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Shell Fights in the Hermit Crab *Pagurus geminus*: Effect of Cheliped Use and Shell Rapping

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Abstract – In shell fights of the hermit crab, *Pagurus geminus*, frequently it is observed that large crabs (attackers) grasp the thoracic appendage of small crabs (defenders) with the major cheliped and pull the smaller crabs out of their shells. If this is a standard occurrence and result, then the interaction should not be called a "negotiation" (Hazlett 1978). The role of cheliped use by the attckers in the eviction of defenders was therefore studied using crabs with tubes on their chelipeds, and the effect of shell rapping, which is thought to be necessary for eviction, was studied using crabs without shells. The experimental crabs evicted the defenders but fighting was significantly prolonged. Therefore, the negotiation model cannot be rejected. Specific aspects of shell fights in hermit crabs are discussed.

Shell fighting of hermit crabs is an interesting phenomenon in that both participants may gain from resulting shell exchanges; shell exchanges between large crabs possessing small shells and small crabs possessing large shells will provide them with shells of more appropriate size. Hazlett (1978) first realized the mutualistic aspect of shell fights in hermit crabs and called the interaction "negotiation" instead of "aggression". Negotiation means that in fights the attacked crab (defender) can choose between meeting and rejecting the attacking crab's (attacker's) requirement to exchange shells, depending on potential gain or loss defined by information about the quality of the attacker's shell (Hazlett 1987). On the other hand, Elwood & Glass (1981) regarded the interaction as aggression because more exchanges occur when the attacker, rather than the defender, will gain from the result.

Though there are exceptions (see Discussion), it is widely known that defenders are sometimes pulled out from their shells by attackers (Allee & Douglis 1945; Orians & King 1964; Hazlett 1966). Shell fights are frequently observed in the Japanese species, *Pagurus geminus*. In most cases defenders are observed being evicted from the shell by being pulled out with attacker's major cheliped (Imafuku 1983). If the defender is always pulled out in shell fights, then the interaction cannot be called negotiation. Thus, I addressed whether the attacker could evict the defender without use of the cheliped or shell rapping which almost inevitably accompany eviction attempts.

Materials and Methods

The hermit crab, *Pagurus geminus*, was investigated. Animals were collected from the beach of Shirahama, Wakayama Prefecture, Japan (33°40′N, 135°20′E) and experimented with in the Seto Marine Biological Laboratory. They were removed from their shells by carefully crushing their shells with a hammer, sexed, and the carapace length was measured. Only undamaged males were used; crabs with any loss of thoracic appendages or infected with parasites were eliminated from the experiments.

Pairs composed of 1 large crab and 1 small crab were prepared. In order to induce shell exchanging attempts, the large crab was either naked (shell-less) or presented with shells 10–30 % smaller than the appropriate size, and the small crab was presented with shells 6–28 % larger than the appropriate size and just suitable for the larger partner. The appropriate shell sizes were previously determined by free-access experiments (Imafuku 1985). Shell sizes were measured by shell widths. The shells used were prepared from freshly collected snails, *Lunella coronata coreensis*, the soft parts of which were removed by boiling. This shell species is one of the most common houses for the present hermit crab species in Shira hama (Imafuku 1984).

Five types of experiments were conducted depending on the conditions of large crabs: (1) Intact; no operation, with shells. (2) Major cheliped tubed; same as "intact" except that the major cheliped of the large crab was covered with a piece of thick silicon tube (2 mm inner diameter). (3) Both chelipeds tubed; same as "major cheliped tubed" except that the minor cheliped was also cov ered with a piece of thin silicon tube (1 mm). (4) Shell-less; shell-less, with free chelipeds. (5) Tubed and shell-less; shell-less and both chelipeds tubed. Detailed conditions are shown in Table 1.

