Behavioural evidence for visual recognition of predators by the mangrove climbing crab *Sesarma leptosoma*

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The climbing crab *Sesarma leptosoma* colonizes the mangrove roots and canopy of East African mangrove swamps, an intricate three-dimensional habitat in which it orients itself visually. To ascertain if vision helps this tree crab to detect dangers such as predators, we used dummy objects: (1) a preserved specimen of its predator, the crab *Epixanthus dentatus* in its typical ambush posture; (2) a piece of wood with real *E. dentatus* claws attached to it, the same size as, and painted to resemble (to the human eye), this predator; and (3) a piece of wood the same size and colour as a live crab but without claws. When these dummies were presented to migrating *S. leptosoma* in the field, they stopped their normal migratory flow only when they were able to see the open claws of the predator. Thus *S. leptosoma* showed a considerable ability to perceive shape, being able to distinguish motionless objects of different shapes but similar size and to associate the detected shapes with the presence of danger.

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Terrestrial and semiterrestrial decapods, with few exceptions (Wellins et al. 1989; Vannini & Ferretti 1997), cannot rely on chemical stimuli for communication and many of their intra- and interspecific interactions involve vision (Hartnoll 1988). Although many semiterrestrial decapods have well-developed visual systems, Zeil et al. (1986) suggested that two different evolutionary pathways have been followed.

Families such as Ocypodidae and Mictyridae bear their eyes at the top of elongated eye stalks, the basal joints of which are close together; thus they are defined as ‘narrow-fronted’ species. Furthermore, the long eye stalks are associated with a narrow zone for vertical resolving power along the horizon of the eyes themselves. Zeil et al. (1986) showed that both features are adaptations to spatial vision in the flat intertidal environments colonized by these species. Field studies by Land & Layne (1995), further discussed in Layne et al. (1997), confirmed that, in fiddler crabs, the band of enhanced vertical resolution images the horizon and is extremely important for recognition of predators and/or conspecifics. In particular, the fiddler crabs showed antipredatory responses only when the approaching experimental items appeared above their built-in horizon, regardless of shape.

The second group of semiterrestrial families, Grapsidae, Xanthidae and Gecarcinidae, are defined as ‘broad-fronted’ species, because they bear their short eye stalks close to the lateral corners of the carapace. Although no detailed work has been done on the visual world of the broad-fronted species, Zeil et al. (1986) suggested that the wide eye separation, the most pronounced amongst arthropods, could strongly enhance binocular stereopsis (see Wehner 1981). No hypothesis has been proposed concerning their ability to perceive shape. Strong depth resolution in binocular stereopsis should be considered an important adaptation that coevolved with the habit of colonizing vertical cliffs and complex three-dimensional mangrove environments, which are inhabited by many broad-fronted species, and is therefore crucial for the mangrove-climbing and canopy-dwelling species such as the Neotropical *Aratus pisonii* and the Indo-Pacific *Sesarma leptosoma* (Warner 1967; Vannini & Ruwa 1994; Cannicci et al. 1996b). Although there is no information about the morphophysiological features of the eyes of these tree crabs nor about their binocular stereopsis and shape discrimination abilities, recent work indicates that both *A. pisonii* and *S. leptosoma* rely on vision: the former to avoid predators and find shelters (Diaz et al. 1995), the latter to orient itself among trees and branches (Cannicci et al. 1996a, 1997). *Sesarma leptosoma*, in particular, shows a strictly diurnal pattern of
activity, and the importance of sight in its everyday life is confirmed by the fact that it becomes active only when the ambient light reaches a certain threshold (Vannini et al. 1995). These findings stimulated our study, in which we used tests with dummy objects in the field to investigate the use of vision by S. leptosoma in its antipredatory behaviour.

