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AN ANALYSIS OF SHELL OCCUPATION BY TWO SYMPATRIC SPECIES OF HERMIT CRAB. I. ECOLOGICAL FACTORS

K. A. MITCHELL

Department of Zoology, The University of Glasglow, Glasglow, G12 8QQ, Scotland, U.K.

To protect itself from its environment, a hermit crab must have a gastropod shell (Reese, 1969; Vance, 1972a) and where numbers of gastropod shells are limited, there is evidence that this limitation reduces the number of hermit crabs an environment can support (Hazlett, 1970; Provenzano, 1960; Reese, 1969; Thompson, 1903). In addition to acting as a limiting factor, the type of shells present in any one place can also determine what size or species of hermit crab is present in that area. Reese (1969, p. 346) states that: "in Hawaii the availability of shells seems to limit the size of individuals in the population", while Markham (1968) found that occupation of small shells by the European hermit crab, *Pagurus bernhardus,* restricted the growth of these crabs. Examples of resource partitioning of hermit crab species on the basis of two different types of shell have also been studied. Grant and Ulmer (1974) and Wright (1973) both found that shells covered by *Hydractinia echinata* were preferred by one out of two sympatric species while Vance (1972b) showed that, of the three rocky intertidal species of the San Juan Islands, Washington, one species preferred short light shells whereas the other two species preferred comparatively taller and heavier shells.

In the present study experiments were performed on two species of hermit crabs, *Pagurus longicarpus* and *Clibanarius vittatus,* which were equally abundant in the intertidal zone at Beaufort Harbor, North Carolina. This area had no empty gastropod shells, thus suggesting that shells were a limiting factor in this area and that resource partitioning of the shells may explain the coexistence of the two hermit crab species. The experiments were designed to answer the following questions. (1) Are shells a limiting factor in this area? (2) Does resource partitioning take place between *P. longicarpus* and *C. vittatus?* (3) If resource partitioning does take place, what factors maintain the partitioning?

Materials and Methods

All animals used in this experiment were taken from the intertidal zone of an area approximately 100 meters long at Beaufort Harbor, North Carolina, next to the Duke University Marine Laboratory dock. This area has a mixture of sand and mud as a substrate and has many living gastropods buried in it. All experiments were conducted during the summer months and no difficulty was encountered in obtaining specimens of either species of hermit crab in this area.

Three series of experiments were conducted. The first series tested the effect of shell limitation on the hermit crabs' occupation of shells, while the second tested the ability of one hermit crab species to obtain a preferred species of shell from the other hermit crab species. The third series of experiments tested the relation between substrate preference of both hermit crab species and the natural occurrence of two living gastropod species on different substrates.

Shell selection

Sixty *Pagurus longicarpus* and sixty *Clibanarius vittatus* were collected in shallow water at low tide on 14th July, 1974. The species of shell which each crab inhabited was noted, and for each of these shells, five empty shells of the same species were put into an experimental tank 120 cm × 70 cm × 20 cm deep. This gave a total of twenty-five *Nassarius vibex,* 315 *Ilyanassa obsoleta,* thirty *Urosalpinx cineria,* ten *Thais haemastoma floridana,* 200 *Littorina irrorata* and twenty *Polinices duplicatus.* All shells put into the tank had previously been collected in the nearby area. The ratio of gastropod shells occurring in nature was used rather than using equal numbers of different shell species so that an idea could be obtained of how a hermit crab would select a shell in nature if there was no competition from any other hermit crab for that species of shell.

After all the empty shells had been placed at random in the tank, three of the sixty *P. longicarpus* and three of the sixty *C. vittatus* were evicted from their shells by holding them over a glass plate under which there was a 100 watt light bulb. *P. longicarpus* came out by tugging on the minor cheliped side of its body, while *C. vittatus* climbed out onto my hand after about a minute of gentle heating. This method proved 100% successful and did not seem to harm the crab in any way. After they were evicted, they were blotted dry of excess water, weighed and then placed in the experimental tank where they were left for 12 hours. It did not seem likely that any of the six crabs would choose the same shell, but to make the risk minimal, an effort was made not to put two crabs of less than 0.05 g difference in the tank at the same time.