Each pair was placed in a plastic cup (8.8 cm in diameter and 4.5 cm high) and their behavior was observed. The following behavior is known to occur in shell fights of *P. geminus* (Imafuku 1983): When 2 crabs meet, one (attacker) approaches to the other (defender) which is usually smaller and retreats in the shell. The attacker holds and turns the defender's shell upside down. After inspecting the defender's shell, especially its interior, the attacker occasionally carries the defender to a suitable place for attack by grasping the defender's shell lip with the minor cheliped. The attacker initiates positioning movements (see Hazlett 1966) by rubbing the defender's shell with its own, using abdominal movements. Immediately after the positioning movement the attacker performs shell rapping which involves a series of 1 to 30 continuous violent hits of the defender's shell with the attacker's shell. The attacker performs shell rapping intermittently, alternating with varied periods of rest. It behaves as if it is waiting for the defender to emerge, keeping the cheliped inside of the defender's shell. When the defender attempts to come out, the attacker moves aside slightly, raps violently, and almost always pulls one of defender's thoracic appendages with the major cheliped. Occasionally the attacker stops attacking and simply leaves the defender, quitting the fight.

In the present experiments, when the large crab held the small crab with ambulatory legs, grasped the shell lip of the partner for carrying, or initiated the positioning movement, both crabs were carefully moved from the plastic cup to the observation tank (33.1 × 5.6 cm, 8.0 cm high) in which their behavior and the sound emitted by shell rapping were simultaneously videotaped. For sound recording a microphone covered with a thin rubber cap was used. Later, the tapes were analyzed with respect to the fighting time, the number of bouts of rapping and total number of raps.

The observation time was limited to 1 h, but when crabs continued to fight, it was extended to record fighting times of up to 1 h. The experiments were carried out from November 1987 to April 1988.

Results (Table 2)

1. *Intact*

Before checking the effect of pulling out with the cheliped and of shell rapping on the eviction of defenders, fighting behavior of intact animals was observed. Out of 23 pairs, 11 initiated shell fights, and in all these cases the large attacker succeeded in eviction of the defender. In most cases the attacker clearly used the major cheliped to pull out the defender as shown in Fig. 1. In 2 cases, however, it appeared that the defender came out without being grasped by the chelipeds of the attacker. It is possible the attacker was using chelipeds inside the defender's shell, which the observer could not detect.

2. *Major Cheliped Tubed*

To check the effect of the major cheliped in shell fights, the attacker's major cheliped was placed in a tube, thereby preventing its use. The operated crab sometimes brought the tubed cheliped to the mouth, as if examining the silicon tube or attempting to remove it. However, once it initiated shell fights, it devoted itself to fighting. Out of 5 attackers, 3 initiated shell fights which resulted in eviction of defenders. In all 3 cases the

Table 1. Crab size and shell size in respective experiments.

Condition of large crabs	N	Crab size (Carapace length)			DR[a] of large crab		DR[a] of small crab	
		Large	Small	Large / Small	Before [b]	After [c]	Before [b]	After [c]
Intact	23	5.4 + 0.4	4.4 + 0.4	1.24	− 23	0	18	− 9
Major cheliped tubed	5	5.8 + 0.4	4.7 + 0.3	1.24	− 25	− 1	17	− 12
Both chelipeds tubed	14	5.7 + 0.3	4.6 + 0.3	1.24	− 25	− 3	15	− 12
Shell-less (= Naked)	18	5.4 + 0.5	4.6 + 0.5	1.18	*	− 1	12	*
Tubed and shell-less	15	5.4 + 0.4	4.2 + 0.4	1.31	*	− 1	22	*

[a] DR: deviation rate from preferred shell size
= 100 × (preferred shell size − current shell size) / preferred shell size.

[b] Before: before shell exchange. After: after shell exchange if it occurred.

*: shell-less.

Table 2. The results of the experiments.

Condition of large crabs	N	Initiation of fight	Eviction [Eviction / Fight]	Failure in eviction	Quitting
Intact	23	11	11 [100%]	0	0
Major cheliped tubed	5	3	3 [100%]	0	0
Both chelipeds tubed	14	9	5 [56%]	1(1)	3(3)
Shell-less (= Naked)	18	12	4 [33%]	3(2[a])	5(3[b])
Tubed and shell-less	15	14	4 [29%]	7	3

"Failure in eviction" means that the attacker could not succeed in eviction of defender within the test time, e.g. continuing fight beyond the observation time. Number in parentheses indicate the number of evictions in the 2nd test.

