



Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae)

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Abstract

Sesarma leptosoma is a small grapsid crab which lives on the roots of mangrove trees of the East African coast and migrates twice a day to and from the canopy, spending the hottest hours of the day and most of the night within the root system. When not feeding on the canopy this crab hides in small crevices which the aerial roots of *Rhizophora mucronata* form on entering the mud surface, or it feeds, at low tide, by scraping the bark on the roots. Crabs marked and released on the tree of capture remained on it throughout the observation period (6 days). Specimens marked and then dislocated to trees 7 m distant were able to return to the tree of origin in a few days. Crabs dislocated 16 m away tended not to remain on the displacement tree, but they were never seen back on their own tree. Observations performed over a 16-day period showed that individually marked crabs, after each of the two daily migrations, went back to one, or at most two, well-defined small root crevices. The short-distance homing ability and the strong fidelity to a well-defined area shown by *S. leptosoma* are interpreted as behavioural mechanisms evolved to avoid high predatory pressure.

Keywords: Homing; *Sesarma leptosoma*; Tree climbing; Tree fidelity

1. Introduction

Among the Brachyura species colonising the mangrove swamps of the Indo-

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Pacific area, the most adapted to climbing trees is surely *Sesarma leptosoma* Hilgendorf, 1869, a small crab found in the mangroves of Tanzania (Hartnoll, 1975; Giddins et al., 1986) and of Kenya (Vannini and Ruwa, 1994). In fact, even if many species belonging to the Grapsidae are known to commonly climb the aerial roots and the first part of the trunks of mangroves (Von Hagen, 1977; Sivasothi et al., 1996; Vannini et al., 1996), only *Aratus pisonii*, a species living in the swamps of tropical and sub-tropical America, and *S. leptosoma* are known to reach the canopy of mature tall trees to feed on the highest leaves.

Although these two species can be considered ecologically equivalent some strong differences in their behaviour must be pointed out. In the American species, the climbing and exploring of the tree-top seems not to have any rhythmicity (Warner, 1967; Von Hagen, 1977) and the only mass movement described for this species is a breeding migration towards the seaward fringe of the swamp, which occurs at new and full moon (Warner, 1967). In contrast, the African *S. leptosoma* performs mass migrations to and from the canopy of *Rhizophora mucronata* twice a day (Vannini and Ruwa, 1994). The first daily migration starts at about 0600 and is followed by a downward flow at about 1000; then the whole population belonging to each tree, sometimes about 200–500 crabs, makes a second upward migration at about 1700 and comes down at dusk spending all the night within the aerial root system of the tree. No seaward breeding migrations have been described for this species.

From the previous observations it is clear that, even if it is a powerful climber, *S. leptosoma* spends most of its time between the roots of the tree, using the crevices formed when the roots enter the mud to hide itself or grazing on the root bark, never very far from its shelters.

The aim of this study was to test if these crabs tend to be faithful to a familiar tree and thus tend to form well-defined tree-related populations.

2. Materials and methods

All experiments were performed in the *R. mucronata* belt of a mangrove swamp near Dabasso, a locality within Mida Creek, 20 km south of Malindi, on the Kenyan coast. Between July and August 1993, about 300 specimens of *S. leptosoma* were captured during their morning downward migration (Vannini and Ruwa, 1994) using a bag-like trap built up around the trunk of five chosen trees. Two of the five trees were used for a short-distance crossing experiment, another two were used for a long-distance crossing experiment, and the fifth tree was used for observations of focus animals. All crabs were marked with Tipp-ex. In each of the crossing experiments, the crabs were not individually marked but instead were divided into four groups: the resident group and displaced group for each of the two trees. The Spearman non-parametric correlation test was applied to correlate these data with time.

2.1. Short-distance crossing experiment

A total of 120 crabs captured on two trees 7 m apart (trees I and II of Fig. 1) were divided into four groups and marked with four different codes. Thirty specimens from the first tree were released back on their own tree, while the other 30 were displaced to the second one; the same method of release and displacement was used for the 60 animals of the second tree. Thus, at the end of the experimental release, there were 30 resident and 30 displaced crabs on each tree.

