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Ecology of the Land Hermit Crab *Coenobita purpureus* on Kikaijima Island II. Breeding behavior, Food, Predator, Orientation and the Environment

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Abstract Breeding behavior and other ecology of *Coenobita purpureus* were investigated on the Kikaijima Island. Copulation and zoea release were observed in the evening during the breeding season in June and July. Two types of copulation postures were confirmed: 1) the male and female crabs leaned out of the shells to embrace each other ventral to ventral, and 2) the male leaned out to attach spermatophores to the female kept withdrawn in the shell using the elongated sperm ducts. Newly landed glaucothoe larvae were found among stranded matter on sandy beaches in the early morning in July. From the footprints made on the sand surface, crab size in shield length was inferred to be about one third of the footprint width. The land hermit crabs fed on dead fish, fruits of *Pandanus* and also fresh flowers. Orientation by moon was proved in the experiment by use of mirror. The effect of recent environmental changes by the human activity on the existence of crabs is discussed.

Keywords Land hermit crab, *Coenobita purpureus,* Copulation, Glaucothoe, Predator, Orientation

Introduction

Previously, I described the breeding site, the breeding season and the migration of the land hermit crab *Coenobita purpureus* Stimpson on the Kikaijima Island (Imafuku 2001). In the present paper, I deal with the breeding behavior, including nocturnal activity, copulation, release of zoeae and landing of glaucothoe larvae, food, predator, orientation by use of the moon, and environmental changes of the habitat of this species.

Breeding Behavior

Observation on the beach

Since aggregation of land hermit crabs to a limited area of the sandy beach at night had been observed by Mr. D. Tanaka on this island (pers. com.), I performed an observation throughout the night on Sakiyama beach on July 9, 1990. This beach was along a small embayment from a large bay, surrounded by high rocky walls of lime stone, as shown in Fig. 1 (for location and landscape, ref. Imafuku 2001).

During the daytime, the land hermit crab, *Coenobita purpureus*, lurked in crevices

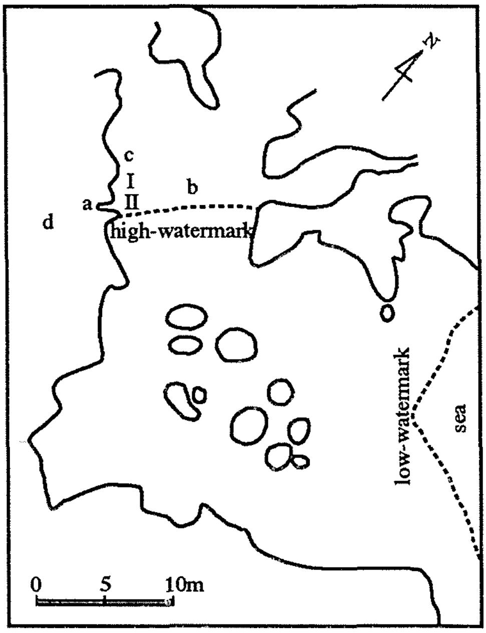

Fig. 1. The coast of Sakiyama. Alphabetical letters: the sampling sites for Table 1. I, II : stations for th survey of the diurnal activity shown in Fig. 2

and under stranded matter with none remaining on the sand surface. When it became dark after dusk to the extent that no objects could be seen with the naked eye, many crabs started to appear, marching in a line from the crevice (a) in Fig. 1 and stopping near the point (b) at the edge of the water. The crabs that followed continued to move and gathered there, coming aside or piling up over the already arrived crabs. Thus, the number of crabs at the edge of the water gradually increased.

When a crab at the edge of the water became washed and submerged by small waves, it rapidly shook its body back and forth. While it pushed out water with withdrawal movements, countless numbers of zoea larvae were emitted from the shell. The crab that had released zoeae came out of the water walking backwards, and then changed its direction to the land. The crab after release moved toward a higher level on the beach. When it became completely dark around 21:00, tremendous numbers of crabs appeared here and there from the surrounding walls, and the beach became heavily crowded with crabs that moved to and from the edge of the water. At that time it was difficult for one to move without stepping on the crabs. The crabs at the edge of the water were wet and roughly covered with sand grains, and thus could be easily identified. Crabs that were returning from the water to the land were frequently captured by other crabs near the rocky wall surrounding the beach. These capturing and captured crabs sometimes separated soon after a struggle, but sometimes stayed still for more than several minutes. During this time, they seem to have copulated, as described later.

Zoea-release behavior was observed from dusk to about 21:00, but was not seen thereafter. However, some crabs were observed to march deeply into the water and to stop there, in contrast to crabs that stopped at the edge of the water to wait for waves to release zoea. Such crabs did not show any body shaking, but returned from the water after a while. This behavior was thought to be "bathing" (Nakasone 1987a). Bathing is said to have such functions as wetting the body to keep the gill from drying out, drinking water, or introducing water into the shell (DeWilde 1973; Page & Willason 1982). Further, it may be preparatory behavior for zoae release, because it occurred a few days prior to genuine release, according to observations made on captive crabs by H. Ikeda in Shirahama, Wakayama.

Numerous crabs covered the sand surface until the next early morning, with several crabs still remaining at around 8:00 when the sun was already high.

Sampling

To study the conditions of crabs found on the beach with respect to breeding, they were sampled from July 9 to 10, 1990, and checked for sex and being ovigerous or not (Tables 1 & 2). Conditions of ovaries were also checked; developed ovaries were orange-colored and could be seen through the thin skin. Crabs lurking in crevices during the daytime were mainly females, and most of them (77%) carried eyed eggs (Table 1, A). Crabs walking on the sand surface at night were composed of fewer males and many ovigerous females (B), and those with wet shells were all females that had mostly developed ovaries without eggs carried on the pleopods (C & D). Thus, crabs with wet shells were thought to have submerged and released larvae. Crabs that captured other crabs at a higher level of the beach were all males (E). Combinations of capturing and captured crabs were pairs composed of males and females, and most of the latter possessed eyed eggs (Table 2). In the previous observation on the beach, crabs captured by other crabs were those that had already released larvae, but in this sampling survey, captured crabs were all females with eggs just before hatching, except for one case (one on the bottom line in Table 2). Thus, captured crabs consisted of those that had already released larvae and those that had not yet released larvae.

