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Response of Hermit Crabs to Sinistral Shells

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Abstract — Shell rotating behavior of the hermit crab *Pagurus geminus* was investigated. In preliminary observations, hermit crabs motivated to change shells rotated presented shells, filled with sand, in a way that dislodged the inside material. In order to determine if this behavior is stereotyped, or flexible and dependent on shell type, hermit crabs were tested with ordinary dextral shells of *Latirulus nagasakiensis* and sinistral shells of *Antiplanes contraria*. Sinistral shells are not normally encountered by hermit crabs. Their rotation of the dextral shell to the left was adequate for sand discharge. Sinistral shells were rotated in both directions. Analysis of recorded videotapes showed that variation in rotation direction could be attributed to variation in the position of the crab relative to the shell. When the crab faced the shell aperture from the inner lip, it rotated the sinistral shell to the right, and to opposite direction when it faced from the outer lip side. The crab always pushed the upper side of the horizontally laid shell, regardless of shell type or its own position.

Hermit crabs are animals that have flourished by taking advantage of gastropod shells (Barnes 1980). Hard shells are thought to be effective in protection against biotic environmental conditions as well as physical harassment (Reese 1969). The size and quality of the shell are known to affect fitness of its occupant (Hazlett 1981; Scully 1983). Probably for this reason, hermit crabs show a high interest in shells, gathering at shell acquisition sites (McLean 1974; Radinovsky & Henderson 1974; Imafuku 1983) or attempting shell exchanges (Hazlett 1966; Dowds & Elwood 1983; Imafuku 1983). Crabs in inadequate shells are ready to enter a new shell of sufficient size and quality. When an otherwise attractive shell is plugged with some materials, crabs usually show some attempt to remove them (Elwood & Adams 1990).

In my preliminary observations, a hermit crab provided with a shell filled with sand rotated it in such a way that the sand was dislodged. This behavior seemed to suggest that the crab has an ability to perceive the shell morphology and to associate the direction of rotation and the discharge of inside materials. If this is the case, the behavior may be regarded as based on something like the insight which is known in higher vertebrates (Eibl-Eibesfeldt 1967).

If crabs have such an ability, they will change their behavior according to situations. Therefore, if crabs have an ability to perceive the shape of shells and to relate it to sand discharge, they will rotate a newly presented sinistral shell in a direction opposite to that needed for the ordinary dextral shell. In the habitat of hermit crabs, sinistral shells are known to be very rare. I conducted this study to examine whether the behavior of hermit crabs is flexible or stereotyped.

Materials and Methods

The hermit crabs *Pagurus geminus* were collected from the beach near Seto Marine Biological Laboratory (33°40'N, 135°20'E) in Shirahama, Wakayama Prefecture, Japan, in April 1989 and in October 1993, and tested within 2 days. Animals were removed from their shells, by carefully crushing the occupied shells with a hammer, and sexed. Shield lengths were measured. Larger individuals (4.1-5.8 mm in shield length) without any injuries or parasites (occasionally *Peltogaster paguri*) were used for the experiments.

The naked crabs were forced to enter small shells (11.3-17.5 mm in outer width of the apeture, measured parallel to the inner lip) of *Nerita albicilla* (the home shell) which are known to be disliked (Imafuku 1985), probably because of the imperfect winding inside. These crabs, motivated to change shells, were then provided with perfectly winding dextral (*Latirulus nagasakiensis*) or sinistral (*Antiplanes contraria*) shells that were filled with sand. The former shells were collected from the Sakai fishing port in Minabe, ca. 6 km north from the laboratory, and the latter shells were purchased from a shell dealer. The 2 species are morphologically similar but with opposite winding direction (Fig. 1). The shell heights were 32.3-49.4 mm for dextral *Latirulus nagasakiensis* and 33.9-52.0 mm for sinistral *Antiplanes contraria*.

One dextral or sinistral shell, filled with sand, was placed with the shell aperture upward on the flat surface of sand substratum in a small aquarium (12.5 by 5.0 cm, 10.0 cm high). A hermit crab was introduced and the behavior was recorded on videotape from a side view.

The crab introduced into the aquarium usually walked next to the side wall, and accidental contacts with the shell usually led to the shell change behavior. Crabs usually contacted with the antenna at first, and then with the chelipeds or the ambulatory legs. After facing the shell aperture, the crabs attempted to insert the chelipeds into the shell interior, and soon initiated trials to remove the sand by picking it up. Frequently they conveyed grains to the mouthparts, and subsequently usually began to rotate the shell. After such behavior, they moved into the presented shells or discarded them.