Following Vannini and Ruwa (1994), we recorded every 10 min the number of marked crabs involved in the daily upward migrations which took place between 0600 and 0830. Two nearly opposite observation points were chosen at a distance of 10 m from the experimental trees, in order not to disturb the regular migrations of the crabs (Fig. 1). From these points observations were carried out for 6 days, starting from the day after the displacement. The two experimental trees and all the trees surrounding them were scanned by observers using binoculars.

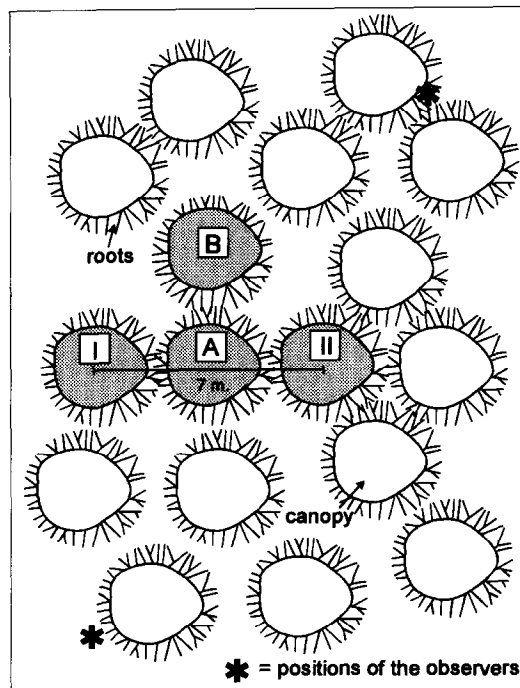


Fig. 1. 'Short-distance experiment'. Crabs were collected and released on trees I and II and observations were carried out from the points indicated. All the represented trees were scanned. Shaded trees were the ones on which crabs were actually recorded.

2.2. Long-distance crossing experiment

The experimental procedure was the same as in the first experiment but with only 100 animals (25 resident plus 25 displaced crabs per tree) on two trees 16 m apart. These two trees were located in an area of lower tree density and there was a path between them (Fig. 2). Two observation points (Fig. 2), situated 10 m away from the experimental trees, were chosen to allow the observers to scan most of the trees surrounding the experimental ones. Observations and records were made using the same technique as in the previous experiment.

2.3. Observations of focus animals

Fifty crabs were captured on a single tree, individually marked and then released on the same tree. A detailed drawing was made of the root system of the *R. mucronata* considered and, during a 16-day period, 10 observation sessions were performed, using a binocular, to locate as many crabs as possible and to record their position on the drawing. All crabs observed were followed during

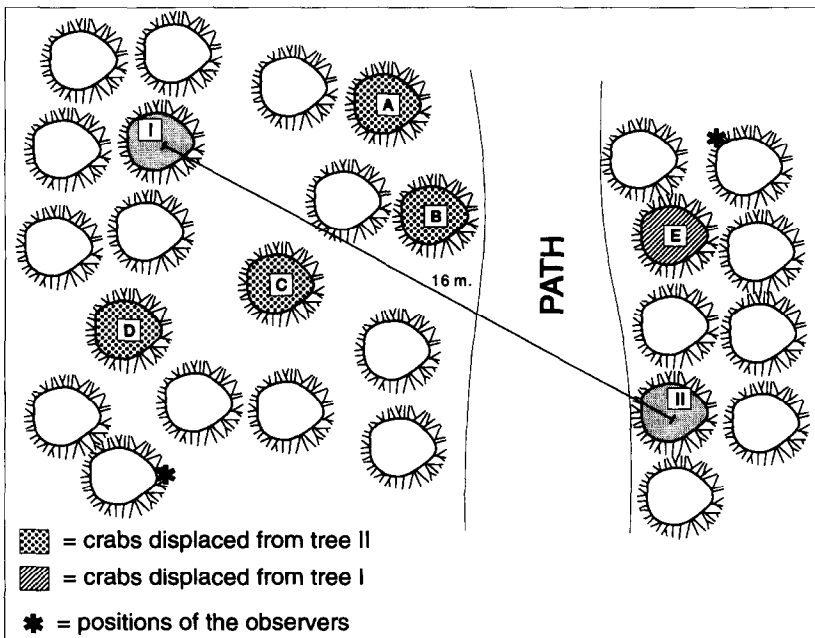


Fig. 2. Schematic view of the relative positions of trees involved in the 'long-distance experiment'. Displacement and experimental trees, observation points, root systems and canopies are represented as in Fig. 1.

their morning downward migrations and their positions were recorded only at the end of the migration, when they stopped on the roots near the mud surface.

