PREDATORY ACTIVITY AND SPATIAL STRATEGIES OF
EPIXANTHUS DENTATUS (DECAPODA: OZIIDAE),
AN AMBUSH PREDATOR AMONG THE MANGROVES

Stefano Cannicci, Renison K. Ruwa, Maddalena Giuggioli, and Marco Vannini

ABSTRACT

The predatory patterns and spatial strategies of *Epixanthus dentatus* were studied in a mangrove creek on the Kenyan coast, together with laboratory analysis aimed at assessing the natural diet. This xanthoid fed on almost all the slowly moving invertebrates common in the forest and actively preyed at night, using an ambush technique. *Epixanthus dentatus* is faithful to individual dens among the roots and to well-defined feeding areas within a 3-m radius, which they shared with an average of 2 other individuals. The high density of *E. dentatus* seemed to affect the behavior of major prey species; various grapsid crab species reduced their climbing activity during the peak activity periods of *E. dentatus*. The density of *E. dentatus* among the mangrove roots was determined both by the number of suitable dens, and, more directly, by the density of prey species.

Decapod crustaceans, together with molluscan species, are among the dominant taxa of the mangrove macrofauna of the Indo-Pacific region (Macnae, 1968). The mangrove decapods are dominated, in both biomass and biodiversity, by the Brachyura, more particularly by the families Ocypodidae and Grapsidae, although some species of Portunidae and Xanthoidea are often present (Davie, 1982; Jones, 1984; Macintosh, 1988).

In terms of their feeding ecology, the mangrove Ocypodidae can be divided into: (1) microalgal filter-feeders, represented by the genus *Uca* and the subfamily Dotillinae (see Hartnoll, 1973; Icely and Jones, 1978); (2) deposit-feeders, such as the Macrophthalminae; and (3) scavengers and predators, such as the ghost crabs of the genus *Ocypode* (see Macintosh, 1988). On the other hand, most of the Grapsidae can be considered generalistic omnivores, although in the mangrove environment they all depend to some extent on mangrove leaves and leaf litter (Warner, 1977; Cannicci *et al.*, 1996c; Dahdouh-Guebas *et al.*, in press).

With few exceptions, mangrove ocypodids and grapsids are semiterrestrial crabs active during low tides (Hartnoll, 1988). Thus, during their activity, they can be considered relatively safe from predation by carnivorous Portunidae common in the channels (Warner, 1977; Hill, 1976; Cannicci *et al.*, 1996a).

Recent studies carried out in Kenya (Dahdouh-Guebas *et al.*, in press) revealed that swimming crabs are not the only brachyurans of the mangrove forests to rely on predation

for survival. In fact, the natural diets of the two xanthoid species common within the Kenyan mangroves, *Eurycarcinus natalensis* (Krauss) and *Epixanthus dentatus* White, are also based on predation upon semiterrestrial species of mangrove crabs and upon gastropods.

In spite of the extensive information about predatory habits of tropical xanthoids active on rocky shores (Vermeji, 1977; Vannini *et al.*, 1989; Seed and Hughes, 1995), nothing, except the preliminary work by Dahdouh-Guebas *et al.* (in press), is known about the biology and behavior of mangrove xanthoid predators. Activity rhythms and peculiar behaviors of herbivorous mangrove species have often been explained as antipredator adaptations (Hartnoll, 1988; Cannicci *et al.*, 1996b), but no data are yet available on the predatory behavior of carnivorous mangrove species.

The aim of this study was thus to evaluate the pressure that *E. dentatus* exerts on the invertebrate fauna of the mangal ecosystem, in order to assess whether this may affect the behavior of prey species.

MATERIALS AND METHODS

Epixanthus dentatus is a medium- to large-sized member of the Oziidae well distributed throughout the Indo-West Pacific region, from East Africa to northern Australia (Guinot, 1967; Davie, 1982). It is always associated with mangroves, but seems to choose different habitats within the forest. Macnae (1968) found this species only under stones or within the crevices of the mangrove scarps of Malaysian forests, while Davie (1985) stated that the primary habitat of *E. dentatus* in Australia consisted of logs, stumps, or trees of the forests. On the Kenyan coast, Vannini *et al.* (in press) recorded a distribution more similar to that observed by Davie in Australia, finding *E. den-*

tatus well distributed throughout the *Rhizophora mucronata* Lam. belt of the swamp.