Around the site where pairs were formed, there were solitary males and females (Table 1, F). There were many crabs on the rocky wall, and they were males and females (G). Crabs found on the sandy beach and the rocky wall about 7:00 in the next morning consisted of males and females (H & I). These results showed that males and females gathered around the beach, females visited the edge of the water for zoea release, and there were many males near the rocky wall to capture returning females from water or solitary females walking around.

Diurnal activity

To reveal the diurnal fluctuation in the number of crabs appearing on the sand surface, 2 fixed points (I & II in Fig. 1) were selected on the sand surface of the Sakiyama beach, and photographed intermittently from 14:00 on July 6 to 11:00 on the next day in 1990. The numbers of crabs counted on the photos are shown in Fig. 2. Crabs started to

Table 1. The number of the land hermit crab, *Coenobita purpureus*, collected on the coast of Sakiyama on July 9-10, 1990.

						Male	Female	Ovary**		Egg	
Code	Condition	Point*	Day	Time	Total n	(shield length, mm)		immature	mature	non-eyed	eyed***
Daytime											
A	lurking in crevice	a	9	15:20	31	5(4.7-7.0)	26(3.8-6.3)	2	2	2	20
Nighttime											
B	walking on sand	b	9	19:25	30	7(4.4-5.9)	23(3.7-6.8)	0	1	0	22
C	with wet shell	b	9	20:25	28	0	28(3.2-6.5)	0	23	2	1+2
D	with wet shell	b	10	20:00	30	0	30(3.7-7.3)	2	24	0	1+3
E	capturing	c	9	20:55	10	10(4.3-7.2)	0				
F	solitary	c	9	20:40	9	3(5.3-7.3)	6(3.8-6.8)	0	1	0	4+1
G	on rocky wall	d	10	19:20	29	14(4.0-8.5)	15(3.7-8.6)	0	2	0	13
Morning											
H	on sand	c	10	7:10	25	16(4.0-7.1)	6(3.8-4.9)	0	2	1	6
I	on rocky wall	d	10	7:15	30	18(4.2-9.2)	12(3.5-6.2)	1	3	0	8

*ref. Fig. 1. **of the non-ovigerous female. ***females with a few eggs (inferred as after release) shown after "+".

Table 2. Combination of pairs. The size (shield length, mm) and the condition of the female.

Male	Female	Ovigerous	Eyed	Ovary
4.7	5.5	○	○	○
4.7	4.2	○	○	○
5.2	4.3	○	○	○
6.2	4.0	○	○	○
4.2	4.5	○	○	○
5.1	3.7	○	○	○
4.6	3.8	○	○	○
5.2	4.7	○	○	○
7.0	5.1	○	○	○
4.9	5.1	○	○	○
4.3	4.3	△	○	○

Ovigerous: ○ =ovigerous, △ =a few eggs carried.
Eyed: ○ =with eyed eggs. Ovariy: ○ =mature.

appear from 20:00 with a peak at around 24:00, and continued activity during the night-time. The number of crabs decreased toward 7:00 in the next morning. Two examples of photos taken at 17:00 and 22:00 are shown in Figs. 3-1 & 3-2.

Copulation

Pair formation where a crab captured another crab was frequently observed on the beach. Such pairs were found to be combinations of males and females (Table 2). Assuming that such pairs would copulate, I continuously observed pairs until they separated, but could not confirm copulation behavior. Similar unsuccessful observations were also made by a cameraman taking pictures of land hermit crabs on Tokunoshima Island. However, I made an interesting observation with respect to copulation of land hermit crabs of this species, *Coenobita purpureus*, in the present survey.

At about 15:00 on June 9, 1990, 2 large individuals both in the *Turbo* shells leaned out of the shell and embraced each other ventral to ventral aside of a large rock on the Nagara beach. The appearance was the same as copulation by aquatic hermit crabs, and thus, the two were thought to be in copula. They remained in this position for about 20 minutes and then separated. A similar posture has also been observed for the same species, *Coenobita purpureus*, in Okinawa (Nakasone 1987a) and for *C. perlatus* in Enewetok (Page & Willason 1982).

Another type of copulation behavior was also observed. At about 19:00 on June 23, 1994, a middle-sized male crab had captured a small female (7.5 mm in shield length) that remained retreated in the shell, but the male inserted the tip of the extended sexual tube just inside the female shell (Fig. 3-3). The 2 crabs separated after about 1 minute. The female was kept in a plastic case and the ventral surface 4 hours later was found to have white sticky material attached which was thought to be spermatophore. Similar events were observed at night on June 24 and 25, 1994, and July 23, 1996. Especially on June

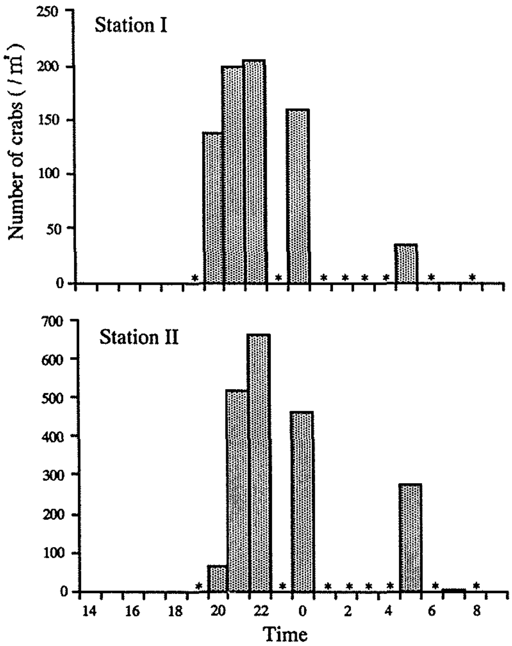

Fig. 2. Individual numbers of the land hermit crab, *Coenobita purpureus*, on the coast of Sakiyama. Positions of Stations I & II are shown in Fig. 1. *: no data.

25, 1994, the male did not release the female even when it was picked up by the observer. The female on that day is shown in Fig. 3-4; spermatophores were attached on the ventral surface of the female and also on the shell aperture. These observations suggest that the pairs observed on the Sakiyama beach were in copula. Copulation by crabs in the shell has not been described previously.