When the 12-hour period of shell selection had elapsed, the species of shell which each crab was inhabiting was noted and each crab was evicted from its shell and discarded from the experiment. The shells were then placed back in the tank ready for three more crabs of each species to be evicted from their "field" shell and placed in the tank for a 12-hour period. It was not thought likely that the shells chosen by the preceding crabs would have been made more or less attractive by their immediately previous inhabitation, as Jensen (1970) did not find this to be true when testing *Pagurus bernhardus,* and there was no evidence to suggest the contrary in the present experiment. There was also no evidence to suggest that those crabs placed in the tank in the mornings selected shells any differently from those placed in the tank in the evenings, as diffuse artificial lighting was supplied during hours of normal darkness, and no pronounced activity rhythms were apparent in either species.

No feeding, other than the detritus on the sand/mud substrate, was provided in the experimental tank, but in the stock tank, crabs were fed on pieces of meat from the blue crab, *Callinectes sapidus.*

Interspecific shell fights

Large specimens of *P. longicarpus* in *I. obsoleta* shells were collected from the Beaufort Harbor region, evicted from their shells, weighed, and then returned to their shells. Crabs below 0.23 g were rejected from the experiment as the results of the shell selection experiment showed that they may not prefer a *Littorina irrorata* shell to their home shell. *C. vittatus* inhabiting *L. irrorata* shells were then collected from the same area, evicted from their shells to check that none were below 0.23 g, and then the first ten collected were given back their home shells. These ten *C. vittatus,* together with the first ten *P. longicarpus* found to be 0.23 g or over, were then put into the experimental tank, this time with all the empty shells removed, and left for 24 hours. The crabs were then taken out of the tank and note was taken of which species of shell each crab was occupying.

The following day the experiment was repeated, this time using ten *C. vittatus* of 0.23 g or over in *I. obsoleta* shells and ten *P. longicarpus* in *L. irrorata* shells. Owing to the lack of *P. longicarpus* found in *L. irrorata* shells in the field, five of the ten *P. longicarpus* used were given the choice of an *L. irrorata* shell taken at random and their *I. obsoleta* shell in which they were found. In four out of five cases the crabs went into the *L. irrorata* shell and in the other case the crab went into a second *L. irrorata* shell offered to it (the first *L. irrorata* shell was noticeably smaller in size than the *I. obsoleta* shell).

Substrate selection

The substrate preference of *P. longicarpus* and *C. vittatus* for mud or sand was tested by dividing the experimental tank into halves by putting mud to a depth of approximately 2 cm on one half of the tank and coarse sand of an equal depth on the other half. The mud was taken from Bird Shoal, an island very near to Beaufort Harbor, and the sand was taken from Beaufort waterfront, directly across from the Bird Shoal collecting point. These sites were chosen because the former is abundant in living *I. obsoleta,* whereas the latter has many *L. irrorata* sticking to the reeds. No live *L. irrorata* were found at the Bird Shoal site, however, nor was *I. obsoleta* found at Beaufort waterfront. A preference for one substrate over the other by *P. longicarpus* or *C. vittatus* would therefore limit its chance of finding shells commonly occurring on the less preferred substrate.

Three categories of experiments were performed on *P. longicarpus* and *C. vittatus.* These were: (a) isolated crabs; (b) intraspecific groups of ten crabs; and (c) interspecific groups of ten crabs of each species. These categories were used as there is evidence that hermit crab behavior is altered both by isolation (Courchesne and Barlow, 1971; Grant and Ulmer, 1974; Hazlett, 1966; Michell, 1973) and by the presence of another hermit crab species (Meadows and Mitchell, 1973).