*2.4. Preliminary observations regarding density and activity of four predators of *S. leptosoma**

It is known from recent studies (Dahdouh-Guebas et al., 1996) that among the crab species colonising the mangal of Mida Creek at least four species commonly prey upon specimens of *S. leptosoma*. These predators are two Xanthoidea species, *Epixanthus dentatus* (White, 1847) (Menippidae) and *Eurycarcinus natalensis* (Krauss, 1843) (Pilumnidae), and two Grapsidae species, *Metopograpsus thukuhar* (Owen, 1839) (Grapsinae) and *S. guttatum* A. Milne Edwards, 1869 (Sesarminae).

In order to calculate a rough index of the actual predatory pressure on *S. leptosoma*, a transect of 60 m was chosen within the mangrove belt inhabited by the tree crab. Along this transect, in four 24-h periods, surveys were performed every 30 min, using electric torches when needed, and all active specimens of the above mentioned predator species were recorded. Two of the 24-h observation periods were carried out in spring tide phases and other the two during neap tides.

3. Results

3.1. Short-distance crossing experiment

Crabs marked and released on the trees of origin (residents) remained constantly on their trees during the whole observation period. The number of records of these crabs, in fact, does not vary with time: Spearman correlation test, $r_s = 0.257$, $n = 6$, $p = \text{N.S.}$, for the first tree and $r_s = 0.814$, $n = 6$, $p = \text{N.S.}$, for the second tree.

The displaced crabs rapidly left the trees ($r_s = -0.9$, $n = 6$, $p > 0.05$, for tree I; $r_s = -0.9$, $n = 6$, $p > 0.05$ for tree II) and returned to the tree of capture ($r_s = 0.986$, $n = 6$, $p > 0.02$, for tree I; $r_s = 0.986$, $n = 6$, $p > 0.02$, for tree II) (Fig. 3A,B). In fact, at the end of the observation period, none of displaced crabs was observed on the foreign trees.

Marked crabs were also recorded on two trees situated between the experimental ones (A and B in Fig. 1). However, since none of the crabs resident on either tree I or tree II were ever seen on trees A and B, these observations were of displaced crabs in the process of returning to the tree where they had been captured. In fact, as seen in Fig. 4, there were no records of displaced crabs on trees A and B after the fourth day of observation. It is important to note that in each of these cases the displaced crabs were taking part in the upward migration on the intermediate tree even though they were generally on their way back to their home tree.

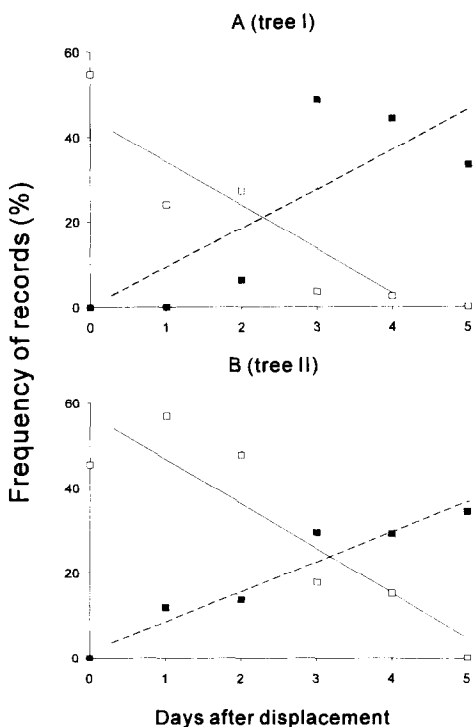


Fig. 3. Number of displaced crabs recorded and regression line for tree I (A) and tree II (B). □, Displaced crabs recorded on the foreign tree; ■, displaced crabs recorded on their home tree after returning to it.