An interesting phenomenon concerning copulation by land hermit crabs is that copulation behavior was performed by females that possessed eggs (Table 2). The same is known for *C. perlatus* in Enewetok (Page & Willason 1982) and *C. purpureus* in Okinawa (Nakasone 1987a). The latter author called this phenomenon "pseudo-copulation". Hermit crabs are different from brachyuran crabs in that the latter can preserve sperm in their body, whereas hermit crabs keep the received spermatophore on the body surface. Such females go into water to shed the developed eggs, which should also wash out the attached material. With respect to copulation of the land hermit crab prior to larval release, it is necessary to examine the effectiveness of this behavior.

Survival time in water

The land hermit crab sometimes entered water to release larvae or bath, and occasionally was washed away by waves to deep water. Frequently, marine hermit crabs in the shallow water were found to carry terrestrial snail shells, which should have been derived from land hermit crabs drowned at larval release. So, I examined how long land hermit

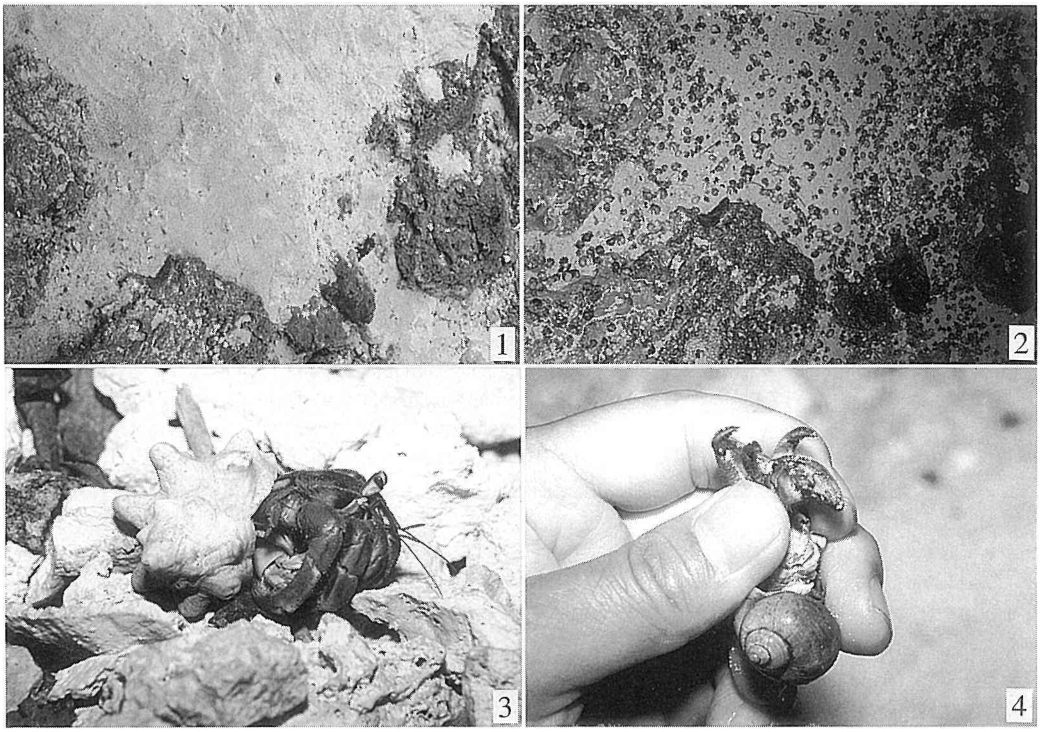

Fig. 3. Daily activity and copulation of the land hermit crab, *Coenobita purpureus*. 1 & 2: The scene of Station II on the Sakiyama coast (ref. Fig. 1) at 17:00 (1) and 22:00 (2) on July 6, 1990. 3: Copulation posture of the male eased out and the female in the shell, with the sexual tube of the former inserted to the shell of the latter (Tekuzuku, June 23, 1994). 4: Sticky white material, probably spermatophres, attached to the ventral surface of the female and to the edge of the shell aperture (Tekuzuku, June 25, 1994).

crabs could survive in water.

Five cabs were kept submerged in water in a 500 ml plastic bottle for 25 hours on July 15-17, 1995. During that period, water was exchanged intermittently. Water temperature fluctuated 27-30°C. The result is shown in Table 3.

The crabs became weak and walked slowly 8 hours after the initiation of submergence, but soon showed recovery when the water was exchanged. At the 16th hour the first crab died. Four of the 5 crabs had died at the 25th hour when the experiment was ended. Thus, it could be concluded that the crabs can survive at least half a day as long as the water is fresh. This result is rather different from that obtained for coconut crabs, *Birgus*; the latter species is said to survive only for a few hours (ref. McMahon & Burggren 1988). It is probable that the thick inner surface of the gill cover developed like a "lung" makes it difficult for the coconut crab to breathe in water. On the other hand, the land hermit crabs are said to respirate by the gills with the aid of water kept in the shell (ref. McMahon & Burggren 1988).

Table 3. Survival time of the land hermit crab in sea water.

Day	Time	Temp. (°C)	Condition
July 15	23:18		5 crabs submerged
July 16	7:40	28.0	all moved slowly
			1 ovigerous female out of the shell
	8:12	27.5	water exchanged
			the naked crab entered the shell after a while
	12:20	29.0	1 crab out of the shell
			water exchanged
	15:21	30.5	1 ovigerous female (5.0 mm in SL) died
			1 male (6.1 mm) in syncope
			water exchanged
			the male recovered after a while
	17:15	31.5	1 ovigerous female (5.4 mm) died
			water exchanged
July 17	0:20	27.8	2 females (6.9 mm ovigerous, 7.5mm) died
			Closed