The procedure for testing the first category was to put a hermit crab on the sand/mud partition, leave it isolated in the tank for five hours, then note which half of the tank it occupied. A minimum of five hours duration in the tank was chosen, as a hermit crab can be very active in a closed container until its has explored its surroundings. Its activity then drops off markedly. In the present situation, this occurred at a maximum of five hours after being placed in the tank.

In addition to testing differences in the hermit crab species' preferences to mud and sand, it was decided to test if a hermit crab occupying a dark shell, such as *I. obsoleta,* was more likely to occur on mud than one inhabiting a white shell, such as *L. irrorata,* or conversely, if a crab inhabiting *L. irrorata* was more likely to occur on sand than mud. This was done by ensuring that half the crabs of both species tested occupied *I. obsoleta* and the other half occupied *L. irrorata.*

TABLE I

Field collection: number of gastropod shells occupied by each species of hermit crab.

Shell species	*P. longicarpus*	*C. vittatus*
N. vibex	5	0
I. obsoleta	50	13
U. cineria	1	5
L. irrorata	3	37
T. haemostoma floridana	1	1
P. duplicatus	0	4

Finally, after ten crabs of both species were tested, the sand and mud halves of the tank were reversed, and another ten crabs of both species were tested in the same way as before. This reversal of substrates established a control for factors, such as light, which may have influenced the distribution of the crabs when they were in the tank.

The second category of experiments was performed in the same way as the first category, the only difference being that ten crabs of the one species were put into the tank at the same time. Similarly the third category was conducted as in the second category but this time ten crabs of both species were put into the tank at the same time.

RESULTS

Shell selection

The results of the field collection of sixty *P. longicarpus* and sixty *C. vittatus* are shown in Table I.

On analysis by the two-tailed binomial test, the probability that there was no difference between the number of shells inhabited by *P. longicarpus* and *C. vittatus* was < 0.001 for both *I. obsoleta* and *L. irrorata*. Differences in the ratio of the two species occupying other shell species were not significant, or alternatively were not tested owing to the small sample size.

The results of the laboratory shell selection experiment for the same sixty crabs of both species are represented in Table II.

Significant differences in selection of shell species were obtained for *I. obsoleta* and *P. duplicatus* ($P < 0.001$). The only other species with large enough numbers

TABLE II

Laboratory selection: number of gastropod shells selected by each species of hermit crab.

Shell species	*P. longicarpus*	*C. vittatus*
N. vibex	4	0
I. obsoleta	44	4
U. cineria	0	0
L. irrorata	12	18
T. haemastoma floridana	0	5
P. duplicatus	0	33

