Ethology 100, 242—252 (1995)
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ISSN 0179-1613

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Homing in the Mangrove Swimming Crab *Thalamita crenata* (Decapoda: Portunidae)

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CANNICCI, S., DAHDOUH-GUEBAS, F., ANYONA, D. & VANNINI, M. 1995: Homing in the mangrove swimming crab *Thalamita crenata* (Decapoda: Portunidae). Ethology 100, 242—252

Abstract

On the Kenyan coast, *Thalamita crenata* confines itself to a defined system of crevices and forages, swimming in a few cm of water, within a radius of about 5 m from its shelter. A field study was designed to analyse this crab's ability to find its shelter after being moved away from it.

Crabs were displaced, being kept under water, with full vision of the sky and landscape and released 5 m away from their refuges, at a maximum depth of 50 cm. They were able to return to their shelters within 1 h and followed initial directions which were well orientated towards home. *T. crenata* was still well orientated and successful in returning home during nocturnal displacements and even after trials in which the landscape was altered. Only blind crabs were neither initially orientated towards home nor successful in returning within two tidal cycles of their release.

The hypothesis that this swimming crab could use orientating information obtained during the outward displacement was then tested. Specimens were dislocated following a non-linear outward path, without vision of the surrounding landscape; other crabs were carried to a false release point and then carried in a closed container to the actual release point. Finally, three kinds of detour experiments were performed. In all these trials the directions chosen by the crabs were still clustered around the home direction and homing success was again high.

These results exclude homing mechanisms based on random search strategies or on egocentric mechanisms, such as path integration. The most probable hypothesis is that *T. crenata* organizes some visual cues in a map-like arrangement and, detecting these cues from any release point within its home range, uses this map to return home.

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Introduction

Many decapods living on the substratum prove to be faithful to a defined area to which they restrict their search for food and in which they find one or a few known shelters where they hide during their resting phases. Like the social and non-social insects that adopt this kind of spatial strategy, many of the central-place foraging decapods show good homing ability.

Unfortunately, in spite of the great quantity of research done to explain the homing ability of insects (WEHNER & WEHNER 1990; WEHNER 1992; UGOLINI & CANNICCI 1995), only a few experimental data are available for an understanding of the mechanisms involved in the homing capability of decapods (HERNNKIND 1983; WEHNER 1992).

Foraging ants and bees are known to rely on two kinds of orientation mechanisms to find their way back to the nest: an egocentric frame of reference, obtained by integrating distances and directions taken during the outward journey (WEHNER & WEHNER 1990) is supported by a geocentric system of navigation. The latter orientation system is actually a group of mechanisms that can be based on the storage of visual landmarks (CARTWRIGHT & COLLET 1983) or on chemical signposts (WEHNER 1992). On the other hand, the hypothesis that insects can use a cognitive map of their familiar area to find their nest (GOULD 1986) is no longer supported by conclusive evidence (WEHNER & MENZEL 1990; DYER 1991).

Information on homing mechanisms in decapods is more scattered and so these mechanisms are difficult to explain. Visual cues proved to be important in the homing of terrestrial species. LINSENMAIR (1967), for *Ocypode saratan*, and HUGHES (1966), for *O. ceratophthalmus*, showed that, to locate their burrows after daytime excursions, these ghost crabs rely on relevant visual cues situated near their refuges or actively built by the crab itself, such as the sand cones of *O. saratan*. Also the intertidal species *Eriphia smithi*, when released 25 m away from its refuge, was able to return home only if allowed to see the sky and landscape (VANNINI & GHERARDI 1989), leading one to infer that visual cues were crucial for its homing performance.

Other decapods give the impression of having a perfect knowledge of their position in space. Both the spiny lobster *Panulirus argus* (HERNNKIND et al. 1975; HERNNKIND & MCLEAN 1971) and the lobster *Homarus americanus* (KARNOFSKY et al. 1989), which perform nocturnal foraging excursions within a 200-m radius, can rapidly return to their den from any point in this area. A high level of knowledge about their familiar area was shown also by males of *Inachus phalangium*, a crab commensal on sea anemones (DIESEL 1986). During the reproductive season, they patrol a defined area, moving only among the sea anemones where females that are ready to spawn hide.