The direction of rotation was defined as follows; right rotation was that in dorsal view of the shell (right or clockwise rotation viewed from the shell apex side), and left rotation the opposite (Fig. 2). Most erabs were tested once but a few were tested twice (see Table 2). Individuals that did not show any shell-change behavior for 5 min were eliminated from the experiments.

Results

1. Dextral Shell (Table 1)

All the crabs tested with the dextral shell of *Latirulus nagasakiensis* rotated it to the left. Number of rotation varied individually from 1 to 4. After rotation, 15 crabs changed the shell, 3 discarded it, and 1 changed but immediately returned to the home shell. Such discarding and returning seemed to indicate that the presented shell was slightly small for that crab.

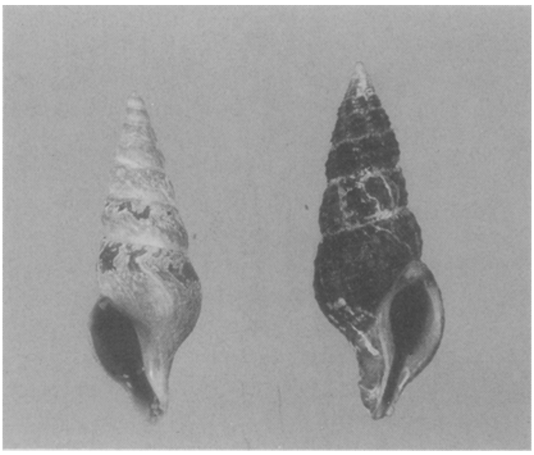

Fig. 1. The sinistral shell *Antiplanes contraria* (left) and the dextral shell *Latirulus nagasakiensis* (right).

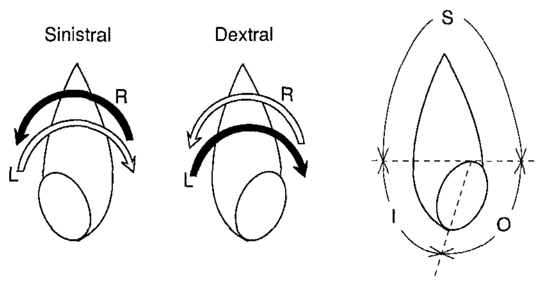

Fig. 2. Definition of the direction of rotation and the position. L: left rotation. R: right rotation. The solid arrows indicate efficient rotation in which the inside material came out. I: inner lip and columellar side. O: outer lip side. S: spire.

Table 1. Behavior of hermit crabs to the dextral shell.

Crab #	Approach	First position	Last position	Rotation direction	Final behavior
431	S	I	I	L	change
432	S	I	I	LL	discard
433	S	I	I	LL	change
434	I	I	I	LLL	change
435	O	O	I	L	change
436	I	I	I	L	discard
437	I	I	I	L	discard
460	I	I	I	LL'L	change
461	I	I	I	LL-LL	return
462	I	I	I	LLL	change
601	O	I	I	LLL-L	change
603	S	S	I	LLL-L	change
605	O	I	I	LL	change
607	O	O	I	L	change
609	O	I	I	LL	change
611	O	O	I	LL-L	change
613	O	O	I	LL	change
617	I	I	I	LL	change
619	O	I	I	LL	change

Approach: the point where the crab first contacted the shell (ref. Fig. 2). First & last position: the position where the crab firstly or lastly contacted the sand in the shell aperture prior to shell rotation. Rotation direction: L: left, R: right, -: successive rotation, ': half rotation with recovery.

2. Sinistral Shell (Table 2)

Of crabs tested with the sinistral shell of *Antiplanes contraria*, 13 performed right rotation, and 3 left rotation. One (Crab 472) attempted to rotate the shell, but stopped. Thus, the direction of rotation varied among individuals.

All 13 crabs that rotated the sinistral shell to the right moved into it. All 3 of the crabs that perfectly rotated the sinistral shell to the left returned to the home shell. When the crab entered the sinistral shell, it kept the shell apex to its left, which is just opposite to the crab in the dextral shell (Fig. 3).