[a] remaining 1 was quit.

[b] remaining 2 were quit and no fight, respectively.

attacker always used the minor cheliped to evict the partner. Reese (1963, 1983) reported the ability to compensate for the loss of appendages in crustacea.

3. Both Chelipeds Tubed

In this experiment, both the major and minor cheliped were placed in tubes. Out of 14 pairs, 9 initiated shell fights and 5 attackers succeeded in eviction; the defender came out of the shell slowly, and at that time the attacker rapped violently. Thus the attacker can evict the defender without use of any cheliped, that is, the defender came out without being pulled by the attacker. In the 4 remaining cases, 1 attacker could not succeed in evicting the defender within 1 h of observation time (failure). The other 3 attackers stopped and quit fighting, simply leaving the defender (quitting).

With respect to the unsuccessful and quitting attackers, a second series of tests was carried out in which the attacker's chelipeds were removed from the tubes, returning the attackers' condition to "intact". In all 4 of these tests, the attacker succeeded in evicting the defender within 1 h of test time.

4. Shell-less

The large crab was removed from its shell to check the effect of shell rapping. Out of 18 pairs, 12 large crabs initiated shell exchange attempts. In the attempt they clearly showed the same movements of the abdomen as in shell rapping, moving as if they still possessed their shells. Four attackers succeeded in eviction of the partner, 3 failed and 5 quit. Thus the shell-less attacker could evict the defender without performing shell rapping with a shell, but the eviction rate was low.

Using 8 unsuccessful and quitting crabs, a second series of tests was carried out in which the crabs were presented with shells as in the intact experiment. Out of 3 unsuccessful crabs, 2 succeeded in eviction and 1 quit fighting. Out of 5 quitting crabs, 3 succeeded in eviction, 1 quit, and 1 did not initiate shell fights.

5. Tubed and Shell-less

Finally, shell fights were observed between normal small crabs and shell-less large crabs with tubes on both their chelipeds. Fifteen pairs were tested and 14 large crabs initiated attacking. Four attackers succeeded in eviction of defenders, 7 failed and 3 quit. The results show that attackers could evict partners without use of chelipeds or shells for rapping.

6. Fighting Time and Number of Raps

In the both chelipeds-tubed and shell-less experiments it was found that attackers could evict defenders without use of chelipeds or shells. However, when attackers were subjected to these operations, eviction rate within the observation

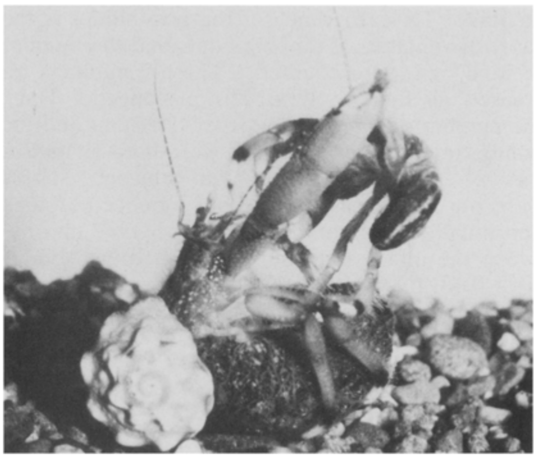

Fig. 1. The attacker pulls out the defender with the right major cheliped.

time clearly decreased (100% for the intact and 29–56% for the operated groups). The difference in eviction rate between the intact and operated groups was thought to be attributable to the fact that fighting time was prolonged in the operated group. To check this possibility, the fighting time was compared between the intact and operated groups. Quitting cases were eliminated from the comparison because quitting seemed to relate to motivational aspects of attackers but not to the effect of the experimental operations. For comparison, the results of the second series of tests, in which conditions were the same as for intact individuals, were added to those of the intact group. The fighting time of unsuccessful cases in which the animal continued to fight beyond the observation time was treated as 3600 s (1 h) for calculation.

In both fighting time comparisons (between the intact and both chelipeds-tubed groups and between the intact and shell-less groups), significant differences were found ($P < 0.05$ for both, Wilcoxon's 2-sample test, 2-tailed). Thus, the fighting time significantly increased when the attacker could not use the chelipeds or shells.