Recently a field study carried out in a Kenyan mangrove swamp demonstrated that the portunid crab *Thalamita crenata* H. Milne Edwards confines its activity within a familiar area with a radius of about 5 m and is faithful to a well-defined number of known refuges (VEZZOSI et al., unpubl. data). A field study was carried out to test the homing ability of this crab, both in its own familiar area and outside it, and, if any homing behaviour could be found, to investigate which kind of orientation mechanisms might be involved.

Methods

Study Area and Tagging Method

The field work was carried out in Mida Creek, a mangrove creek 20 km south of Malindi on the Kenyan coast, during Oct.—Nov. 1992, Jul.—Aug. 1993 and Jul.—Aug. 1994.

Thalamita crenata inhabits the intertidal flat (a fossil reef) in front of the mangroves, amongst which it swims in search of food during ebb and flow tides (VEZZOSI et al. 1995). In the crevices of this fossil madreporic plateau, the water remains in a permanent system of tidal pools where a large population of *T. crenata* can hide waiting for the flow tide. The platform area with the maximum number of crevices exploited by *T. crenata* was chosen and a 40 × 40-m grid (composed of 100 squares, 4 × 4 m each) was traced using nylon and wooden poles.

A total of 500 crabs (150 in 1992, 200 in 1993 and 150 in 1994) were captured, their carapace length and sex were recorded, and then they were individually tagged by glueing to the cardiac region of the carapace a 30 cm red wire ending with a numbered tag. This tagging method allowed us to locate the crabs during surveys made at low tide, when they were sheltering in their crevices. Inhabited shelters were also marked with wooden poles (20 cm long) and flags.

All experiments were performed using crabs that proved to be faithful, for at least 10 d, to no more than three refuges situated within a 2 × 2-m area.

Displacement Experiments

Control tests. The first group of experiments was designed to test the ability of *T. crenata* to return home after a passive displacement performed with vision of the sky and the surrounding landscape. When the crab was emerging from its refuge, i.e. at the beginning of a flow or ebb tide, it was held by means of the attached wire and towed, always underwater, to a point about 5—6 m away. After release, an observer, situated about 3 m away from the crab, followed its movements and recorded on a map the overall path that the crab followed. Release points were randomly distributed in space.

All crabs that did not reach their goal stopped anyway after about 50—60 min from the time of release. After this time span, either no water was left on the reef or the water level reached about 50 cm. In either case, all *T. crenata* rapidly hid themselves in any kind of crevice (VEZZOSI et al. 1995). Seventeen of these trials were performed during daytime.

Nocturnal tests. A total of 18 trials (six at full moon, six at half moon and six at new moon) were carried out at night, using the same technique and adding a Starlite (photo-chemical light for fishing) to the crab's tag to better follow it.

Landscape modification tests. The landscape perceived by the crab was altered during both the displacement and the homeward journey. In 13 trials, a piece of cloth 8 m long and 2 m high was placed between the crabs and the mangroves, before the crabs were displaced as described above.

Blind crabs. Before the displacement, two pieces of dark rubber were glued to the orbits of 16 crabs, care being taken not to damage the antennae.

The next group of experiments was designed to test whether the crabs were able to obtain some kind of directional information en route and to rely on such information during the homeward journey.

Non-linear displacements in an open container. Sixteen crabs were kept for a few min in an open bucket and then, still in the bucket, were carried to the release point along a convoluted path. They were thus not allowed to obtain any kind of inertial or optokinetic information during the displacement.

False displacement tests. A false displacement method, as used by UGOLINI (1987) for paper wasps, was applied to 19 crabs. The crabs were displaced with the control technique, but once arrived at the 'false' release point they were carried back home in a closed bucket, and moved in a direction orthogonal to the first one to the 'true' release point. These crabs could visually acquire information about the home direction only during the false displacement and then, if they relied on the en-route information, they should have followed a wrong direction to return home.

Detour displacements with vision of the sky and landscape. Some displacements were performed with the control procedure but following a U-shaped path to show whether this procedure could affect the initial direction followed by the specimens (n = 20).

Detour displacements with vision of sky and landscape only in the last one-third of the path. Another 19 crabs were kept in a closed bucket for the first two-thirds of the displacement route and were able to see the sky and landscape only in its final third.

Detour displacements in the dark. Eighteen crabs were kept in closed containers that were rotated on their main axis during the outward path.