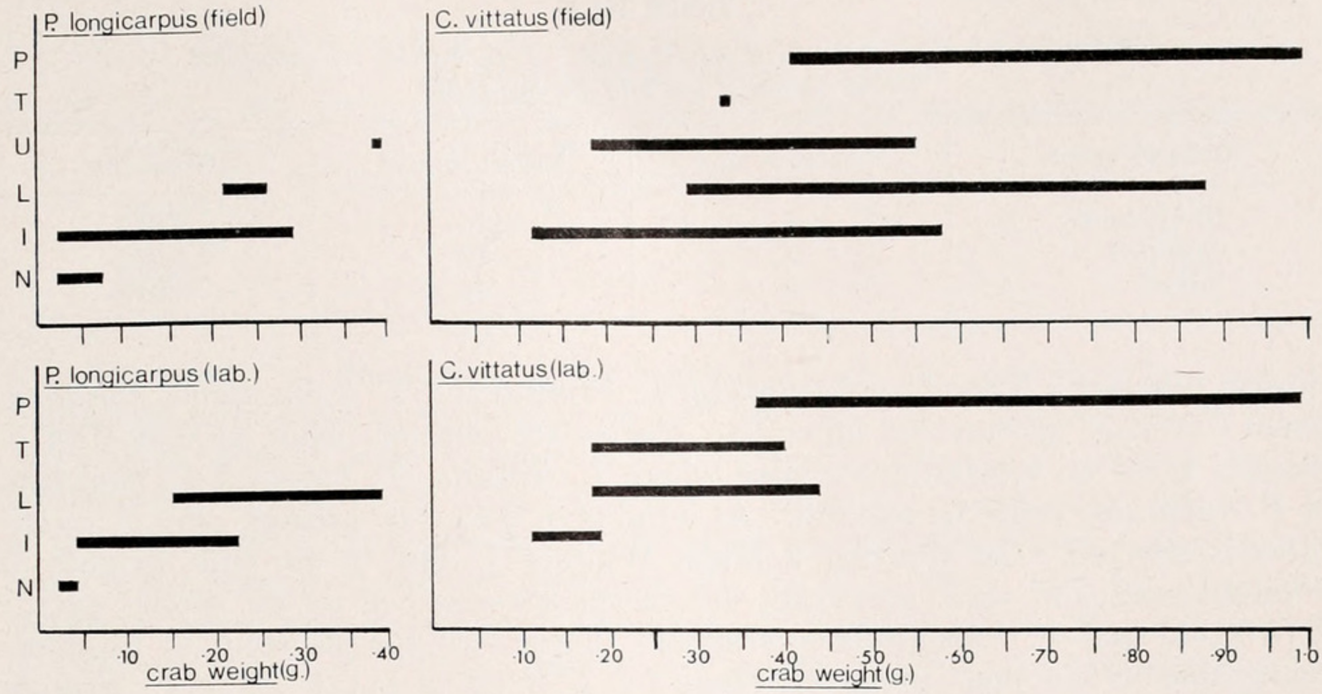

FIGURE 1. Effect of increasing weight of crab on shell species inhabitation. Black bars represent the weight range within which crabs inhabit a species of shell. Abbreviations of shell species are: P, *Polinices;* T, *Thais;* U, *Urosalpinx;* L, *Littorina;* I, *Ilyanassa;* N, *Nassarius.*

selected to test hermit crab species preference was *L. irrorata.* No significant difference was recorded for this species of shell ($P = 0.36$).

There is, therefore, little doubt that resource partitioning of shells takes place both in the restricted selection conditions of the field, and in the unrestricted choice of shells in the laboratory. The partitioning which takes place in the field is not the same as that in the laboratory, however, as there is a significant increase in the number of *P. longicarpus* selecting *L. irrorata* in the laboratory over those occupying *L. irrorata* in the field ($P = 0.036$). Similarly with *C. vittatus,* there is a significant increase in the numbers selecting *P. duplicatus* in the laboratory ($P < 0.001$), but with an accompanying significant decrease in the numbers selecting *I. obsoleta* ($P = 0.05$) and *L. irrorata* ($P = 0.015$). The two-tailed binomial test was again used to calculate all probabilities.

The influence of crab size on shell selection is shown in Figure 1. *P. longicarpus* shows a clear pattern in the laboratory selection of shells. As its size increases, so the species of shell which it prefers changes. Up to 0.04 g it prefers *Nassarius vibex.* From 0.05–0.15 g it prefers *I. obsoleta.* There is then an indeterminate zone from 0.16–0.22 g in which the crab may choose either *I. obsoleta* or *L. irrorata.* Finally, at 0.23 g or greater, it prefers *L. irrorata.*

The weight ranges of *P. longicarpus* inhabiting different species of shell in the field are basically similar to those of the laboratory but with *I. obsoleta* making up for the lack of *L. irrorata* shells. Nevertheless, a Mann Whitney U test shows that the weights of *P. longicarpus* in *L. irrorata* shells are significantly larger than those in *I. obsoleta.*

C. vittatus also shows a clear pattern in the laboratory. At a size range of 0.12–0.17 g, *I. obsoleta* is preferred. At a weight of 0.19 g, three shells can be