SL=shield length

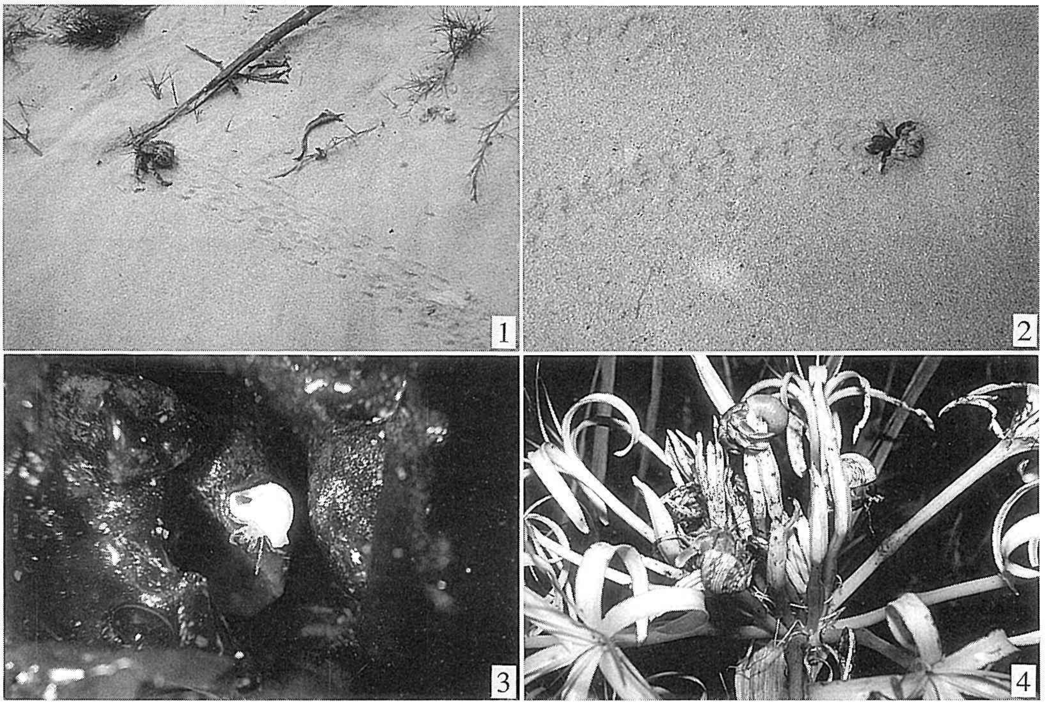

Fig. 4. Footprints, a glaucothoe and adult crabs on plants. 1: Footprints of the land hermit crab composed of a combination of short parallel lines (Sugira, July 23, 1996). 2: The crab walking backward on a slope (Sugira, July 23, 1996). 3: A glaucothoe larva on the stranded algae (Nagara, July 20, 1996). 4: Crabs devouring the petals of the *Crinum* flower (Somani, June 29, 1995).

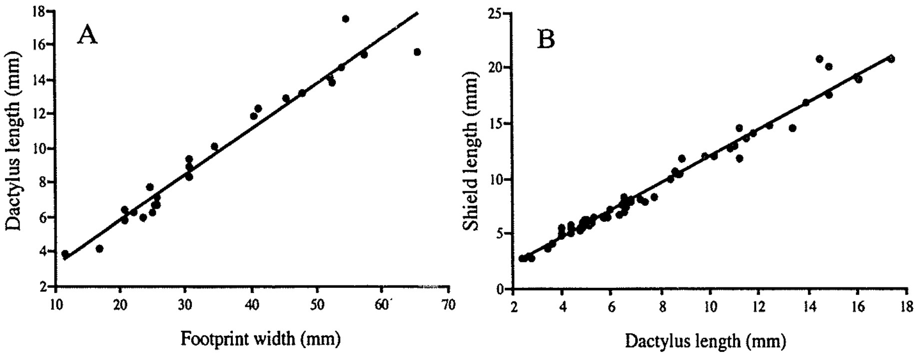

Fig. 5. The relation between the dactylus length and the footprint width (A) and between the shield length and the dactylus length (B).

Footprints

Land hermit crabs appeared on the sandy beach for larval release or other activities at night. They left footprints after such activities. Thus, we can confirm their nocturnal activities by daytime observations on footprints made on the substratum, as shown in Fig. 4-1. Further, we can obtain information from the footprints about the size of the crab and the direction to which it should have moved.

On July 9, 1994, crabs were allowed to walk on the sand substratum of the Sugira beach. The footprint was a shape that was composed of some nearly parallel short lines made by the legs on both sides. One end of the 2 outermost lines was nearer than the other ends, and the wider end was the direction to which the crab proceeded. The relation between the widest width of the 2 lines and the dactylus length of the 3rd left leg is shown in Fig. 5-A. The equation is:

$$[\text{dactylus length of the 3rd left leg}] = 0.26 \times [\text{footprint width}] + 0.56 \text{ mm}$$

The relation between the dactylus length and the shield length is shown in Fig. 5-B, with the following equation:

$$[\text{shield length}] = 1.23 \times [\text{dactylus length}] - 0.36 \text{ mm}$$

Thus,

$$[\text{shield length}] = 0.32 \times [\text{footprint width}] + 0.33 \text{ mm}$$

Briefly, the shield length is about one third of the footprint width.

Interestingly, crabs walked backwards, when it climbed a sandy slope (Fig. 4-2). Such backward walking was also observed when they came out of the water after larval release, and also found in the video images on a TV screen of aquatic species, *Pagurus ochotensis*, attempting to escape from the underwater camera. These observations suggest that retreating is less resistant, probably because the pointed shell apex, instead of the opened shell aperture, is faced to the moving direction. The validity of this explanation should be examined by measuring the resistance with a shell pulled to the shell-apex direction and the shell-aperture direction.

Landing by gaucothoe

Zoea larvae of the land hermit crab, *Coenobita purpureus,* develop into glaucothoe larvae within 17 days at fastest (Nakasone 1987b). According to Mr. Keio Ôi of the Kasari Primary School in Amami-Ôshima, newly landed graucothoe were found in the morning. So, I attempted to find newly landing larvae from early morning on Kikaijima Island.

Ten individuals of glaucothoe larvae in tiny shells (1.8-2.5 mm in shell width, 2.5-3.5 mm in shell height) were found on the beach of Isaneku in an observation from 5:40 to 7:00 on July 26, 1994. At 7:30 on 27, 5 individuals were found on the same beach. All of them were found from cluster of algae stranded around the high-water mark. I attempted to find on the same beach from 6:35 to 7:05 on July 20, 1996, in vein. However, 1 individual was found from the stranded algae on the beach of Nagara at 7:27 on the same day (Fig. 4-3).

Food

Kinds of food

In the present investigation, the hermit crabs, *Coenobita purpureus*, were observed to gather to fish and plants. In the evening on June 20, 1995, the surgeonfish, *Acanthurus pyroferus* Kittlitz, bought at a store was put on the beach of Isaneku, and then several crabs gathered to it within several minutes. After a few ten minutes, the fish was covered with a crowd of numerous crabs. Such a crowd was seen until the next morning.