**METHODS**

**Study Area and Species**

We carried out the experiments in the mangrove swamp of Dabaso, within Mida Creek, 20 km south of Malindi, on the Kenyan coast, in October–November 1997 and 1998. This swamp, about 80–100 m in width, is composed of mature Rhizophora mucronata trees up to 15 m tall. It is flooded twice a day and is colonized by a large population of S. leptosoma (Vannini & Ruwa 1994). The crabs migrate up and down the tree trunks twice a day.

**Bridge-crossing Experiment**

We designed this experiment to test whether visual and tactile modification of the everyday migratory paths of the climbing crabs would affect their behaviour. At night, that is, when the crabs were not active, we covered 70-cm-high portions of the trunk of two test trees with PVC sheeting. On the PVC, we placed a strip of raffia palm lacework 20 cm wide as a bridge to allow the crabs to cross the experimental obstacle. This was the only passage the crabs could use to get to the canopy where they feed. The use of a raffia strip was suggested by direct observation of many mangrove crab species, which often explore and easily climb on these laceworks laid down in the swamp by local fishermen. In view of the highly synchronized migratory behaviour of S. leptosoma, we were able to videotape (Sony Hi8 Camcorder) both of the upward migrations on the first, second and sixth mornings after the experimental modification (a total of ca. 500 crabs). Later, the six recording sessions were analysed with a Sony VCR with stop-motion and slow-motion functions.

For every session, we recorded the total number of crabs crossing the bridge and, for each of the crabs, noted the following parameters: (1) the number of stops on the bridge (Stops); (2) the duration of the stops (s, Stop time); and (3) the total time needed by each crab to cross the bridge, excluding Stop time (Cross time). We assumed all these parameters to be closely related to the difficulties the crabs faced in approaching and then crossing the bridge.

With the described modification of the tree trunk, we never had to manipulate directly, or even touch, the crabs inhabiting the experimental trees. The crabs were always observed or video-recorded while moving freely on the raffia strip during their natural downward migration from the mangrove canopy.

**Experiments with Dummies**

To study the visual shape discrimination of S. leptosoma, we took advantage of the ambush habits of its most common predator in the study area, Epixanthus dentatus (Eriphiiidae). As shown by Cannici et al. (1998), this medium-size semiterrestrial crab climbs the aerial roots of the mangrove and stands still for hours, with its claws wide open, waiting for smaller crabs to get too close. In view of the high density of E. dentatus in the swamp, S. leptosoma must probably cope with this danger frequently when active. We therefore designed experiments involving different kinds of dummies to test the way in which vision might help the climbing crabs avoid predation. The first dummy (Epixanthus) consisted of a specimen of E. dentatus (preserved in 70% alcohol) set in the typical ambush posture and coated with Araldite (Fig. 1a). This dummy closely resembled, in both colour and shape, a live predator while hunting. The second dummy (Clawed-rectangle) was a solid wooden rectangle, painted in the natural colours (as they appear to a human observer) of an E. dentatus carapace to which were glued two real claws of a preserved specimen; the whole was coated with Araldite (Fig. 1b). The third dummy (Trapezium) was a solid wooden trapezium the same size as a living E. dentatus and coated with Araldite; it was the least like the real crab, resembling it (to the human eye) only in colour and general dimensions (Fig. 1c). All dummies were kept for a week under the mud of the swamp so that they would acquire the general mangrove smell. We also smeared them with mud just before the experiment, since the real E. dentatus are always covered with mud when hunting.

Before presenting these dummies to the crabs living on four selected trees, we covered a 70-cm-high section of the trunk of each tree with a PVC sheet and set up a raffia palm lacework, as in the previous experiment. The raffia bridge ended where the highest aerial root of the mangrove tree joined the trunk (Fig. 2). We drew a scale showing the distance from the dummy’s position in units of 10 cm on the raffia lacework to facilitate the observations, and the whole experimental set-up was left in place for 2 weeks before the dummy tests. This period of time was sufficient to allow these climbing crabs to get used to strong modifications of their path to the mangrove canopy (Cannici et al. 1997).