TABLE III

Substrate selection of Pagurus longicarpus. *Probabilities are calculated by the binomial test and are two-tailed.*

Category tested	Number on sand	Number on mud	Probability
Individually	5	15	0.042
Grouped	3	17	0.002
Mixed	4	16	0.012

chosen, however. These are *I. obsoleta, L. irrorata* and *T. haemastoma floridana.* From 0.20–0.37 g, only the latter two species are selected, while at 0.38–0.44 g, there is again an indeterminate zone where *L. irrorata, T. haemastoma floridana* or *P. duplicatus* could be selected. At weights of 0.45 g or greater, only *P. duplicatus* is selected. On applying a Mann Whitney U test to the crab weights in different species of shell, significant differences are obtained for all species except *L. irrorata* and *T. haemastoma floridana.* These two species seem to be interchangeable within their preferred range for *C. vittatus* but whereas *L. irrorata* shells were twenty times more common than *T. haemastoma floridana* in the experiment tank, they were only chosen 3.6 times more than them. A binomial test shows that a selection of 5 : 18 is significantly different from the expected ratio of 1 : 20 ($P = 0.002$). Hence there is reason to believe that *C. vittatus* prefers the general shape of *T. haemastoma floridana* to that of *L. irrorata.*

The field results of size of crab against species of shell show a similar though less clearly defined pattern. It is interesting to note that *U. cineria,* although occurring over a wide size range of crab in the field, is not selected at any size range in the laboratory.

Interspecific shell fights

At the end of 24 hours, the ten *P. longicarpus* and ten *C. vittatus* still occupied the same species of shell as when they were first put into the tank. This was the case in both series of experiments. In the first series, the ten *P. longicarpus* were in a species of shell unsuitable for their size compared with the *L. irrorata* shells occupied by *C. vittatus,* whereas in the second series, the opposite was true. It was assumed that, if any shell swaps between species did occur in nature, it would be between individuals in a similar situation to those used in the experimental tank. Since no shell swaps did occur in the tank, it can be assumed with a fair degree of certainty that shell swaps between these two species at Beaufort rarely, if ever, occur in nature.

Substrate selection

The results are presented in Tables III and IV. No significant differences were obtained for either species of crab inhabiting either species of shell against sand or mud when tested by a two-tailed binomial test. The results were therefore pooled for each species of crab. Similarly, no significant difference was found between the results obtained before and those obtained after the sand/mud halves of the tank were reversed. These results were also pooled, so that the table shows

TABLE IV

Substrate selection of Clibanarius vittatus. *Probabilities are calculated by the binomial test and are two-tailed.*

Category tested	Number on sand	Number on mud	Probability
Individually	8	12	0.504
Grouped	11	9	0.814
Mixed	11	9	0.814

only the results of the twenty crabs tested for each category in either species. Significant differences in preference of mud over sand were obtained in *P. longicarpus* regardless of what category was being tested, whereas *C. vittatus* had no preference in any category. To test whether presence or absence of the same or of the other hermit crab species had any effect on substrate choice, a chi-squared test of homogeneity was performed on the ratio of sand : mud for the three categories tested in both species. Neither *P. longicarpus* ($P < 0.80, > 0.70$) nor *C. vittatus* ($P < 0.70, > 0.50$) showed any significant change in preference in the three categories.

Discussion

The results of the shell selection experiment indicate that two major factors operate in determining shell inhabitation by both species of hermit crab in this area. The most obvious factor is that the species of shell which a hermit crab prefers is related to the size (weight) of the crab. In the laboratory there is a clear pattern of shell species inhabitation which is similar for both species of crab. That is, given a crab of a certain weight, it can be predicted which species of shell it will prefer compared with another species. Only in overlap zones (for example, in *C. vittatus* from 0.38–0.44 g) is there some doubt as to the preferred species. It still remains to be discovered, however, whether this apparent species preference is related to the dimensions or specific shape of the shell. This problem is the subject of a second paper on shell occupation of these species (in preparation).