Yellow flowers of *Hibiscus tiliaceus* L. were commonly seen around the beach where crabs bred. Some crabs were observed to devour a dropped half-withered flower of this species on the Isaneku beach at night on July 29, 1995. Further, when I put a fruit of the screw pine, *Pandanus odoratissimus* L., known as a favorite of hermit crabs, on the sand surface aside a tree on the same beach at 19:30 on July 23, 1996, soon many crabs gathered. Crabs were also found to climb plants to devour flowers of *Scaevola frutesches* Krause and *Crinum asiaticum* L. Especially on the Somani beach, a lot of crabs were observed on the flowers of *Crinum* planted along the promenade (Fig. 4-4), and some plants had become bald at the top.

Similar to the crabs on Kikaijima Island, the land hermit crabs in the South Pacific and Caribbean Sea have been reported to feed on flowers and fruits, and also dead fish and turtles (ref. Page & Willason 1983). *Coenobita perlatus* in Enewetok Atoll have been observed to clear out a fallen tern to feather and bones within a night. Further, isolation of deposited meat from the activity of land hermit crabs through settlement of wire nets induced generation of maggots, evidenced the activity of hermit crabs as "cleaners" (Page & Willason 1983). An interesting study about the feeding behavior of land hermit crabs was made by Thacker (1996) who revealed that crabs showed a tendency to avoid food that they had recently eaten, and as a result, they fed on various types of foods.

Possibility of pollination by crabs

From the fact that land hermit crabs frequently climbed up and visited the *Crinum* flower, it was expected that they might play a role in pollinating of this flower. This was examined in 1995. Twenty five stocks of *Crinum asiaticus* were planted along a straight promenade on the Somani coast. For these stocks, I examined whether climbed crabs frequently changed one stock to another.

From 20:30 to 23:30 on June 27, 10 crabs on the flower were marked. On the next day, the flowers were checked from 22:30 to 23:30. Out of 28 crabs found, 3 possessed marks and they were all from the same stock as found in the previous day. The newly found 25 individuals were marked and checked from 22:45 to 23: 15 on the next day of June 29. On this day, 59 crabs were found with 5 marked individuals. Out of these marked crabs, 3 were from the same stock as the previous day, and 1 from the same sock as that obtained 2 days before, and 1 was the crab that was marked on the next stock on the previous day.

As a whole, 8 crabs marked on the flower were recaptured and only 1 was found from a different stock. Therefore, it is not likely that land hermit crabs are contributing to pollination of the *Crinum* flowers. However, the present observation was limited to a short period of a day, and thus, it is probable that crabs might have climbed more frequently at different times from the present survey. Furthermore, the *Crinum* plant possesses a few stalks in a single stock, and crabs may have moved between flowers of different stalks. This plant has plural numbers of flowers on a single stalk, and thus, crabs may have come and gone among different flowers. Such possibilities should be examined in future.

In the present survey, some insects and other animals were found from flowers; 2 moths, 2 mantises, 3 tettigoniid katydids and 3 geckos. These animals are candidates for pollinators of this plant. However, the most frequently observed animal was the hermit crab. The contribution of the land hermit crab to *Crinum* flowers needs to be examined by comparing the fruition rates between stocks with an isolating fence at the base and those without.

Flower visiting individuals

In the previous survey, crabs obtained from flowers were small individuals of 2-3 cm in shell width. A survey was made for size and sex of the flower-visiting crabs in the same place as the above survey at about 21:30 on June 30, 1995. A total of 52 males (5.6-11.4 mm in shield length) and 3 females (5.3-7.9 mm) were collected from the *Crinum* flower. Females were all ovigerous. This bias toward males may give an impression that males prefer flowers. This conclusion, however, requires further survey of the sex ratio of crabs in the vicinity of this plant. There may be a possibility that males are more abundant in areas far from the edge of the water where the females gather to breed, as expected by the results shown in Table 1, and also as described by Yamaguchi (1938).

Predator

Predator of larvae

When I observed release of zoea by females on the beach of Nagara at night on July 12, 1995, I found some small individuals of the mullet, *Lisa macrolepis* (Andrew Smith), frequently gathering to the site. At the moment of release, the fish rushed at a mass of zoeae just emitted. Clearly the larvae were subjected to predation by the fish.

A similar scene was observed on the beach of Isaneku at night on July 22, 1995. Underwater video recordings revealed some mullets swimming just in front of the camera, busily opening and closing the mouth, through countless numbers of larvae suspended. Further, small shrimps, *Palaemon* sp., frequently raised both of the chelipeds alternately in water and brought them to the mouth. Two species of gobiid fish popped up as if they rushed at larvae.

Predator of adult crabs

According to the observations by Mr. Yonezo Ikeda in Iriomotejima Island, Okinawa, land hermit crabs on that island were eaten by the ruddy kingfisher, *Halcyon coromanda* (Latham). This bird violently hit the crab against a large stone or an iron tube to break the shell. As the ruddy kingfisher is known in Kiakijima Island also, I examined whether it was a predator of the hermit crab.

A basin (26 cm in diameter, 10 cm high) containing some crabs was put aside the spring of Tekuzuku where the kingfisher was occasionally observed to visit and bathe. A large stone was also put next to the basin for the bird to use it to break the shells.

At 17:30 on September 26, 1995, 3 hermit crabs were put in the basin, and 1 crab disappeared by 9:30 the next morning. The 2 other crabs disappeared by 12:30 on September 27. For disappearance of these crabs, the activity of crows was suspected, because some crows were frequently observed on the tree, *Ficus macrocarpa* L., hanging over the spring.

At 12:00 on September 28, 5 crabs were put in the basin, and the site was continuously observed from a distance. A crow appeared on the *Ficus* tree aside the spring at 12:36 and flew down to the site at 12:38. When the crow flew away from the site at 12:40, only 1 crab remained inside the basin. I continuously observed the site until 17:40, but no change occurred.

In the periods of July 1-4 and 20-23, 1996, I set a video camera at the site in the morning and evening for 4 hours a day. Some crows appeared from 7:42 to 7:48 on July 4. They picked up the crabs out of the basin and sometimes dropped them. At that time, 2 crabs were taken away. Again, 2 others were taken away from 9:49 to 11:10. As a crow was found to tilt the basin by stepping on the rim and throwing the crabs out, I put a weight for diving or a stone in it. At 17:32 on July 20, 2 naked crabs and 2 shelled crabs were set, and the ruddy kingfisher appeared 4 times in a period of 10 minutes from 17:48 to 17: 58. At every instance, it took away 1 crab (Fig. 6-1). The bird did not discriminate shelled crabs from naked crabs. It did not break the shells.