Displacements to longer distances. By the control procedure, 21 and 16 crabs were displaced to points situated 20 and 50 m, respectively, from their shelters. Only the crabs released at 20 m from home started to move during the minutes that followed the displacement. The crabs in the other experimental group just hid themselves in the sand. However, in these experiments, it was not possible to choose at random the directions of the displacements, as in the above trials, and the experimenters needed to maintain directions parallel to the coast.

Data Analysis

In all displacement trials the crabs were considered to have returned home either if they went back to the capture site or if they went to the hole in which they had been recorded in the majority of the surveys previously conducted. Moreover, the crabs that did not immediately succeed in returning were divided into two groups: those found back in their hole during the surveys performed on the day following the experiments, and those that never returned home. The G-test was used to analyse the homing success data from different trials.

The directions followed by the crabs in the first 50 cm were calculated. These directions were related both to the home direction and to the initial directions expected if the crabs could rely on information gained en route (in the false displacement and U-shaped path trials). All circular distributions obtained were analysed using the circular statistical tests suggested by BATSCHELET (1981).

Results

Homing within the Home Range

A high percentage of crabs displaced with vision of the sky and landscape were able to reach home within 50 min and only one crab out of the 17 did not succeed in returning to its shelter (Fig. 1). Homing ability was not affected in nocturnal displacements or with a barrier that altered the landscape (Fig. 1, Table 1). However, the temporarily blinded crabs were not able to locate their refuges, even within the following day. The percentage of returns by crabs subjected to a non-linear displacement in a bucket, in the false displacement trials and in the U-shaped path trials were not significantly different from the control trials (Table 1). Only the crabs dislocated along a U-shaped path while being rotated in a closed bucket were less successful in returning home.

The return paths taken by the crabs were moderately straight (Fig. 2a,b), while only the blinded crabs showed rather convoluted paths (Fig. 2c).

Fig. 3 shows that the initial directions followed by crabs in control trials (Fig. 3a), night-time experiments (Fig. 3b; crabs tested in different stages of the lunar

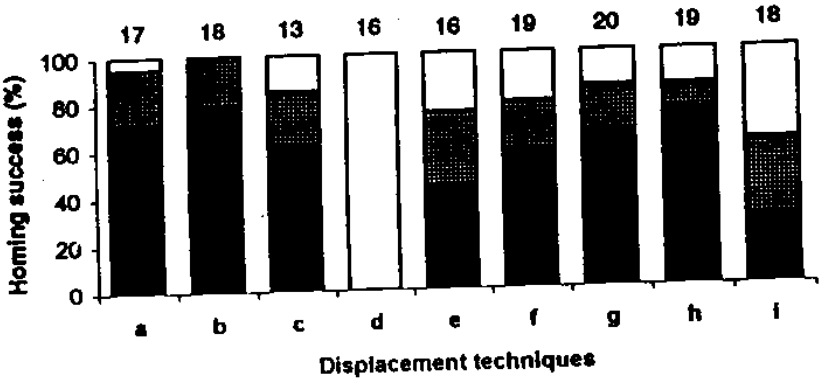

Fig. 1: *T. crenata* homing success (relative frequency of successful returns; n shown atop each column is number of crabs) for different displacement conditions. a, Control trials; b, nocturnal trials; c, trials with modified landscape; d, blind crabs; e, non-linear displacement in containers; f, false displacement trials; g, detour trials with vision of the landscape; h, detour trials with two-thirds of the displacement in the dark; i, detour trials with the whole displacement in the dark. Black, returned within 1 h; hatched, returned after two tides; white, did not return within two tides

Table 1: Homing success in *T. crenata*. Comparison between percentage of returns in the control displacements (a) and in the other experimental displacements (b–i). For meaning of letters see Fig. 1

Trial	G	df	P
b	1.18	2	>0.1
c	0.67	2	>0.1
d	32.33	2	<0.001
e	3.08	2	>0.1
f	1.71	2	>0.1
g	0.77	2	>0.1
h	1.60	2	>0.1
i	7.90	2	<0.02

cycle were cumulated because of the great homogeneity of the results), trials with altered landscape (Fig. 3c) and non-linear displacements (Fig. 3e) were not distributed at random and that there was a tendency to cluster around the home direction (respectively $u = 2.364$, $p < 0.01$; $u = 4.149$, $p < 0.01$; $u = 2.454$, $p < 0.01$; and $u = 3.065$, $p < 0.01$, V-test). On the other hand, the initial directions taken by the blinded crabs were randomly distributed ($u = 0.084$, ns, V-test) (Fig. 3d).