Study Area and Methods.—Collections, observations, and experiments were conducted in the Dabaso forest, located within the Mida Creek, 20 km south of Malindi, Kenya. The study site was tidally flooded twice a day. At High Water Neap Tide (HWNT) the more seaward tree roots were covered by 80 cm of water, while the landward fringe was covered by only a few cm; at High Water Spring Tide (HWST) sea levels were 170 cm and 100 cm, respectively.

From 1992–1994, 19 specimens were collected for analysis of the stomach contents. Immediately after collection, the sex and carapace width of all specimens were recorded. They were then placed in 70% alcohol. The analysis took place within 1 month of sampling. The stomach contents were washed with alcohol into a petri dish and examined under a binocular microscope. Animal remains found in the stomachs were identified to the finest possible taxonomic level.

The morphology of the gastric ossicles was analyzed with SEM. Gastric mills of specimens were removed and the gastric ossicles were dehydrated by sequential washes in 95% and 100% alcohol, dried, and then mounted on SEM stubs.

The first observations on patterns of predation and activity rhythms of *E. dentatus* were carried out in July–August 1994. A transect of 60 m was chosen within the *Rhizophora* belt, where this species is most common. We performed linear surveys every 30 min, regardless of the tidal phase, using torches and diving goggles when needed. During these sessions, carried out in two 24-h periods around Spring tide and 2 around Neap tide, all the active *E. dentatus* were recorded, together with their position with respect to the water level and, when possible, the kind of prey on which they were feeding.

A second session of observations and experiments was carried out in November–December 1995, along the transect used during the previous observations. All trees surrounding the path were marked with numbers and a total of 58 *E. dentatus*, found among the roots of these trees, were captured, measured with calipers, individually marked, and released on the tree where they were captured. All crabs observed and marked were adult specimens, with carapace widths ranging between 26 and 47 mm; no subadult or smaller specimens were observed within the transect. Moreover, females (*N* = 44) were more than 3 times as abundant as males (*N* = 14).

Two numbered pieces of Dymo tape were attached with Superglue® to the cardiac region of the carapace and to the major claw. We employed this double-marking procedure because, although very often the number on the carapace was easily recorded when the crabs were active on the roots, the tag on the major claw was the only one visible when the crabs hid themselves inside their burrows.

During the following 3 weeks, day and night surveys were performed in which the position and behavior of the marked specimens were recorded, together with the presence and behavior of unmarked specimens. During the daytime surveys, the dimensions and general shape of the dens occupied by the marked *E. dentatus* were measured, together with all the crevices and dens of the same shape and dimensions found among the root systems of *Rhizophora mucronata*.

Spontaneous excursions of single specimens were quantified by measurement of the distance between the 2 most distant points at which they were found during the surveys.

The number of active specimens of one of the most common prey of *E. dentatus*, the tree crab *Sesarma leptosoma* Hilgendorf, was chosen for comparison with the number of *E. dentatus* found active on living and dead trees. Information about the number of *S. leptosoma* migrating toward the canopy of living and dead trees of the experimental transect was collected with the techniques described by Vannini and Ruwa (1994). Data on the 2 species were standardized on the basis of maximum numbers of specimens per tree, because of the strong difference in the numbers of crabs of the two species recorded per tree.

After the activity patterns of *E. dentatus* had been assessed, 15 crabs were captured and experimentally displaced to points 6–15 m distant from their dens. Their positions were then recorded during all the following surveys.

RESULTS

Predatory Activity

Pictures taken with SEM show that the urocardiac ossicle of the stomach of *E. dentatus* has a large single dorsal tooth (Fig. 1A) and the two zygocardiac ossicles have large anterior lateral teeth, typical of carnivorous crabs (see Warner, 1977) (Fig. 1B).

Fifteen of the 19 stomachs analyzed were empty, while the other four contained animal prey that was strongly crushed but still identifiable as *Littorina scabra* (L.), *Clibanarius longitarsus* (de Haan), *Metopograpsus thukuhar* (Owen), and a specimen of the genus *Uca*.

