, the degree of interspecific competition can be calculated simply as the ratio of interspecific/intraspecific fights for a species; either as fights participated in, fights started, or fights won:

$$\alpha_{ij} = \frac{\text{interspecific fights between i and j}}{\text{intraspecific fights by i}}$$

$$\alpha'_{ij} = \frac{\text{interspecific fights started by j against i}}{\text{intraspecific fights by i}}$$

$$\alpha''_{ij} = \frac{\text{interspecific fights between i and j won by j}}{\text{intraspecific fights by i}}$$

For the laboratory situation, where the population densities were equal, the α_{ij} are as given in Table 9. A second way of measuring the effect of one species on a second would be to count only the fights started by the first species (α'_{ij}) or to use only the fights won by the second species (α''_{ij}). In this latter formula, j winning should be counted as both a fight started by j which results in j getting a new shell, and fights started by i, in which j does not come out of its shell. Values for the second and third values of

TABLE 9

COMPETITION COEFFICIENTS, α_{ij}, BETWEEN PAIRS OF HAWAIIAN HERMIT CRABS BASED UPON ALL INTERSPECIFIC SHELL FIGHTS PARTICIPATED IN FOR EACH SPECIES PAIR AND FOR ALL INTERSPECIFIC FIGHTS FOR A SPECIES

	SPECIES j			
SPECIES i	*Cal. laevimanus*	*Cli. latens*	*Cal. zebra*	BOTH OTHER SPECIES
Cal. laevimanus	1.00	0.71	2.43	3.14
Cal. latens	0.18	1.00	0.64	0.82
Cli. zebra	2.43	2.71	1.00	5.14

alpha are given in Table 10. In the laboratory situation of equal densities, both *Calcinus* species represent a greater "threat" to *Cli. zebra* than *Cli. zebra* does to itself—interspecific fights are more frequent than intraspecific. Based upon shell fights won, the interaction coefficients are as shown in parentheses in Table 10. The effect of the *Calcinus* species upon *Cli. zebra* is similar no matter which *alpha* coefficient is calculated. When the values from Tables 9 and 10 are adjusted for differences in field density, the values are as presented in Table 11; to determine the field α_{ij}, the proportion of interspecific fights participated in (or won) was multiplied by the ratio of field densities i/j.

It is clear that the effect of competition for shells between the *Calcinus* species and *Cli. zebra* would be very detrimental to *Cli. zebra* if the field densities of the three species were approximately equal. Such an effect would be further exaggerated by the fact that individuals of *Cal. laevimanus* are able to win fights against *Cli. zebra* that are larger than they are. The problem of relating *alphas* based on fighting to demographic pressures is an important one that is now being worked upon.

It is important to remember that all the data for the present study were obtained from the populations of hermit crabs inhabiting one area on one small sand bar in Kaneohe Bay. If the specimens had been gathered from an area where the field densities of the three species were markedly different, it is probable that the results of all three experiments would be different.

Since the data on shell fighting suggest that the *Calcinus* species have an advantage in the study area, other factors must be responsible for the observed differences in field densities of the three species. All three species are reproductively active for a number of months of the year

TABLE 10

COMPETITION COEFFICIENTS, α'_{ij}, BETWEEN HERMIT CRAB SPECIES BASED UPON NUMBER OF SHELL FIGHTS STARTED BY SPECIES j ONLY AGAINST i, AND UPON NUMBER OF SHELL FIGHTS WON BY SPECIES j

	SPECIES j			
SPECIES i	*Cal. laevimanus*	*Cal. latens*	*Cli. zebra*	BOTH OTHER SPECIES
Cal. laevimanus	1.00	0.18 (0.14)*	0.00 (0.57)	0.18 (0.71)
Cal. latens	0.14 (0.14)	1.00	0.03 (0.53)	0.18 (0.67)
Cli. zebra	2.42 (1.86)	2.57 (0.57)	1.00	4.99 (2.43)

* Values for fights won (see text) are in parentheses.

TABLE 11

COMPETITION COEFFICIENTS, α_{ij}, FOR HERMIT CRAB SPECIES, ADJUSTED FOR DIFFERENCES IN FIELD DENSITIES

	SPECIES j		
SPECIES i	*Cal. laevimanus*	*Cal. latens*	*Cli. zebra*
Cal. laevimanus	1.00	2.54 (0.50)	0.20 (0.05)
Cal. latens	0.05 (0.04)	1.00	0.01 (0.01)
Cli. zebra	29.16 (22.32)	119.23 (25.08)	1.00

NOTE: The values in parentheses are for fights won (α''_{ij}), the other valures for fights participated in (α_{ij}).

(Reese, 1968*b*), although *Cli. zebra* would seem to be the most temporally limited of the three. August was the only month in which more than 50 percent of the females of this species examined were berried, compared with April through October for *Cal. laevimanus* (Reese, 1968*b*). C. K. Barry (unpublished data) measured the temperature tolerance of several *Calcinus* species, and found that *Cal. latens* was not able to withstand as high temperatures as could individuals of *Cal. laevimanus*. Attempts to rear larvae of these species in the laboratory, under identical conditions, showed clear differences in survivorship to the first crab stage (Hazlett, unpublished data). Over 15 percent of the *Cli. zebra* zoea obtained in the laboratory successfully molted to crabs, while only about 1 percent of the *Calcinus* species zoea lived to that stage. Moreover, the time from first zoea to first crab stage was less than 5 weeks for *Cli. zebra* at 27°C, while the time for the *Calcinus* species was about 6 weeks.

These data on shell fighting clearly indicate that interspecific agonistic interactions are important for the species of hermit crabs studied. Individuals of *Clibanarius zebra* are at a decided disadvantage in shell fights with sympatric *Calcinus* species, and where population densities are (for other reasons) nearly equal, the competition against *Clibanarius zebra* is very strong.

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