Five crabs that rotated the sinistral shell to the right (Crabs 470, 471, 477, 478 & 479) were further tested with the dextral shell. Of them, one (Crab 477) did not show any shell-change behavior within the observation time. Three crabs adequately rotated the secondly presented dextral shell to the left. Another crab (Crab 479) rotated the dextral shell to the right. Thus, 3 crabs changed the rotation direction according to the shell types, and 1 maintained the same rotation direction with both types of shells.

3. Position of the Crab

The rotation direction varied among the crabs tested with the sinistral shell. It appeared to be determined by the position of the crab with respect to the shell. The crabs manipulated the shell from the inner lip side (position I, see Fig. 2) or from the outer lip side (position O). In Table 3, the direction of rotation and the position are shown for dextral and sinistral shells. From this table the relation of the rotation direction to the position is clear; when the crab performed the rotation movement in position I, it rotated the dextral shell exclusively to the left, and the sinistral shell exclusively to the right. Crab in position O rotated the shell in directions opposite to these. The results indicate that the crab always pushed, but did not pull, the upper side of the horizontally held shell, regardless of its position or of the winding direction of the shell.

Table 2. Behavior of hermit crabs to the sinistral shell, and to the dextral shell in the second test for some crabs.

Crab #	Approach	First position	Last position	Rotation direction	Final behavior
For sinistral shell					
470	I	I	I	R	change
471	S	O	I	R'RR	change
472	S	O	O	L'	discard
474	S	O	O	LLLL-LL-L	return
475	S	I	O	L	return
476	?	O	O	L	return
477	I	I	I	RR-R	change
478	S	O	I	RR	change
479	S	I	I	RRR	change
604	O	O	I	R	change
606	O	O	I	R'R	change
608	S	S	I	R	change
610	O	O	I	R	change
612	I	I	I	R	change
614	O	O	I	R	change
618	I	I	I	R	change
620	S	I	I	R'R	change
For dextral shell					
470	O	O	I	L-L	return
471	S	O	I	L'L'L-L	change
478	I	I	I	L	discard
479	O	O	O	RR'RR	change

For abbreviations see Table 1.

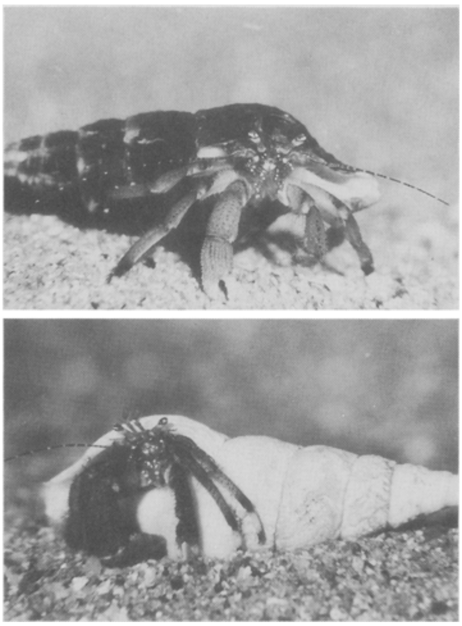

Fig. 3. Posture of crabs in the dextral shell (top) and in the sinistral shell (bottom).

Table 3. The relationship between the position of the crab to the shell and the direction of rotation.

Shell	Dextral		Sinistral	
Rotation	Left	Right	Left	Right
Position I	22	0	0	13
Position O	0	1	4*	0

*involves the imperfect rotation of Crab 472.

Then, how is the position determined? The videotapes of the crabs were checked for the initial approach and the position where the crab made the first and last contact with the sand in the shell aperture prior to rotation movements (Tables 1 & 2). Approach and first position varied for both types of shells, but the last position was almost always I for the dextral shell. Thus, for the dextral shell, 5 crabs changed position prior to shell rotation. For the sinistral shell, 6 crabs changed position from O to I, and 1 crab (Crab 475) did the opposite. Examples of shell rotating behavior are shown in Fig. 4.

Discussion

The hermit crabs almost always rotated the dextral shell to the left, but the sinistral shell was rotated in various directions. Thus, it could not be concluded that the hermit crabs have an ability to know the shell morphology and to react accordingly. If they have such an ability, they would have clearly switched the rotation direction according to shell type.

Analysis of the videotapes revealed that the direction of rotation is not fixed, but that rotation technique is. Crabs always pushed the upper side of the horizontally laid shell, regardless of shell type or of the position they were in. For the dextral shell, they almost took position I and rotated it in this way, which automatically produced left rotation and led to sand discharge. For the sinistral shell they took varied positions from which they performed a pushing movement that resulted in various rotation directions of the sinistral shell. Questions at present are (1) why the crabs take positon I for the dextral shell, (2) why the position varies for the sinistral shell, and (3) why crabs push, rather than pull, the upper side of the horizontally held shell.