Field observations revealed that, while preying, *E. dentatus* stands still, with its claws wide open and with the cardiac region of the carapace flattened against the base of the aerial roots (Fig. 2), in a posture reminiscent of the defense posture of many xanthoids. It grasps the base of the roots with the walking legs, ready to strike and catch any slowly moving invertebrates that come within reach, including animals larger than itself (Table 1). The major claw is used to crush the shell or carapace of small prey, such as *Littorina scabra* or *Sesarma leptosoma*, or to grasp at the larger crab species, such as *Thalamita crenata* H. Milne Edwards or *Neosarmatium smithi* (H. Milne Edwards), while the minor chela is used to cut into the carapace and open it. Although *E. dentatus* usually stood still in their ambush posture for almost all the activity period, on two occasions specimens moved to vertebrate carrion (a puff adder and a chicken) and to feed on it.

At low tide, the crabs abandon their dens and can be observed half-sunk in the mud among the roots of *R. mucronata*, in the position described above. During the ebb and

Fig. 1. SEM photomicrographs of the stomach ossicles of *Epixanthus dentatus*. Dorsal view of the urocardiac ossicle (A) and lateral view of one zygocardiac ossicle (B). Scale = ×30.

flow of the tide and at high tide, active *E. dentatus* left the mud surface and climbed to the higher roots. They maintained themselves in the same open-clawed position, but stood between 20 cm above and 10 cm below the water level, to a maximum recorded height of 170 cm above the substrate. In spite of their good climbing ability, no *E. dentatus* was observed on the more seaward trees at HWST, when the water completely covered the root system and only the trunk was still above the water.

The Dabaso population of *E. dentatus* was significantly more (approximately 10 times) active during the night than in daytime (Table 2). During the night the crabs were active both at low and high tide, and there were no significant differences between the number of active crabs recorded at Spring versus Neap tide.

Spatial Strategies

Eighty-one % (*N* = 47) of the marked crabs were observed in the transect three or more times, and only six unmarked crabs were recorded on the experimental trees during the three weeks of observation.

The length of the spontaneous excursions was independent of the duration of the observation period both in males (*R* = 0.07, *d.f.* = 8, *P* = 0.86) and females (*R* = 0.21, *d.f.* = 35, *P* = 0.22) (Fig. 3), although the spontaneous excursions of males (12.77 m ± 5.09)

Fig. 2. Schematic drawing of the predatory position assumed by *Epixanthus dentatus* during its ambush activity.

Table 1. Number of prey captured by *Epixanthus dentatus* during observation sessions.

Prey	Observations
Polychaeta	1
Littorina scabra (L.)	4
Merguia oligodon (de Man)	1
Clibanarius laevimanus Buitendijk	2
Clibanarius longitarsus (de Haan)	1
Thalamita crenata H. Milne Edwards	5
Uca sp.	1
Metopograpsus thukuhar Owen	3
Sesarma guttatum A. Milne Edwards	2
Sesarma leptosoma Hilgendorf	6
Neosarmatium smithi (H. Milne Edwards)	2
Total	28

Table 2. Difference in the number of active *Epixanthus dentatus* recorded during different tidal (high/low and Spring/Neap) and light conditions. Average number of crabs recorded per condition and number of surveys performed, *N*, are also shown. Three-factor ANOVA with logarithmic transformation. None of the interactions among the three factors was significant.

Source of variation	N		Average number		F	d.f.	P
Day versus night	39	37	0.72	7.59	48.185	1	< 0.0001
High versus low tide	19	57	4.89	3.79	0.188	1	0.666
Spring versus neap tide	24	52	4.33	3.50	0.006	1	0.939

were significantly longer than those of females (3.23 m ± 1.38) ($G = 9.416$, $d.f. = 3$, $P < 0.05$, G-test) (Fig. 4). There was no significant relationship between the length of the spontaneous excursions and the size of the crabs ($R = 0.09$, $d.f. = 45$, $P = 0.547$) (Fig. 5).

No marked specimen visited more than three trees of *R. mucronata* during the observation period, and 66% ($N = 31$) of the reobserved *E. dentatus* were always resting or in the predatory posture on the same tree.

Epixanthus dentatus were never observed actively digging or maintaining their dens. They simply used natural dens formed by the last junctions of the roots as they enter the mud. However, not every crevice seemed to be suitable. Out of 30 measured dens, 25 were funnel-shaped dens with narrow entrances of approximately 10 cm^2 and an approximate average volume of 105 cm^3 (Fig. 6A), which remain drained of water at low tide. The other five crabs sheltered in small depressions in the mud situated among thick and densely packed groups of roots (Fig. 6B).

The results of the experimental displacements show that 11 (91.7%) of the 12 displaced females were able to return to their dens within a week, while only one of the three males returned home in the same period. Homing times, i.e., the number of days each

crab needed to return to its den, were not correlated with the displacement distances ($R = 0.22$, $N = 12$, $P = ns$) (Fig. 7).