The other major factor operating in determining shell inhabitation is the availability of certain shells. Evidently some species of shells are not available in the numbers that would allow every hermit crab to be in a preferred shell. If this had been the case then there would have been no significant differences between the numbers of shells each species picked up in the field and the numbers of shell species selected in the laboratory. It is worth noting, however, that the ratio of shell species found in the field agrees much closer to that found in the laboratory in the case of *P. longicarpus* than *C. vittatus*. Of the sixty crabs of each species tested, forty *C. vittatus* chose a shell of a different species from the one they were inhabiting in the field compared with only fifteen *P. longicarpus* changing shell species. This indicates that the finite number of shells in this area affects *C. vittatus* more than *P. longicarpus*.

The results of the interspecific shell fights experiment show that *C. vittatus* did not obtain a preferred shell from *P. longicarpus* in the laboratory. Conversely, *P. longicarpus* was unable to obtain a preferred shell from *C. vittatus*. The former result is somewhat surprising in relation to the results of Wright (1973). Wright found that *C. vittatus* was able to obtain the shells of *P. longicarpus* even when *P. longicarpus* was the larger crab. The only instance he cited of *C. vittatus* not being able to do so was when *P. longicarpus* occupied a shell on which living *Hydractinia echinata* were present. No *H. echinata* were present on any of the shells used in the present experiment, however. Provenzano (1959) records a break in the distribution of *P. longicarpus* at Southern Florida, and also records differences in pigment and overall color between Eastern Atlantic specimens and those from the west coast of Florida. From this evidence he divided them into subspecies and it may be that these subspecies have different behavioral as well as morphological properties. Provenzano (1959, p. 404) suspected this when he wrote "experiments in comparative behavior of morphologically similar and dissimilar members of the same genus might yield interesting results" in relation to *P. longicarpus* and *Pagurus pollicaris*. One other possibility is that *P. longicarpus* is in the middle of its geographical distribution at Beaufort, North Carolina, whereas *C. vittatus* is at the northern extremity of its distribution. In Texas where Wright worked, the opposite is the case. *P. longicarpus* is at the southern extremity of its distribution whereas *C. vittatus* has been reported as far south as Brazil (Provenzano, 1959). It may be that a species is more aggressive when it is in an environment which is better suited to its physiological needs.

The shell selection and aggression results help to explain most of the observed shell inhabitation of the two species of hermit crabs but do not entirely explain the small percentage of *P. longicarpus* occupying *L. irrorata* in the field. Approximately one in three of the *P. longicarpus* tested was large enough to occupy an *L. irrorata* shell compared with almost all the *C. vittatus* being large enough. This should therefore have given an *L. irrorata* species distribution of about 1 : 4 in favor of *C. vittatus*. The actual distribution, 3 : 37, is significantly above this ratio so that some factor other than chance seems to be responsible. This factor is probably the substrate preference of *P. longicarpus* for mud rather than sand. Since *C. vittatus* does not have this preference, a *C. vittatus* individual is much more likely to come across an empty *L. irrorata* shell than a *P. longicarpus* individual, assuming that *L. irrorata* shells are not washed far from the sand substrate on which they occur naturally.

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Summary

Three series of experiments were conducted on *Pagurus longicarpus* and *Clibanarius vittatus* at Beaufort, North Carolina. The first series showed that the preferred species of shell by either species of crab is determined by the size of the crab and that certain species of shells are not available in preferred numbers for the hermit crab species. This affects *C. vittatus* more than *P. longicarpus*. The

second series showed that shell fighting is not an important factor in determining which species occupies which kind of shell while the third series showed that a substrate preference for mud by *P. longicarpus* may limit it from obtaining a preferred species of shell that occurs naturally on sand.

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