Taking Position I for the Dextral Shell

Prior to shell changes, hermit crabs almost always insert their chelipeds into the shell interior for examination (Reese 1963; Kinoshita & Okajima 1968). Position I is suitable for this behavior because the crabs can only flex their chelipeds ventrally (Fig. 5). Crabs sitting in position O could not deeply insert the cheliped into the shell.

Position I allows contact of the sternite of the cephalothorax with the hump of the first whirl of the shell, and seems to provide the sternite with some stabilizing stimulus.

Variation in Rotation Direction of the Sinistral Shell

According to the above explanation, crabs should also take position I for the sinistral shell, because it would allow them to perform deep cheliped insertion. Why did they occasionally take position O for the sinistral shell?

For the dextral shell, the crab in position I faces the shell aperture and maintains the main shell body to its left, that is with the left ambulatory legs on the shell body and the right ambulatory legs below, on the substratum, as seen in Fig. 5. In nature, almost all shells are dextral, and crabs attempting to perform cheliped insertion will have a sense of the left legs being higher, or of keeping the shell body to their left. In order to get the same sense for the sinistral shell, they should assume position O. With the sinistral shell, a conflict is evident be-

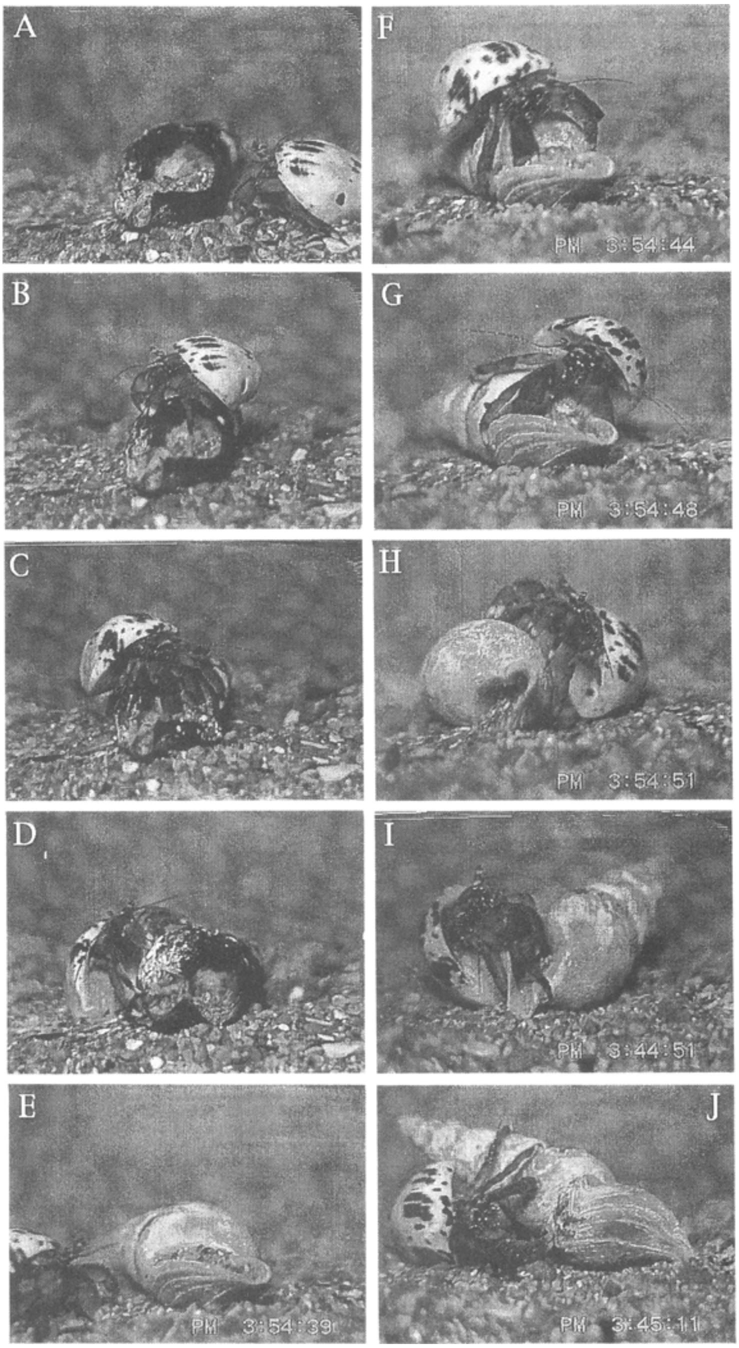

Fig. 4. Examples of the shell rotating behavior for the dextral (A-D) and for the sinistral shell (E-J). The crab approaches the dextral shell from the outer lip side (A). After the first contact with the sand in the shell aperture it moves to the inner lip side (B), from which it inserts the chelipeds into the shell aperture (C). It retreats down to the substratum and begins to push the upper side of the shell for left (adaquate) rotation (D). The crab in E approaches the sinistral shell from the outer lip side, moves to the inner lip side (F), inserts the chelipeds into the shell aperture (G), and rotates the shell adequately for right rotation (H). The crab in I performs the cheliped insertion into the shell aperture of the sinistral shell from position O. It begins to push the upper side of the shell, producing left (inadequate) rotation of the sinistral shell (J).

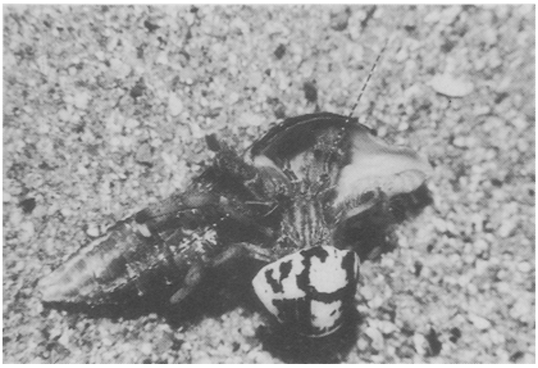

Fig. 5. The crab inserting its cheliped from position I. Crabs can perform deep insertion from this position.

tween the crabs' tendencies to keep the shell body on their left (thus coming to position O) and to receive the assumed stimulus on its cephalothorax sternite (leading to position I). This discrepancy seems to be a cause of the varied positioning of crabs exposed to the sinistral shell.

Shell Rotation by Pushing the Upper Side