When the intact and the tubed and shell-less groups were compared, a very significant difference ($P < 0.01$) was detected. On the other hand, there were no significant differences between the both chelipeds-tubed and the tubed and shell-less groups nor between the shell-less and the tubed and shell-less groups. These results may be due to the fact that in unsuccessful cases the observed period of fighting was limited to 1 h. Of the longer fights exceeding 1 h, there was 1 in the both chelipeds-tubed group, 3 in the shell-less group, and 7 in the tubed and shell-less group.

In the operated groups, fighting time was significantly prolonged. This may be attributed to operations effecting a decrease in aggressiveness of the attacker or less success of aggressive behaviors. To learn which of the possibilities is the case, the number of rapping bouts and the number of total raps were counted. These 2 numbers increased as fighting time was prolonged. Thus, the number of rapping bouts per time unit and the number of raps per time unit were used as indicators of aggressiveness of the attacker. There were no differences in the bout number per time unit nor the total number of raps per time unit between the intact and both chelipeds tubed groups ($P > 0.18$, $P > 0.19$ respectively, t-test), indicating that the operation does not suppress aggressiveness of the attacker.

Discussion

From the both chelipeds-tubed experiment, it was found that defenders come out from their shells without being pulled out by attackers. The results do not eliminate the possibility of negotiation in shell exchange attempts. Eviction with no body contact between participants has been observed in both species, *Clibanarius tricolor* (Hazlett 1966) and *Pagurus bernhardus* (Hazlett 1970). These results may suggest that defenders accede to vacating their shells when they will gain from shell exchanges, or persistently endure attacks when the attacker's shell is expected to be of less value for them. However, when the chelipeds of the attackers were free to use, fighting time (the time required to effect eviction) significantly decreased, indicating that pulling out has some effect on the eviction of defenders. Probably defenders are usually grasped by attackers when attempting to come out. In the both chelipeds-tubed experiment, some defenders occasionally hesitated to emerge from their shell entrance, there were also crabs which appeared once at the entrance and then withdrew back into their shells. Thus, decision-making by defenders to leave their shells seems to be somewhat inconclusive. In a normal situation, attackers with free chelipeds could immediately evict defenders, and thus shorten the fighting time.

In the both chelipeds-tubed experiment, some defenders gave up their shells, without being pulled out. Why do they leave their shells? In the tubed and shell-less experiment, some defenders left their shells without being pulled out nor being rapped to leave their shells. During fights, defenders were kept turned upside down and forced to confinement in the shells. This restricted situation in confinement, devoid of free movements or perhaps lacking oxygen (Dowds & Elwood 1985), may be the causes.

Though shell-less attackers could evict defenders, the fighting time was significantly longer when attackers could not perform rapping. Similar results were obtained in *P. bernhardus* (Elwood & Glass 1981). Thus, rapping should have a quantitative effect on the eviction of defenders. With respect to rapping, 2 effects may be expected; one is discomfort (Dowds & Elwood 1985) and the other is information (Hazlett 1987). Rapping is a series of strikes with hard material which may impose discomfort on the defending animals withdrawn in their shells. Rapping may also convey information about the attackers' strength and/or shell quality to the defender. Since hermit crabs are known to show submissive behavior (Reese 1962, 1983), it indicates that communication between crabs is involved. On this question, further investigations are needed.

In the operated groups, attackers occasionally quit fights; in the intact group, once hermit crabs initiated fights, they almost always continued to attack until defenders discarded their shells. One reason for the operated attackers' quitting fights may be the enlargement of chelipeds with tube covers. Hermit crabs are known to measure the size of empty shells with cheliped movements in the interior of shells (Reese 1963; Kinoshita & Okajima 1968). The tube cover made the palm width of the major cheliped ca. 30% larger and the thickness ca. 40% larger, which may cause a misjudgment in the evaluation of the partner's shell as smaller. In the shell-less experiment, the reason for quitting fights should be different. Inconvenience in movements or lack of confidence to win fights without a shell may be causes.