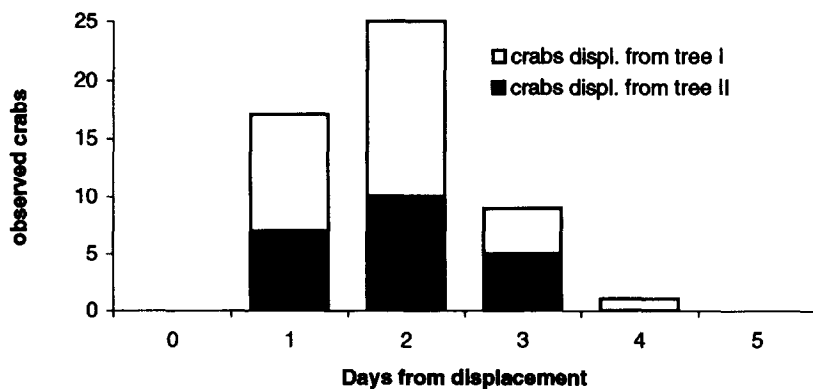


Fig. 4. Cumulated number of crabs recorded for each observation session on trees A and B (Fig. 1).

3.2. Long-distance crossing experiment

Also in this experimental situation resident crabs proved to be faithful to their own tree ($r_s = 0.2$, $n = 6$, $p = \text{N.S.}$, for the first tree and $r = 0.543$, $n = 6$, $p = \text{N.S.}$, for the second); in fact none of them was observed on trees other than the capture one. However, marked differences, with respect to the previous experiment, occurred in the behaviour of the displaced crabs. In the 6-day period of observation, no crab returned to its home tree even though on both trees I and II the relative frequency of records of displaced was significantly lower than of the resident ones ($G = 38.031$, $df = 5$, $p < 0.001$, for the first tree and $G = 47.048$, $df = 5$, $p < 0.001$ for the second; G -test) (Fig. 5A,B). The tendency to leave the foreign tree is confirmed by the fact that only displaced crabs (Fig. 6) were observed, at distances up to 6.50 m, on the trees surrounding the two experimental ones (trees A, B, C, D, E of Fig. 2).

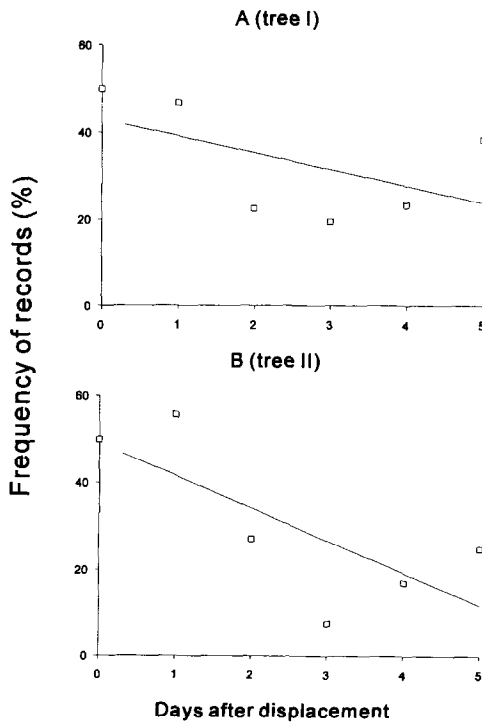


Fig. 5. Number of displaced crabs recorded for tree I (A) and tree II (B). □, displaced crabs recorded on the foreign tree. There were no returns.

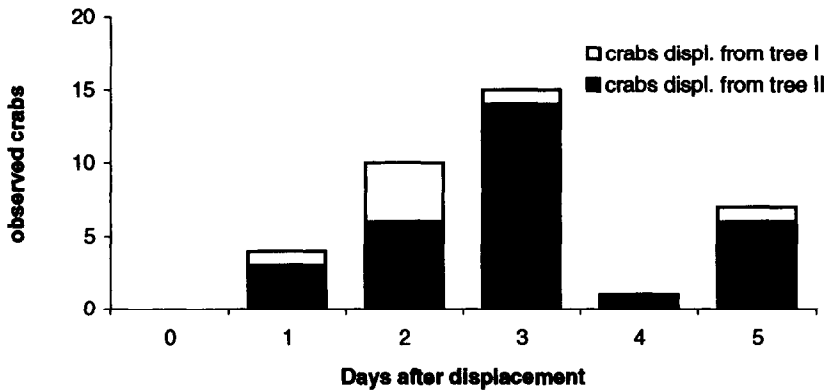


Fig. 6. Cumulated number of crabs recorded on trees A, B, C, D, E (Fig. 2).