The results of the false displacements (Fig. 4a) and all the detour experiments (Fig. 4b,c,d) show that directions are still non-randomly distributed and that points are clustered around the true home direction and never around the expected direction (Table 2).

Homing outside the Home Range

As shown in Table 3, about 40 % of the crabs displaced to a distance of 20 m

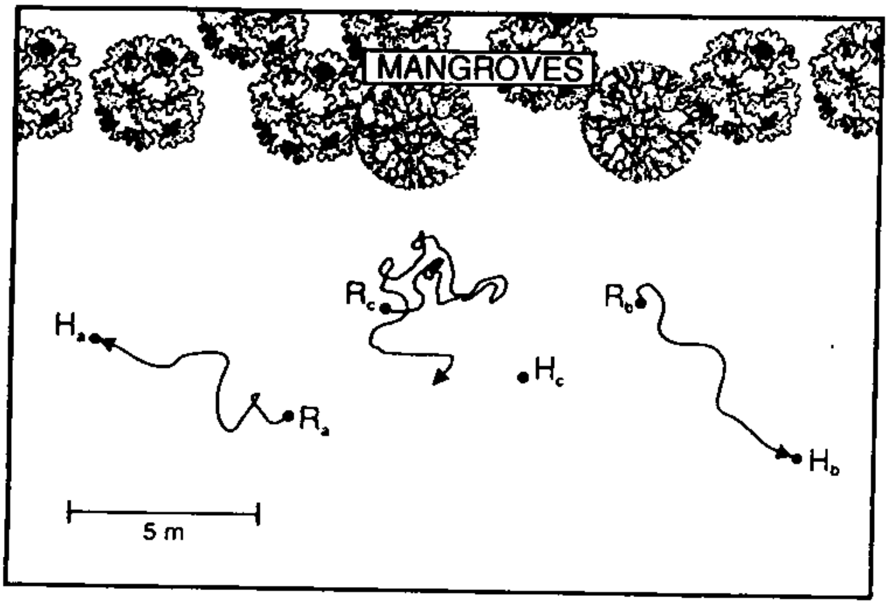

Fig. 2: Three examples of paths taken by *T. crenata* after daytime displacement (control) (a); nocturnal displacement (b); and with blinded specimens (c). For each path the release point (R) and home site (H) are indicated

were able to return to their refuge during the experimental session, while none of the specimens released 50 m away did so. Statistical analysis of the data shows that the homing ability of *T. crenata* is strongly affected by the distance of release (Table 3).

In the 20-m displacements, the distribution of the initial directions of the whole sample is still significantly different from a random distribution and maintains a tendency to cluster around the home direction ($u = 1.834$; $p < 0.05$, V-test) (Fig. 5b).

Discussion

Both during the day and at night, *T. crenata* is initially well orientated towards home and can rapidly return to its shelter if displaced, within its home range, with vision of the sea and landscape (Figs 1, 3a,b). As can be seen from Fig. 3(c) and Table 1, alteration of the perceived landscape does not disorientate the crabs, which proved to be well orientated even when placed in a bucket and taken to the release point along a non-linear path (Fig. 3d).

The straight and well-orientated paths covered by the crabs (Fig. 2a,b) exclude the use of systematic or random search strategies (WEHNER 1992). A high homing success after passive displacements indicates that *T. crenata* does not rely on egocentric systems based on information stored on the outward journey, such as the path-integration systems used by desert ants (WEHNER & WEHNER 1990). Moreover, the only experimental procedure that strongly affected the initial orientation and the homing ability of *T. crenata* was to blind the crabs (Figs 1, 3e).