At 10:35 on July 22, I observed an interesting behavior by a crow. The crow picked up one crab, and put it on the concrete surface aside the basin. Then, it put another crab aside the first one. When the first crab started to move, the crow pinched it lest the first should move (Fig. 6-2), which made an impression that the crow attempted to arrange crabs on the concrete surface. Such behavior seemed to have no fixed purpose, but to suggest that the crow was simply playing with them. Finally, the crows took one crab away and swallowed another.

In these observations, the kingfisher took away a crab whenever it appeared. Thus, it probably utilized it as food, though it did not use a stone to break the shells. The bird seemed to do this at other places. A crow was seen swallowing a crab once, and taking some crabs away. The destiny of the latter was unknown. However, it is not unlikely that crows actively take crabs as food, because they frequently showed seemingly play behavior on them.

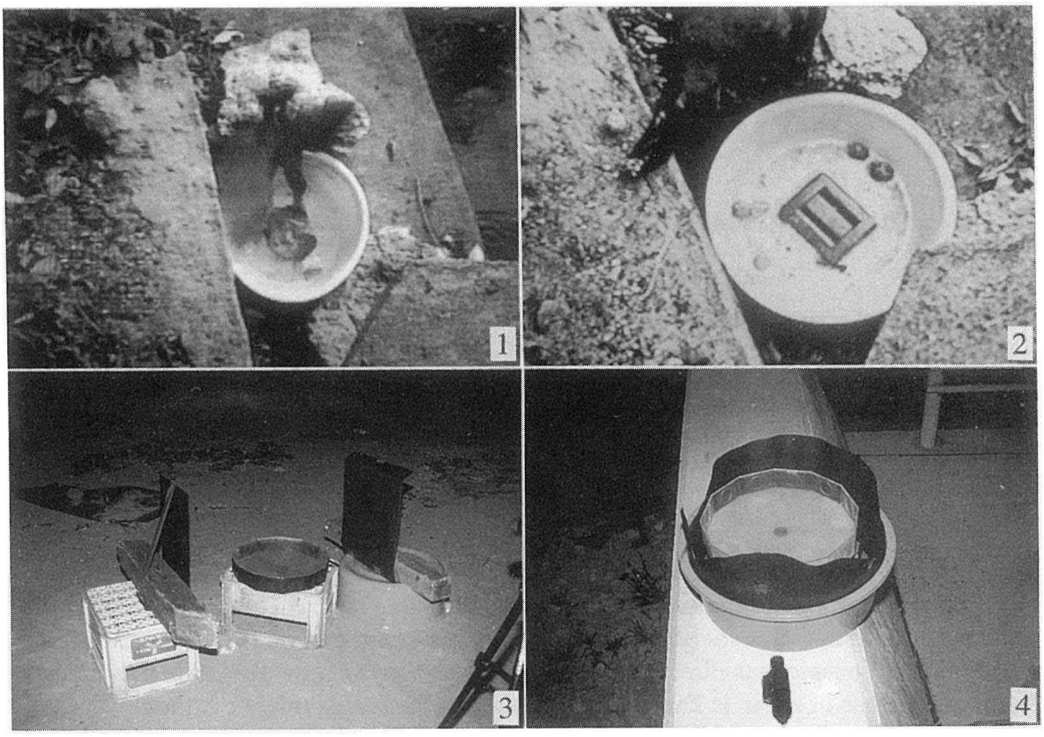

Fig. 6. Experiments on the predator and the orientation of the land hermit crab. 1: The moment of the ruddy kingfisher capturing a crab in the basin (Tekuzuku, July 20, 1996). 2: The crow arranging crabs on the concrete; the pinched crab is the first one and the second crab just above it (Tekuzuku, July 22, 1996). 3: The experimental system for the moon orientation; the 12-gonal vessel at the center was shaded with a vertical black board on the right and illuminated by the moon on the mirror of the left side (Isaneku, July 24, 1994). 4: The system for the silhouette orientation; the vessel was surrounded by walls made of black paper imitating the natural landscape (Isaneku, July 27, 1994).

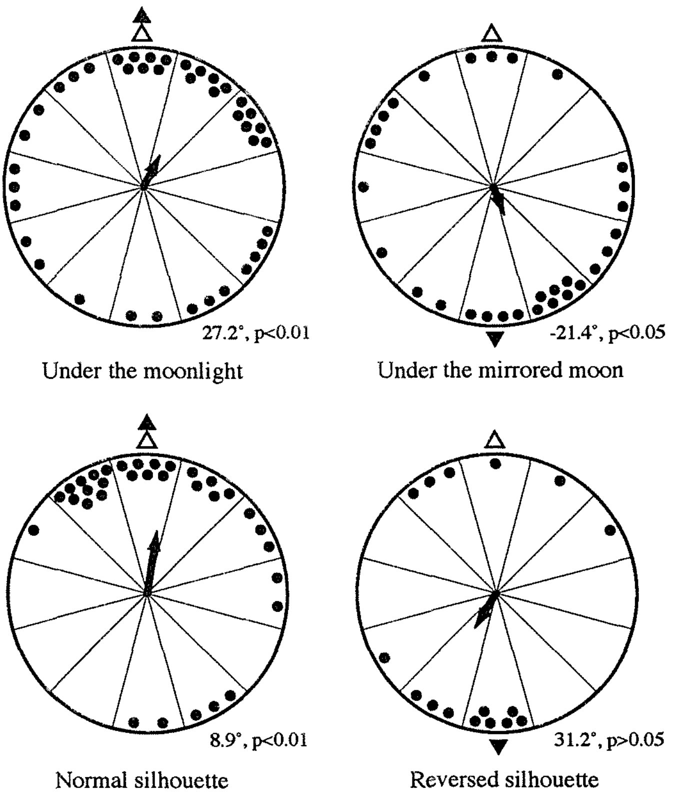

Fig. 7. Results of orientation experiments. Black dots in each circle show directions taken by the crab. The arrow at the center indicates an averaged direction with the length expressing a strength of tendency. The open and solid triangles outside each circle indicate, respectively, the direction taken by the crab on the beach and that expected in the vessel if the crab oriented with the assumed cue. Numbers outside the circle are angles of the averaged direction and p-values by V-test (ref. Zar 1984).