3.3. Observations of focus animals

For 20 out of the 50 crabs marked, it was possible to follow the daily downward journey more than five times and to record the crevices where their migration stopped. Fig. 7 shows that, for each of these 20 crabs, the number of holes visited is not dependent on the number of times the crab was recorded ($t = 1.013$, $df = 18$, $p = \text{N.S.}$, Spearman non-parametric correlation test). Fifteen of these crabs (75%) proved to be faithful to two holes (Fig. 8), while five crabs (25%) always migrated to a single hole. The total number of holes visited by the marked crabs was 37; thus, the theoretical probability of reaching only two well-defined crevices for a crab migrating five times and moving at random is $1.44 \text{ E-}07$. For crabs observed more than five times, this value is much lower.

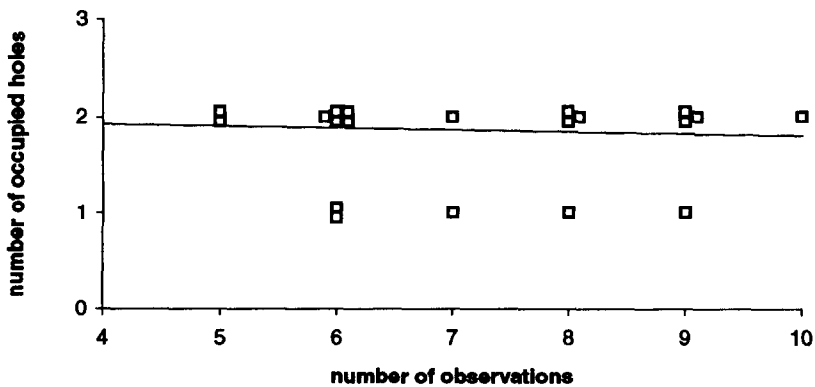


Fig. 7. Relationship, for each of the 20 crabs which were observed for at least five times, between the number of observations and the total number of holes visited by the crabs.

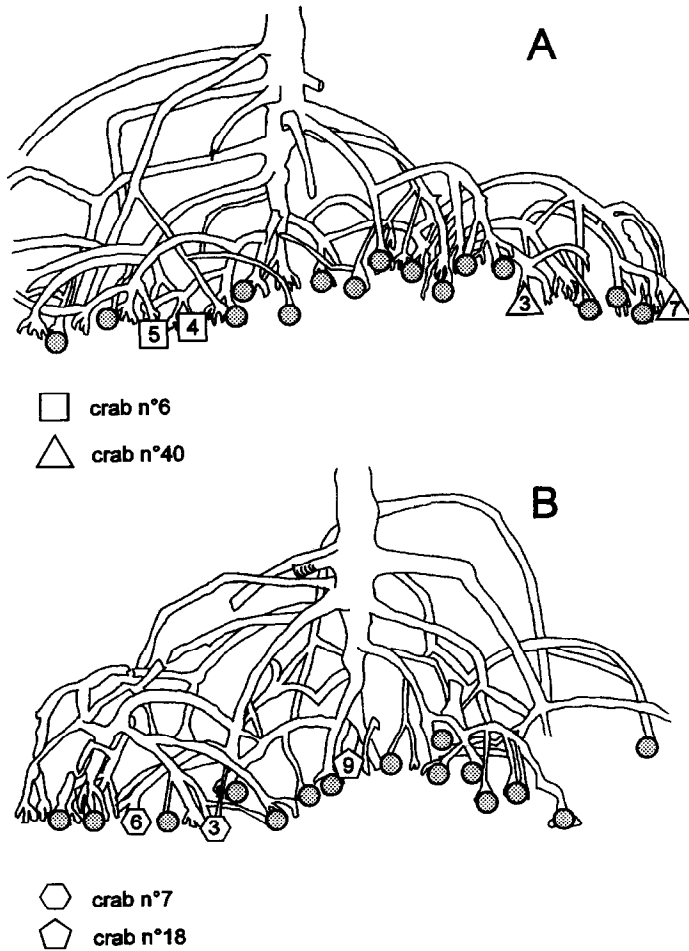


Fig. 8. Map of the two sides, A and B, of the root system among which the observations of focus animals were performed. Shaded circles = holes visited at least once by the marked crabs; white polygons = holes visited by the represented crabs, the numbers of visits are also indicated.