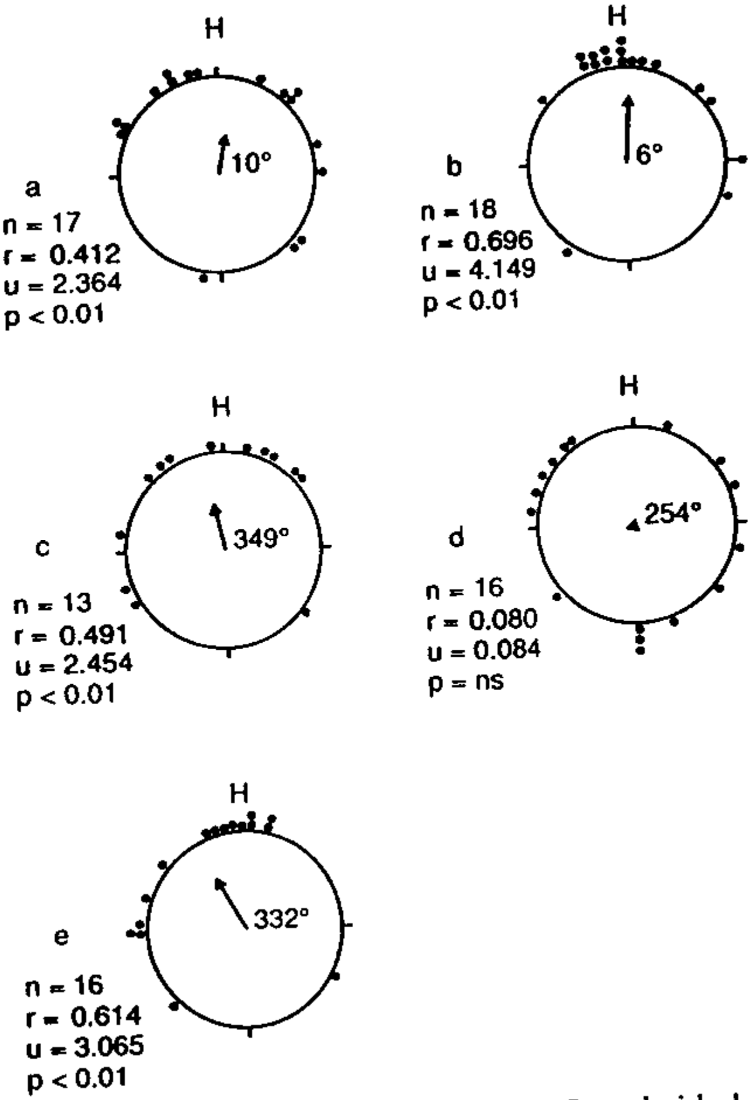

Fig. 3: Initial orientation after displacement in *T. crenata*. a, Control trials; b, nocturnal trials; c, trials with modified landscape; d, blind crabs; e, non-linear displacements in containers. For each distribution, the cumulated home direction (H), the number of trials (n), the length (r) and direction of the mean vector and the values of the V-test (u and p) are given

Although blinding the crabs might induce greater stress than simply displacing them, it is important to note that blind crabs were not able to locate their shelters even during the following day, when presumably the stress would not have been so great. Thus, these results lead one to infer that the role of vision is important for the homing capability of this swimming crab.

T. crenata cannot use relevant visual signposts situated near the den, such as the sand cones built by *Ocypode saratan* (Linsenmair 1967), and, moreover, it seems not to utilize the distant landscape as *Eriphia smithi* does (Vannini & Gherardi 1989); in fact, specimens were still well orientated even when not allowed to see the distant landscape during the displacement (Fig. 3c). Thus *T. crenata*, when displaced within its home range, probably uses nearby landmarks to establish the home direction.