Orientation

Orientation by the moon

Land hermit crabs appeared from crevices and among the bush to visit the edge of the water and returned there at night. In darkness, they migrated on the flat sand surface without any conspicuous directional cues. How do they find the direction they should move? Release of zoeae is known to occur around the spring tide, or at the time of full moon or new moon (Nakasone 1987a). Especially at the time of full moon, the moon stays in the sky throughout the night, rising in the east at dusk, illuminating the sandy beach the whole night, and sinking in the west at dawn. Thus, crabs are thought to use the moon as a cue for orientation.

A 12-gonal plastic vessel (40 cm in diameter, 6 cm high) was settled at the center of the sandy beach under moonlight illumination, and the proceeding direction of a crab put at the center of the vessel was recorded. The sides and the ceiling (lid) of the vessel was transparent, and the bottom opaque milky white. As it was known from a preliminary test that the direction to which the crab moved in the vessel largely depended on the direction to which it was settled by the experimenter, the test crab was dropped in the shallow hollow made of a film case that was attached at the center of the bottom floor, and allowed to rise by itself. The depth of the case was adjusted by poring sand in it.

The crab that walked straight in a direction at least 20 cm on the beach was used for the test. The observation of walking and the collection of crabs were made with naked eyes or by use of a torch lamp made dim with an opaque cover. Immediately after the test crab was dropped in the hollow of the vessel, the vessel was closed with a lid and observed through a noctovision (Litton, M-911A). The observer located in the direction of hills, not to be seen from the vessel. A direction on the beach or in the vessel was expressed with a number, allocated to each of 12 sectors with 0 to the seaward, 6 to the landward, 9 to the left in facing the sea, and so on. The proceeding direction in the vessel was determined when the crab reached a sidewall. Crabs were used once. For the test of orientation by the moonlight, the vessel was shaded with a vertically held rectangular board and illuminated with the mirrored moon from the opposite direction (Fig. 6-3). The experiment was carried out on the Isaneku beach on July 22-25, 1994.

The results are summarized in Fig. 7. The direction taken by the crab on the beach was reproduced in the test vessel, and the direction taken in the vessel was reversed when the moon was reflected with a mirror.

Moon orientation was shown in a classical experiment for sand hoppers by Papi & Pardi (1959), and was supported by Enright (1961). For animals to orient by use of the moon, they should compensate the movement of the moon in time, and this ability was proved in the sand hopper. Such ability was not examined in the present hermit crab.

Orientation by silhouette

The land hermit crab was also active around new moon when the moon did not rise at night. At that time, they could not use the moon for orientation. When I tried to see in a moonless night, I could discriminate a hill or trees from the background sky. If the hermit crab had a similar keenness of sight, then they could orient even in the moonless night. So, I made a silhouette model imitating the natural landscape such as hills and trees with black thick paper, and examined whether the crabs could perform orientation using the silhouette.

The test vessel, used in the above experiment, was settled at the center of a large basin (52 cm in diameter), adjusting the level of the vessel floor to the rim of the basin, and the silhouette model was attached along the rim of the basin. The test was carried out on the top of a concrete breakwater which was the highest point of the beach, thus without interference by the natural landscape (Fig. 6-4). The basic methods were the same as the above test for the moon orientation. In this experiment, crabs were tested when the silhouette was settled just in the same direction as the natural one, and also in the 180° reversed direction. The observation was made with noctovision through a small hole made on the hill of the imitation model. The experiment was carried out on the beach of

Isaneku on July 27, 1994, and June 29, in 1995.

The results are shown in Fig. 7. The hermit crab could orient when the silhouette was positioned in the same direction as the natural one. However, the result was insignificant when the silhouette was reversed, though many crabs tended to move in the expected direction. The insignificant result seems due to shortage of test numbers. There is an experiment that indicates the orientation by use of geographical sight for diurnal sand hoppers (Ugolini *et al.* 1998). However, there seems to be no such experiment for nocturnal animals, except for the present hermit crab. In that sense, it is necessary to repeat this experiment in the hermit crabs, along with examination of the threshold of light sensitivity in this animal.

Change in the environment

Adults of land hermit crabs live on land, whereas their larvae develop in the sea. Thus, they should cross the coast twice in their lifetime; when they were released into water as zoea larvae, and when they land as glaucothoe larvae. Therefore, destruction and