For each living tree, all dens in which an *E. dentatus* was recorded to hide for at least a full low tide were identified as "suitable dens." On the other hand, for dead trees, the suitable dens were subjectively defined by the observer on the basis of the measurements collected for the living trees. The number of *E. dentatus* faithful to living marked trees ($N = 2.81 ± 0.70$) was highly correlated with the number of suitable dens recorded among the tree roots ($N = 2.96 ± 0.31$) ($R = 0.594$, $N = 29$, $P < 0.01$); the average number of specimens faithful to seven dead trees and the number of suitable dens were, respectively, $0.29 ± 0.36$ and $4.2 ± 1.84$. While the average number of living trees in a 100-m^2 area of the Dabaso forest is nine, the average number of active *E. dentatus* living in the same area is about 25.3.

ANOVA with log transformation (due to the Poisson-like data distribution) of the numbers of *E. dentatus* and *S. leptosoma* active on living and dead trees (Table 3) shows a significant decrease in the number of individuals present on dead trees for both species ($F = 90.17$, $d.f. = 1$ and 35, $P < 0.001$), together with an obvious difference in the frequency of the two species (*S. leptosoma* be-
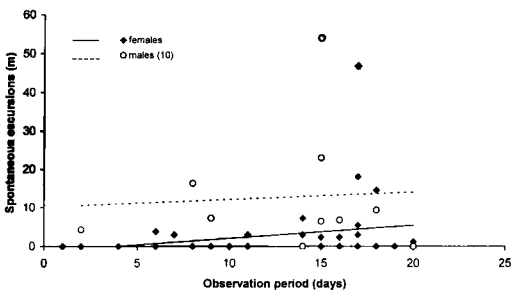

Fig. 3. Relationship between total days of observations and total length of spontaneous excursions performed by female and male *Epixanthus dentatus*. Regression lines for both females and males are shown.
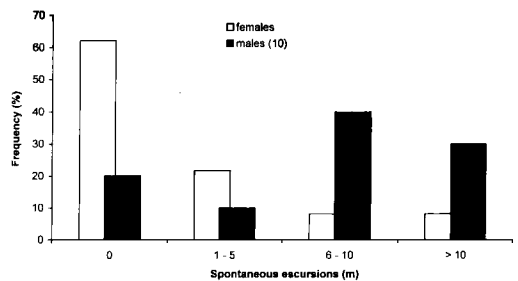

Fig. 4. Percentage frequency of spontaneous excursions of different length performed by individually marked females and males of *Epixanthus dentatus*.
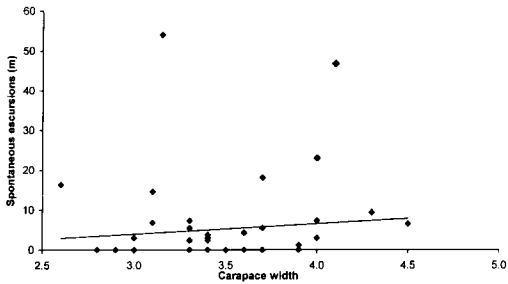
Fig. 5. Relationship between body size and total length of spontaneous excursions performed by marked *Epixanthus dentatus* (males and females pooled data). Regression line is shown.

Fig. 7. Relationship between the homing times of experimentally displaced *Epixanthus dentatus* and the distances of the release points (displacement distance). Regression line is shown.

ing the more frequent one ($F = 61.12$, $P < 0.001$) and a significant interaction ($F = 25.94$, $P < 0.001$; the frequency decrease being more intense for *S. leptosoma*).