We did the dummy tests during the morning downward migrations. For each of the four trees we conducted four trials: the presentation of the three dummies, randomly sorted for each tree (Table 1) and placed at the base of the aerial root where the bridge ended (Fig. 2), plus one control session in which we recorded the migratory behaviour of the crabs without presenting a dummy.

During each trial, an observer, situated at least 8 m from the tree, followed the whole downward migration taking place on the experimental tree and observed the crabs for ca. 3 h, the exact duration depending on the weather and air temperature (see Vannini et al. 1997 for a detailed description of S. leptosoma migratory habits). Two observers carried out the tests simultaneously on two different trees; thus an 8-day period was necessary to...
perform all 16 trials. In each trial, the observer recorded: (1) the number of crabs crossing the bridge; (2) the number of stops of each crab (Stops); (3) the approximate duration of the stops (s) with a stopwatch (Stop time); and (4) the distance from the dummy at which each stop occurred.

To avoid pseudoreplication, all observations collected during each trial on each tree were treated as a single observation. The measures, for each trial on each tree, were: (1) the proportion of crabs stopping; (2) the mean number of Stops per crab; (3) the average Stop time per crab.

All statistical tests are two tailed.

RESULTS

Bridge-crossing Experiment

There was no significant difference between the two trees for any of the parameters (Kruskal–Wallis test; Stops: $\chi^2_{1}=0.12, P=0.73$; Stop time: $\chi^2_{1}=0.052, P=0.818$; Cross time: $\chi^2_{1}=0.386, P=0.534$; for each parameter $N=120$). Therefore, in the following analysis we merged the data for the two trees.

The three parameters varied significantly with time (Fig. 3). As the time from the manipulation day increased, the crabs passing over the bridge stopped less often (regression test: $F_{1,118}=35.18, P<0.0001$; Fig. 3a), spent less time standing still (regression test: $F_{1,118}=28.56, P<0.0001$; Fig. 3b) and spent less time crossing the bridge (regression test: $F_{1,118}=46.48, P<0.0001$; Fig. 3c).

Experiments with Dummies

As all three measures, that is, the proportion of crabs stopping, the mean number of Stops per crab and the average Stop time per crab, had equal variances and were normally distributed (Cochran’s test: $C=0.63$, NS; $C=0.34$, NS; $C=0.59$, NS, respectively), we applied a one-way ANOVA to each measure. The proportion of crabs stopping differed between treatments (ANOVA: $F_{3,15}=4.86, P<0.02$; Fig. 4a); in particular, significantly more crabs stopped during the Epixanthus and Clawed-rectangle trials than during the control tests (Dunnett test: $C=0.13, P<0.05$ and $C=0.04, P<0.05$, respectively). The mean number of Stops per crab also differed significantly between trials (ANOVA: $F_{3,15}=4.66, P=0.02$; Fig. 4b), although in this case only during the Epixanthus
trials were the Stops/crab significantly higher than in the control tests (Dunnett test: C=0.15, P<0.05). The same trend was revealed by analysis of the average Stop time per crab (Fig. 4c): this measure varied between treatments (ANOVA: F3,15=5.20, P<0.02) but was significantly higher than the control value only during the Epixanthus trials (Dunnett test: C=0.12, P<0.05).

The number of first stops by crabs at the different distances from the dummy differed strongly between trials (G test: χ^2=23.11, P<0.01; Fig. 5). During the control test, the distribution of these first stops along the raffia bridge was uniform (G test: χ^2=5.24, NS; Fig. 5a) and the distribution remained uniform during the Trapezium trials (G test: χ^2=4.23, NS; Fig. 5b). However, a nonuniform distribution of stops was recorded during the Clawed-rectangle trials (G test: χ^2=57.49, P<0.001; Fig. 5c) and Epixanthus trials (G test: χ^2=53.13, P<0.001; Fig. 5d), with a strong increase of stops at 30 cm and then at 20 cm from the dummy. Therefore, the crabs changed their behaviour at a distance of about 30 cm from the dummy, but only when the dummy was one of the two bearing E. dentatus claws. Considering the average height of the S. leptosoma eyes and the size of the dummy, this detection distance means an angular height of 8.5° and an angular width of 18° on the crab’s retina.