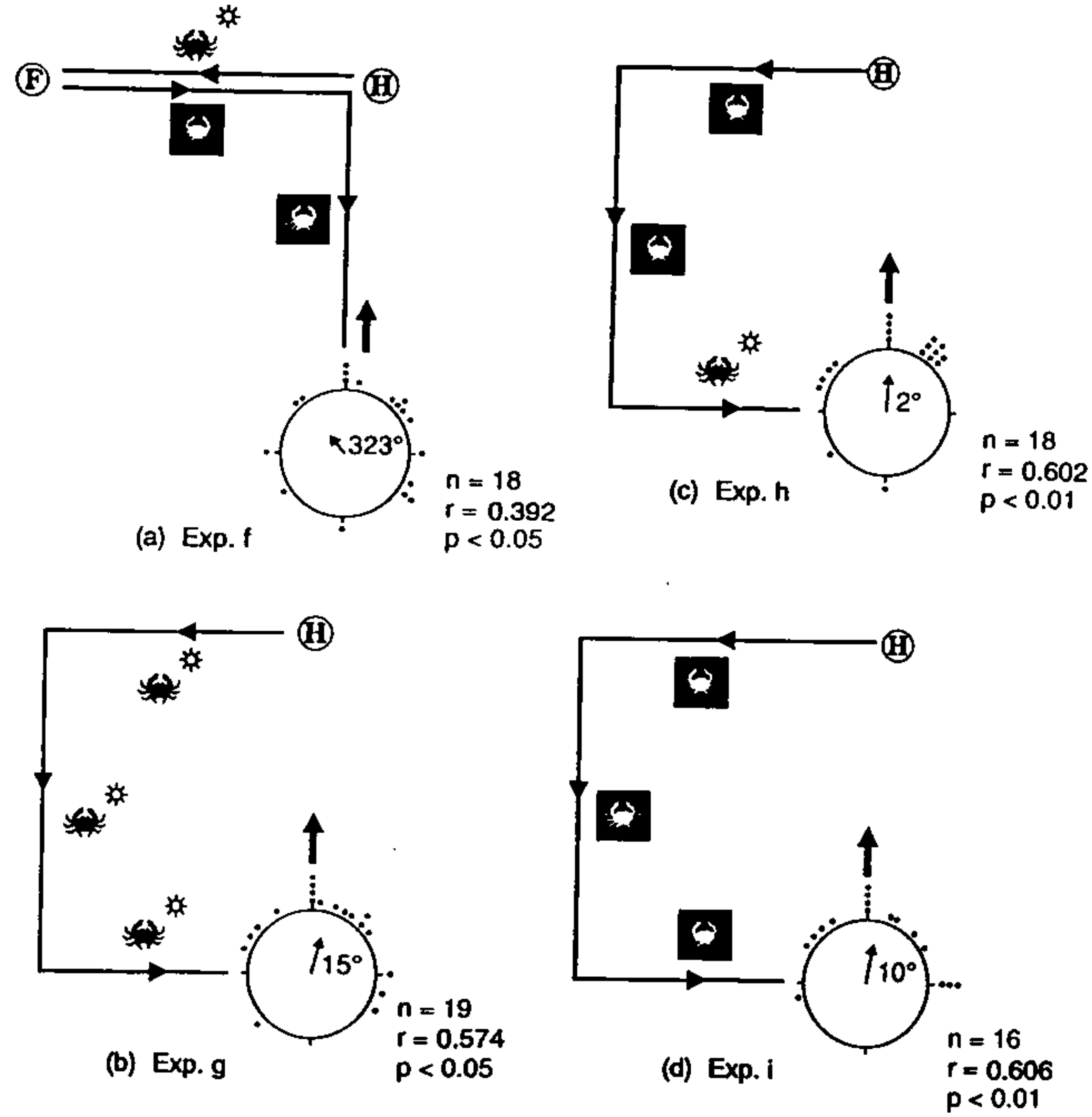

Fig. 4: Initial orientation of *T. crenata* with respect to the home site (black arrows: cumulated home direction), integrated in a schematic representation of the displacement route followed in false displacement and U-shaped path trials. F, false release point; H, home site. Black crabs and sun mark the segments performed with full vision of the sun and landscape; white crabs in black boxes are segments conducted in closed containers. For further details on distribution data, see Fig. 3

Table 2: Initial orientation in *T. crenata*. The initial directions followed were calculated first with reference to the homeward direction and second to the direction expected if the crabs had relied on visual information obtained en route. For meaning of letters see Fig. 1

Trial	Home direction		Expected direction	
	u	p	u	p
f	1.879	<0.05	0.608	ns
g	3.425	<0.01	1.087	ns
h	3.608	<0.01	1.647	ns
i	3.383	<0.01	0.571	ns

Table 3: Homing success in *T. crenata*. Number of crabs returned (ret.), returned within two tides (ret. 2 tides) and not returned (not ret.) in, respectively, the control trials, 20-m and 50-m displacements. Results of a comparison between controls and the two long-distance displacement groups are also given

Trial	Ret.	Ret. 2 tides	Not ret.	G	df	p
Controls	12	4	1	—	—	—
20 m	8	5	8	6.3	2	<0.05
50 m	0	4	12	25.9	2	<0.001