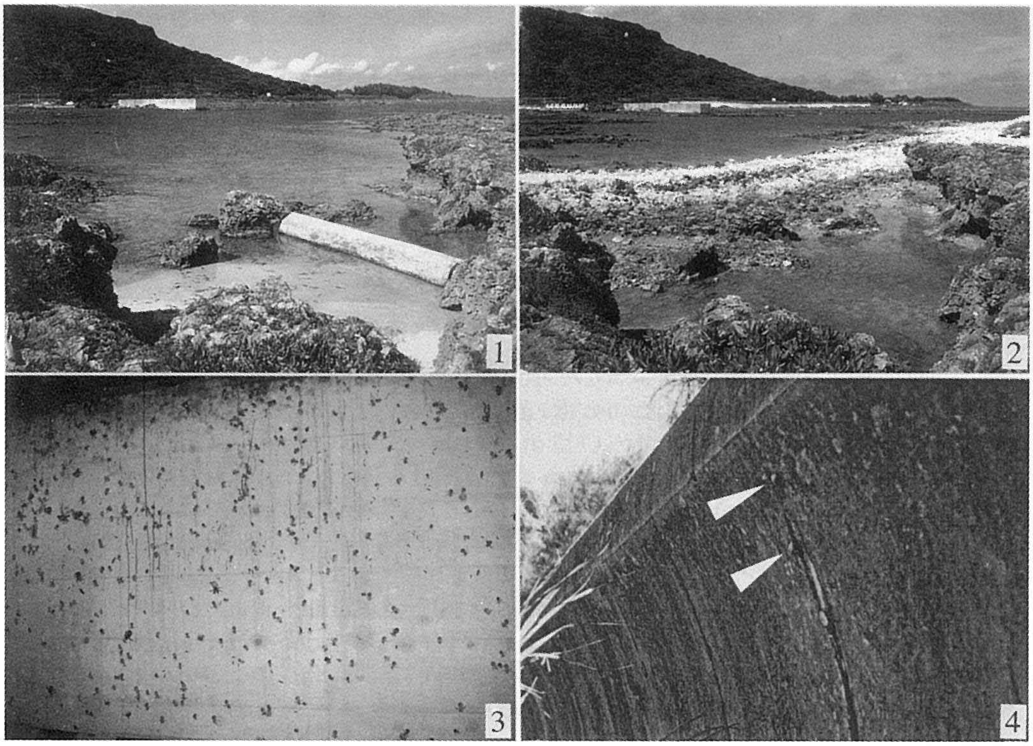

Fig. 8. Conditions of the Sakiyama coast and crabs on the modified coast. 1 & 2: Photos of the Sakiyama coast taken on July 22, 1990, (1) and on July 19, 1996, (2); a pass made of mud and sand has been constructed over the beach in 1996. 3: Crabs crowding on the vertical concrete surface on the Tekuzuku coast (July 15, 1995). 4: Some crabs walking down the vertical surface of the breakwater of the Keraji coast (shown with white triangles, July 22, 1996).

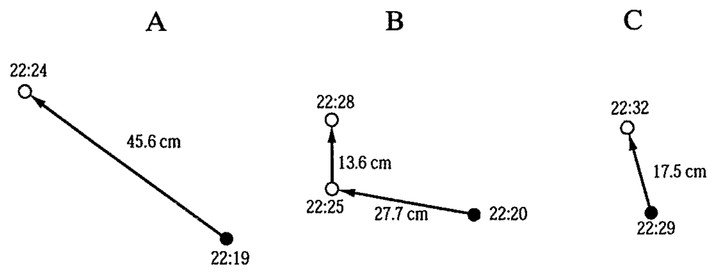

Fig. 9. Migration of 3 land hermit crabs (A, B & C) on the vertical concrete surface.

modification of the coast by human activities should impact on their survival.

In the period of the present survey, the coast was largely modified in Sakiyama and Tekuzuku. Ports and breakwaters had been constructed in Somachi and Keraji before the present study was initiated. The situation of these coasts is described here.

Sakiyama

Countless numbers of hermit crabs covered the sand surface of the Sakiyama beach in July 1990 when I first visited this place. The breeding site on this beach where zoea release had been made (Fig. 8-1) was covered with earth and sand to make a pass for breakwater construction from 1991 to 1992 (Fig. 8-2). When I visited there in the breeding season of 1995 and 1996, some crabs were found hiding in crevices of the rocky wall in the daytime and releasing larvae at the edge of water that was isolated from the open sea by the pass newly made at night. Clearly the number of crabs was extremely decreased. A part of crabs were also found to breed on the open sea side.

As the water level of this tide pool was changing in parallel to that outside, the water in pool was thought to connect to the open water through spaces of stones and mud under the pass. It is necessary to examine whether the larvae can metamorphose to advanced stages within the pool, whether they can pass into the open water, or whether they have to die in the confined pool before landing.

Tekuzuku

Many crabs were breeding on this coast in 1990 when I initiated the present study, but

Table 4. Walking speed of the land hermit crab on the concrete, sand and rock surface.

	Concrete			Sand			Rock	
#	Time*	Speed**	#	Time*	Speed**	#	Time*	Speed**
A	5 min	9.2	E	14 sec	64.3	H	7 sec	102.9
B	8 min	5.2	F	11 sec	81.8	I	5 sec	180.0
C	3 min	5.8	G	16 sec	56.3	J	13 sec	55.7
D	11 min	0						

*sampling time. **cm/min.

in 1994-1995 the breeding site was placed under the new concrete port. In the breeding season of 1995, a lot of crabs walked here and there on the port where the breeding site was located. A part of the crabs attempted to climb down on the vertical surface of concrete toward the edge of the water (Fig. 8-3). Other crabs that came from a hill directly entered into water to release larvae at a site different from the previous site. It was thought that the concrete surface was difficult for them to walk. They attempted to move by inserting the tip of the leg into a tiny hole made on the concrete surface. I compared the walking speed between on the concrete surface and the ordinary beach surface (Fig. 9 & Table 4). The walking speed was 4.0 cm/min on average on the vertical concrete surface, whereas it was 90.2 cm/min on the horizontal coast surface. Thus, it took time more than 20 times to walk on the vertical surface. Clearly, a concrete surface largely limited their activity.

Not always a walking speed, but other activities also should be affected by modification of the breeding site which had been utilized for many generations. It is necessary to trace whether the population there will continue to survive in the future or soon be led to extinction.

Somachi

On this beach, a port was constructed in 1990, and many crabs were observed to crowd over the road aside the port just after construction, according to the native people. When I visited the site on July 20, 1996, some crabs were found walking on the asphalt road and some clinging to the vertical surface of the concrete construction to release larvae at the water level.

Keraji

On the Keraji beach, a long breakwater about 2 m high had been constructed. The breakwater divided the landside and the seaside. Some crabs were observed to release larvae at the edge of the water on July 20, 1996. It was unclear whether they came from the landside of the breakwater crossing over it or from a narrow front area. However, I observed some crabs were crossing over it in the daytime on July 21 and 22, 1996 (Fig. 8-4). Thus, at least a part of the crabs came from the landside. The breakwater slightly concaved on the seaside surface, and thus, to cross over it crabs should walk down on this side as if they hung from the surface, especially near the top of it. Interestingly, they selected to walk on a narrow asphalt line between the concrete plates of the breakwater.

In the 4 beaches described above, some crabs were observed to breed even though under the influence of human activity. It was clear that the number of crabs had decreased markedly from the previous condition in 1990. Thus, no modification of environment is clearly preferable for them. In order to coexist with the land hermit crab, we should be careful when building a construction. If inevitable, we should consider, for example, to select a place outside their breeding site, or to make the construction with blocks on which they could easily climb over or a construction containing holes at the base through which they can pass. Such devices should be useful not only for the land hermit crab but also for such other crabs as saramids that come and go between the sea and land. Prior to making constructions on the beach, we should know what animals live there, and how the site is utilized, by survey for over a whole year. After that, we should consider the place and type that affects their lives least.

Kikaijima Island is rich in nature from mountains to the sea. Such a fact seems to yield more crabs than the neighboring Amami-Ôshima (ref. Zeze & Suzuki 1986).

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