Regardless of whether shell exchange attempts are negotiation or aggression, the fact that both participants have a chance to gain from "fights" is very interesting. Here, I describe the cause of the unique outcome of mutual gain in hermit crab fights, because it may be a rule in fights of most other animals that the defeated individuals suffer a loss. There are 2 unique aspects in shell fights; one is that the end of fights result in a form of exchange, and the other is that the value of what participants fight for is different for different individuals. In hermit crab fights the winner obtains the partner's shell but must give up its own shell. Thus the outcome results in an exchange of shells. In order for both participants to gain form exchange, the "property" to be exchanged—the shell—should have a different value for each crab. If the shell has the same value for both, mutualistic exchanges would not occur, because attackers would never leave a shell of similar or higher value in exchanges with for a shell of lower value, and defenders would not have a change to gain from exchanges. In the case of shells, the value is different for different individuals. Large shells are valuable for large crabs and of low value for small crabs and vice versa. Another possible aspect of variance of shell value may be shell species and morphology. Elwood et al. (1979) found that hermit crabs tend to move into shells of species that have been occupied previously, and assumed that newly moulted crabs may mold their bodies to the shape of the currently occupied shell. If this is the case, there should be individual differences in preference for shell types, that is to say, shell types should have different values for different individuals. If there are animal fights which satisfy these 2 factors of exchange and "property" having different value for different individuals, then there is a chance for mutualistic outcomes, regardless of the appearance of interactions being negotiated or aggressive.

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References

Allee, W.C. & M. B. Douglis 1945 A dominance order in the hermit crab, *Pagurus longicarpus* Say. *Ecology 26*: 411–412.

Dowds, B. M. & R. W. Elwood 1985 Shell wars II : the influence of relative size on decisions made during hermit crab shell fights. *Anim. Behav. 33*: 649–656.

Elwood, R. W. & C. W. Glass 1981 Negotiation or aggression during shell fights of the hermit crab *Pagurus bernhardus*? *Anim. Behav. 29*: 1239–1244.

Elwood, R. W., A. McClean & L. Webb 1979 The development of shell preferences by the hermit crab *Paurus bernhardus*. *Anim. Behav. 27*: 940–946.

Hazlett, B. A. 1966 Social behavior of the Paguridae and Diogenidae of Curacao. *Stud. Fauna Curacao 23*: 1–143.

Hazlett, B. A. 1970 Tactile stimuli in the social behavior of *Pagurus bernhardus* (Decapoda, Paguridae). *Behaviour 36*: 20–48.

Hazlett, B. A. 1978 Shell exchanges in hermit crabs: Aggression, Negotiation, or both? *Anim. Behav. 26*: 1278–1279.

Hazlett, B. A. 1987 Information transfer during shell exchange in the hermit crab *Clibanarius antillensis*. *Anim. Behav. 35*: 218–226.

Imafuku, M. 1983 New shell acquisition in the hermit crab, *Pagurus geminus*. *J. Ethol. 1*: 91–100.

Imafuku, M. 1984 Quality of shells occupied by the hermit crab *Pagurus geminus*: How many hermit crabs are satisfied with their shells? *J. Ethol. 2*: 31–36.

Imafuku, M. 1985 Shell exchange of the hermit crab *Pagurus geminus*. *Nankiseibutu 27*: 70–74. (In Japanese with English abstract)

Kinoshita, H. & A. Okajima 1968 Analysis of shell-seaching behavior of the land hermit-crab, *Coenobita rugosus* H. Milne Edwards. *J. Fac. Sci. Tokyo 2*: 293–358.

Orians, G. H. & C. E. King 1964 Shell selection and invasion rates of some Pacific hermit crabs. *Pac. Sci. 18*: 297–306.

Reese, E. S. 1962 Submissive posture as an adaptation to aggressive behavior in hermit crabs. *Z. Tierpsychol. 19*: 645–651.

Reese, E. S. 1963 The behavioral mechanisms underlying shell selection by hermit crabs. *Behaviour 21*: 77–126.

Reese, E. S. 1983 Evolution, neuroethology, and behavioral adaptations of crustacean appendages. In: S. Rebach & D. Dunham (eds.) *The behavior of higher crustacea*. pp. 57–81. John Wiley & Sons, New York.

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