Apart from the quantitative measures analysed above, the behaviour of S. leptosoma also differed qualitatively between the four trials. Crabs were often observed to climb and step on the Trapezium dummy during their downward path to the roots, while they never touched the Epixanthus or Clawed-rectangle dummies. When they confronted these dummies, they changed their path in one of two ways. Some crabs moved sideways on the trunk at the edge of the PVC sheet and eventually found another root on which to proceed downwards, while other crabs grasped the under part of the root and walked upside-down to cross the portion of the root occupied by the dummy. Both these behaviours strongly retarded the crab’s migration and neither was observed during the control trials.

**DISCUSSION**

Our results show that S. leptosoma hesitates when approaching dummies representing one of its most specialized brachyuran predators, E. dentatus, thus indicating that it uses vision to recognize a predator. Our field trials, although based only on behavioural responses of the descending crabs, enabled us to gather data on the visual recognition and active avoidance of particular shapes, that is, the open claws (Fig. 4), and on the distance at which this recognition seems to occur (Fig. 5).

The bridge-crossing experiment was designed as an exploratory investigation preliminary to the experiments with dummies. Although it was already known that S. leptosoma can cope with strong artificial modifications of its path to the mangrove canopy (Cannicci et al. 1997), this preliminary test was crucial to identify behavioural responses directly connected with the hesitation that S. leptosoma might exhibit when facing a new situation. The results showed that S. leptosoma had problems in crossing the bridge, but the hesitation in climbing clearly tended to disappear with increasing experience with the obstacle and the frequency of the behavioural parameters that we chose agreed well with this trend (Fig. 3). In addition, this preliminary trial allowed us to establish the number of stops and the amount of hesitation that could be considered normal during migration on the experimental bridge, before we could assess whether extra stops and hesitation were caused by the dummies during the following experiments.

The experiments with dummies revealed that, with respect to the control tests, a higher proportion of crabs encountering the Epixanthus dummy at the end of the raffia strip stopped at least once (Fig. 4a). Furthermore, the crabs stopped more often (Fig. 4c), and for longer (Fig. 4c); thus the crabs showed a clear hesitation along their path. Similarly, the proportion of crabs stopping at least once during the Clawed-rectangle trials was significantly higher than during the control tests (Fig. 4a). There were no significant differences in behaviour between the control S. leptosoma and those facing the dummy without real claws (Fig. 4). Thus, the simple obstacle represented by a wooden trapezium of the same general size and colour as their ambush predator did not significantly increase the hesitation of the crabs. Instead, they had to recognize...
the overall shape of the predator or, to a lesser extent, the 'open claws' visual stimulus before showing fear of a predator.

The data suggest that recognition of the predator's visual characteristics started at a distance of about 30 cm (Fig. 5), meaning an angular height of about 8.5° and an angular width of about 18° on the S. leptosoma retina. A similar detection distance was reported for males of Uca pugilator: their behaviour began to change when a conspecific approached to within about 30 cm of their territory. However, in those field trials, the conspecifics were actively moving and they subtended an angular width of about 3.7° on the eye's surface (Land & Layne 1995). Furthermore, at that distance, the U. pugilator males could not recognize the sex of the approaching crab, information that in these fiddler crabs is probably based on visual perception of the large claw of the males (Layne et al. 1997).

Table 1. Experiments with dummies

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Order of presentation of the four treatments, that is, the three different dummies plus the control session with no dummy, on each of the four experimental trees. For the description of each dummy, see the text.