3.4. Preliminary observations regarding the density and activity of four predators of *S. leptosoma*

The results of the four 24-h observation periods (Fig. 9 and Fig. 10) show that all four species are active during low tide (at high tide, fishes reaching the swamps are possible predators). *Epixanthus dentatus* shows a nocturnal activity pattern (Fig. 9 and Fig. 10) while the other species are more diurnal, although they are quite active even during the night. Based on the number of predators recorded during their activity peak and the number of trees along the transect, a rough

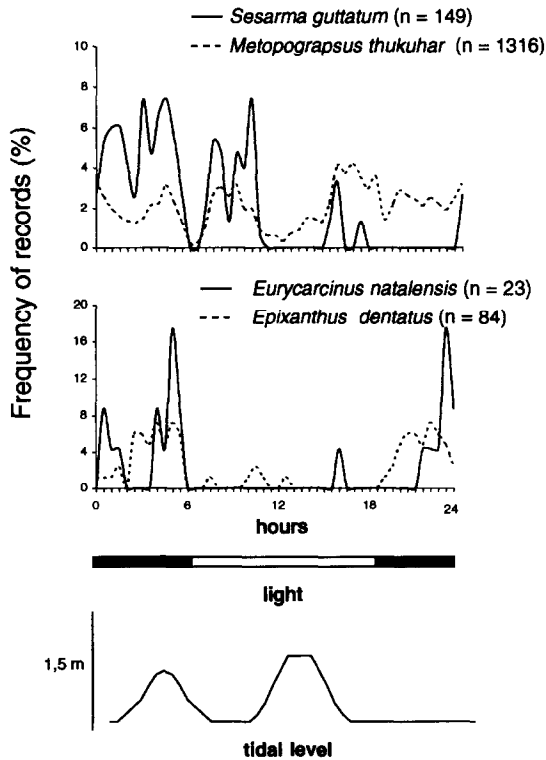


Fig. 9. Daily activity, as the frequency percentage of active specimens observed, of the two Xanthoidea and the two Grapsidae crab species which are the most common predators of *S. leptosoma*. The figure shows the number of crabs recorded during two 24-h periods of observation carried out at neap tide. The hour of day, light intensity and water level are also shown.

estimate of the number of predators active per tree is about 0.9 for *Epixanthus dentatus*, 0.7 for *Epixanthus natalensis*, 2.9 for *M. thukuhar*, and 1.1 for *S. guttatum*. Thus the predatory pressure on the small *S. leptosoma* can be estimated at 5.6 predators \cdot tree⁻¹, active both during the day and at night.

4. Discussion

4.1. Why is *Sesarma leptosoma* so faithful to a specific tree and to certain shelters?

The *Rhizophora* belt of the swamp in which the experiments were performed was 70–80 m wide and trees were abundant and uniformly distributed in space. Moreover, the root systems of all trees were overlapping to a great extent and no ecological factors seemed to change drastically between different parts of the