Crabs always pushed the upper side of the shell during rotation, regardless of its winding direction or of the position of the crab relative to the shell. One explanation for this behavior may be that hermit crabs can not rotate the shell by pulling the upper side; however, this should probably be discounted. When crabs walk, they "pull" the ground nearer, a movement comparable to shell rotation by pulling. Crabs have also occasionally been observed to rotate the shell by pulling, when they searched for the shell aperture prior to shell interior investigation (personal observation). A switch from pushing or pulling to solely pushing occurs after the location of the shell aperture. Thus, they can rotate the shell by pulling the upper side.

Then why do they always push the upper side of the shell for rotation after location of the shell aperture? This way of shell rotation is suitable for sand discharge by crabs that have a tendency to take position I, and should be attributable to natural selection, or learning during growth in which they have frequent chances for shell changes. For this problem, examinations of the behavior of the crabs reared without any experience of such shells that are filled with sand or other materials are necessary.

Adaptive Behavior

The hermit crab *Pagurus geminus* rotated dextral shells to the left, which is suitable for sand discharge. A similar behavior was observed in *Pagurus bernhardus* (Elwood & Adams 1990). Thus, the behavior of shell rotation to evacuate particles may be ubiquitous for hermit crabs.

The shell rotating behavior, which appeared to require an intellectual ability to relate certain behavior to its result, was revealed to be composed of 2 simple reactions to the shell; locating the shell aperture from the inner lip side (taking position I) and pushing the upper side of the shell. However, what makes the situation more complex is the use of this pushing reaction after the crab located the shell aperture; that is, a switching. Another interesting behavior is that shell rotation is effective for shells filled with sand that may pour out. *Pagurus bernhardus* adopted such activities more frequently when the shell was filled with sand than when it was blocked with a piece of gravel or dental cement (Elwood & Adams 1990).

These activities of hermit crabs, adoption of rotation behavior and switching of rotation direction, may provide us with an impression that they behave with some expectation about the outcome of their behavior, thus having a degree of intellectual ability. Similar seemingly intellectual behavior may be seen in other invertebrates, for example crouching behavior in hunting ants (Masuko 1984). However, analyses of such complicated but adaptive behavior in lower animals may disclose that tactics adopted by them to solve a problem are different from those used by higher animals.

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