(a) Number of stops

(b) Stop time (s)

(c) Cross time (s)

Days from manipulation

Figure 3. Bridge-crossing experiment. The relationship between (a) number of stops, (b) the duration of the stops, Stop time, and (c) the total time each crab needed to cross the bridge, excluding the duration of the stops, cross time, and the number of days after the initial manipulation.

(a) Nonstopping/stopping crabs

(b) No. of stops/crab

(c) Duration (min) of stops/crab

Days from manipulation

Figure 4. (a) Mean ratio of nonstopping versus stopping crabs, (b) mean number of stops per crab and (c) average duration of stops recorded on the four experimental trees during the four trials. Error bars represent 95% confidence intervals.
behavioural response dependent on the sex of the approaching crab at a distance of 10–15 cm, that is, at an angular width of 8°. These fiddler crabs reacted with the same intensity to approaching dummies of different shapes but the same size; thus Land & Layne (1995) concluded that ‘the actual shape of the crab is unimportant’. In our trials, S. leptosoma reacted to motionless visual stimuli, but only when the ‘open claw’ was detected at a 30-cm distance; no increase in stops was recorded when an object with the size of the predator but not the overall shape was detected. Although in laboratory arenas both fiddler crabs (Langdon & Herrkind 1985) and the other mangrove climbing crab A. pisonii (Diaz et al. 1995) could differentiate between refuges and predators on the basis of the horizontal extent of the test shapes, visual discrimination in S. leptosoma (as we have documented here) is specifically concerned with predator detection.

Our results, especially the difference in shape discrimination between the tree crabs and fiddler crabs, must be discussed in relation to Zeil et al.’s (1986) hypothesis. These authors proposed that the visual system of semiterrestrial crabs evolved to allow the crabs to take advantage of the visual features of the habitats in which they live. In fact, mud flat dwellers, such as the fiddler crabs, bear their eyes on long eye stalks and the eyes themselves have a narrow zone for vertical resolving power (Zeil et al. 1986), which acts as an artificial horizon and helps the crabs to detect predators (Land & Layne 1995; Layne et al. 1997). The proposed mechanism is simple: all small approaching objects whose images on the retina do not intersect the artificial horizon are harmless and could be a potential mate, while objects with large vertical angular size are potentially dangerous and induce escape reactions. On the other hand, the Grapsidae inhabiting mangrove swamps (e.g. tree crabs) and rocky cliffs do not have such an artificial horizon built into their eyes (Zeil et al. 1986). No hypothesis has been proposed concerning the ability of these crabs to perceive shapes. Dummy conspecifics whose claws were experimentally waved in front of the river crab Potamon fluviatile elicited more attack–defence reactions than immobile ones (Vannini et al. 1983), although the crabs also reacted differently to an immobile medium-sized dummy conspecific wearing large or small claws when presented from no more than 30 cm. River crabs were also able to perceive small differences between rectangular notched and non-notched tags (Vannini & Gherardi 1981).

Our data suggest that the vision-related abilities observed in river crabs have been particularly enhanced in climbing crabs inhabiting the complex three-dimensional habitat of the tree canopy. They are not only able to perceive the shape of a motionless object waiting for them, but also to associate it with a visual template stored in the central nervous system and representing, most probably, the shape of the open claws of the dangerous predator. The presence of such an ability in unrelated families such as Potamidae and Grapsidae suggests that it may be widespread among Brachyura; appropriate experiments could easily reveal it in other semiterrestrial species.

The visual abilities of S. leptosoma are likely to help this daytime climber during its feeding activity; indeed they probably coevolved with its climbing and feeding habits, under the strong pressure exerted by brachyuran predators. In fact, at least four species of crabs commonly hunt and ambush our population of S. leptosoma, with densities up to six predator crabs per tree in the study area (Cannicci et al. 1996a). These numbers mean that if a climbing crab fails to estimate distances exactly and falls from the tree branches or cannot perceive the shape of an ambushing crab, it will probably not have a second chance for survival.

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References