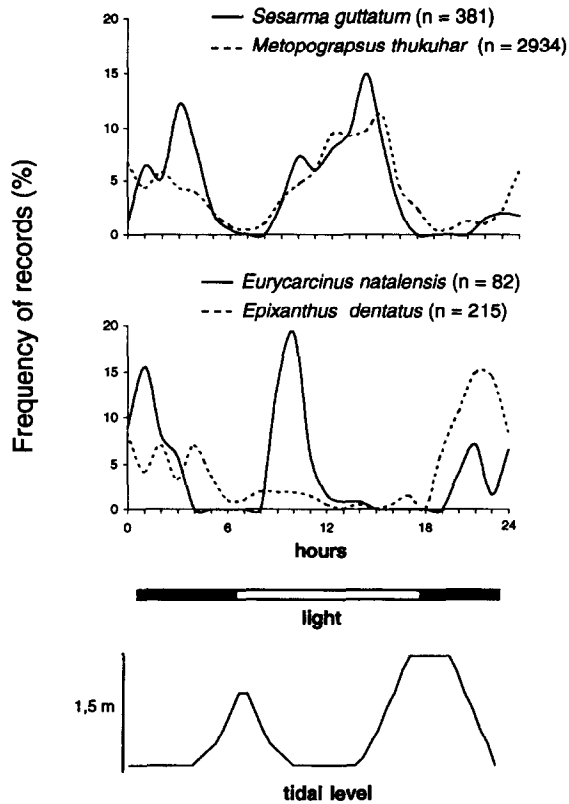


Fig. 10. Daily activity of the two Xanthoidea and the two Grapsidae crab species which are the most common predators of *S. leptosoma*. The figure shows the number of crabs recorded during two 24-h periods of observation carried out at spring tide. For further details see Fig. 9. The hour of day, light intensity and water level are also shown.

swamp. There are at least two possible explanations for the high fidelity that *S. leptosoma* shows for its own tree. First, it is known from recent studies that this species is faithful to a specific feeding area among the branches of its own tree to which it migrates twice a day (Cannicci et al., 1996); i.e. crabs tend to be faithful to a tree where they find suitable feeding areas. Second, the results concerning the faithfulness to a specific shelter among the roots suggest that crabs are faithful to a tree also because they need to shelter in a known hole at its base.

4.2. How is a crab able to return to its home tree when displaced 7 m away?

It is more difficult, at present, to answer this last question. The overlapping root systems in which crabs had to find their way back seem to be both uniform, in terms of chemical, tactile and visual cues that might help the crabs in their task, and, on the other hand, amazingly complex: the crabs would seem to have a rather

small chance to find the right root in that chaos. Long-distance experiments showed that crabs, at least five days after displacement, did not return to their home tree. Our data for the short-distance experiment allow us, for the moment, to exclude a random search strategy (Papi, 1992); first because the crabs returned very quickly to their home tree, and second because they always seemed to be oriented towards home since the start of their trip back (in fact they were observed only on trees that were between the displacement tree and the home tree).

Although the long-distance experiment was carried out in an area with lower tree density the displaced crabs were able to recognise that the tree they were placed on was not the familiar one and thus tended to abandon it, while the residents were strongly faithful to their tree.

Displacement experiments have been performed also with *A. pisonii*, the other canopy crab which inhabits the American red mangrove *R. mangle* (Dunham and Gilchrist, 1988). The authors displaced blinded, partially blinded and control animals within 3 m of a mangrove root system and found a difference between blinded and control crabs in the time needed to reach the roots, but no difference between the two groups in the time needed to climb the trunk. Thus, vision seems to be important in orienting crabs toward the trees, while negative geotaxis is sufficient to climb the trunk. The results of these experiments are difficult to compare with those performed on *S. leptosoma* because they did not test whether *A. pisonii* had a real home tree or not, and the whole study was focused on a kind of zonal orientation.

4.3. Why is *S. leptosoma* faithful to a few specific shelters?

Many other terrestrial or semi-terrestrial crabs inhabiting mangroves dig burrows and are faithful to them (Macnae, 1968; Micheli et al., 1991). The most important differences between *S. leptosoma* and these species are:

1. The tree crab covers daily vertical distances up to 15 m from its shelters while the other species limit their activity to a small area immediately surrounding the hole and excursions outside this area are rare;
2. *S. leptosoma* seems neither to dig nor to restore its shelters; thus, the number of crevices suitable can be considered a limiting factor. Most of the other mangrove crabs actively dig and maintain their burrows.

If this is true, a possible explanation for such strong fidelity to a shelter and such good homing ability is the predatory pressure to which these crabs are subjected. In fact, the four preliminary surveys carried out in the swamp of Dabaso (Fig. 9 and 10) show that the density of the four decapod species that prey upon *S. leptosoma* is quite high and that their activity is well distributed throughout the day and the night. Under such strong predatory pressure the development of a homing mechanism that would allow the climbing crabs to return to a well-known and suitable shelter would probably be strongly adaptive.

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