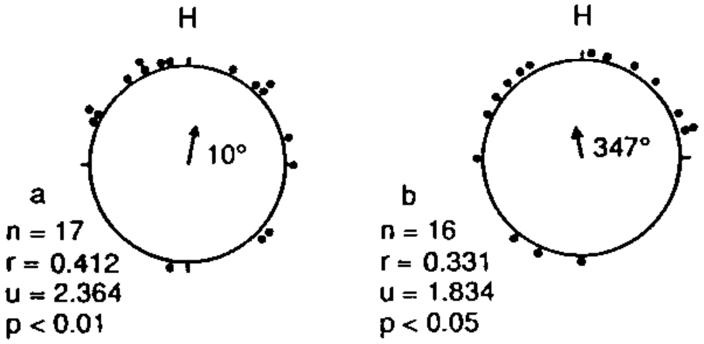

Fig 5: Initial orientation after releases from 5 m (a, same data as Fig. 3) and 20 m (b). For further details, see Fig. 3

Another source of orientating information might have come from the flow of the landscape (optokinetic reaction) and even of the water (crabs were always kept underwater). The importance of visual information gained en route is known for insects; paper wasps rely on directional information stored during passive displacement (UGOLINI & CANNICCI 1995), while, on the other hand, recent experiments by GEIGER et al. (1994) showed that foraging bees did not direct themselves towards the hive even if they were displaced in a way that allowed them to see the sky and landscape.

Regarding the information gained during passive displacement, the results show that crabs displaced in a bucket (thus with vision of only a small portion of the sky), those displaced along a U-shaped path (thus with information stored en route that contrasted with the visual cues perceived at the release point), and finally those tested with the false displacement technique, were all initially well orientated towards home (Figs 3, 4).

The homing success obtained in all these trials was still high (Fig. 1), with the exception of crabs kept in rotating containers. However, these specimens were still well orientated towards home and probably failed to reach their den because of the strong stress induced during the displacement. In fact they started their return journey only after a long resting period.

Therefore, it seems that orientational cues gained en route are not used to determine the home direction, as was found also in bees (GEIGER et al. 1994).

T. crenata thus shows good knowledge of the position of its refuges within the home range. The most reasonable hypothesis at present is that this crab can perceive some orientational cues, probably visual landmarks, and organize them in a map-like arrangement (sensu PAPI 1992) which allows it to return home from any given point within its home range.

Although insects do not use cognitive maps for their homing performances (WEHNER & MENZEL 1990; DYER 1991), *T. crenata* would not be the first decapod to show a map-based behaviour. WEHNER (1992), reviewing the works of HERNNKIND et al. (1975), KARNOFSKY et al. (1989), VARJU & SANDEMAN (1989) and DIESEL (1986), noted that *P. argus*, *H. americanus*, *Cherax destructor* and *I. phalangium* probably can arrange orientational cues, of different sources in the cited species, in a sort of cognitive map and they can use this arrangement to return to their shelters or to find the shelters of females.

Although the homing ability of *T. crenata* when released at points 20 m away from its refuge appears still to be good (Table 3), these results are preliminary and little can be inferred about the mechanisms involved. However, it is difficult to imagine that the hypothetical cognitive map of a crab that confines its normal activity within a radius of 6 m can extend over an area of 1200 m^2. Hence, other orientating mechanisms must be supposed. Moreover, in these releases the crabs were still initially well orientated (Fig. 5) and thus, assuming that they had no useful information available at the release point, the role of information obtained en route must be analysed in future research.

Acknowledgements

Many thanks are due to Dr E. OKEMWA, Director of KMFRI, and Professor P. POLK, K. B. P. c/o Vrije Universiteit Brussels, for encouraging the study of mangrove ecology in Kenya. We would also like to thank Dr A. UGOLINI, University of Florence, for his friendly help in the early planning of this research. We need to thank all the wonderful friends that made enjoyable the heavy field work in Sita: Claudia BARELLI, Matteo BONAZZI, Adam and Festus LENGA, Peter REYNIERS, Silvia RITOSSA, Cosimo TENDI, Marc VERNIERT and Roberto VEZZOSI. We are grateful for financial support from an EEC (STD-2) grant and from MURST (60 % and 40 % funds).

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Received: November 8, 1994

Accepted: January 24, 1995 (W. Wickler)