Epixanthus dentatus was able to prey upon practically all the invertebrate fauna common in the Dabaso swamp (Table 1), including prey equal in size or larger than itself, such as *Thalamita crenata* and *Neosarmatium smithi* (H. Milne Edwards). Among the commonest species of the swamps, the only one not eaten by *E. dentatus* is the large snail *Terebralia palustris* L., which was very com-
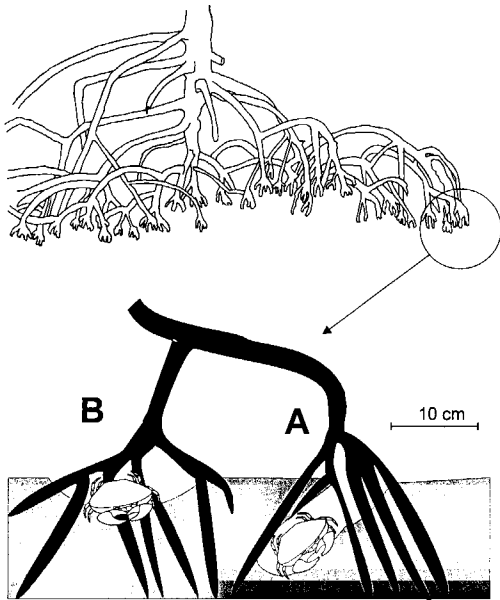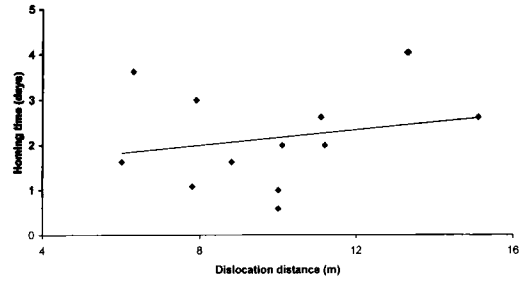

Fig. 6. Schematic drawing representing the two typical kinds of natural crevices utilized by *Epixanthus dentatus* as dens.

mon on the mud surface. Its shell is probably too strong to be broken. Fiddler crabs, although very common in the swamp, do not seem to be an important resource for this crab, probably because *Uca* spp. are strongly diurnal (Icely and Jones, 1978; Hartnoll, 1988) in their activity and never climb on the root system of *R. mucronata* (Vannini *et al.*, in press). Thus, they would not be available to a predator with nocturnal habits (Table 2) and good climbing ability, such as *E. dentatus*.

The shape of the gastric mill ossicles confirms the predatory nature of this species. The urocardiac ossicle bears a single dorsal tooth (Fig. 1A), as in the majority of carnivorous crabs (see Warner, 1977). This tooth can crush solid food with the help of the large anterior lateral teeth present in the zygocardiac ossicles (Fig. 1B).

Although the diet of *E. dentatus* is based on a wide variety of items, only four of the 19 stomachs analyzed had contents. This suggests that either *E. dentatus* has a poor success rate, or it has a very rapid stomach clearance rate, typical of predatory species (see Hill, 1976). Probably it is due to both these factors.

The activity of *E. dentatus* was affected by the water completely covering the roots of *R. mucronata*. This can, however, be explained by the fact that *E. dentatus* is not physically able to grip the trunk of the tree with its walking legs and must therefore stay on the roots, where it can maintain a good hold. Thus, when the root system is submerged, this crab cannot maintain itself near the water level and it gives up trying to ambush, probably to avoid more powerful swimming predators. A few preliminary observations on specimens with Light Emitting Diodes (LEDs) attached seemed to support this hypothesis. In fact,

Table 3. Average numbers and SE of *Epixanthus dentatus* and of migrating *Sesarma leptosoma* recorded per tree.

	Living trees			Dead trees		
	Average number of crabs	SE	Number of trees	Average number of crabs	SE	Number of trees
Epixanthus dentatus	2.8	0.37	24	0.4	0.25	5
Sesarma leptosoma	72.5	18.60	7	2.3	1.86	3

marked crabs not only gave up ambushing, but they also disappeared deeply within their burrows during maximum high tides.

The data on both the number of specimens actively preying, and on the number of suitable dens, show a 0.25 ind./m^2 density. This value is high with respect to estimates for smaller crabs common in mangal ecosystems (see Jones, 1984; Macintosh, 1988) and indicates that *E. dentatus* is a significant predator of arboreal crabs within the study area.

Finally, our preliminary observations suggest that habitat preferences of the prey can be a limiting factor for the survival of the predator itself. In fact, the females of *E. dentatus* relied on well-defined and long-standing feeding areas (Figs. 3, 4), to which they are able to return if experimentally dislocated (Fig. 7). The feeding and activity range is shared with an average of two other females, and consists of the entire aerial root system of a tree of *R. mucronata*. Such a root system also shelters an average of 300 individuals of *S. leptosoma* (Vannini and Ruwa, 1994). The abandonment of dead trees by *S. leptosoma* (which feed on fresh mangrove leaves) (Cannicci *et al.*, 1996c) was recorded, together with the disappearance of *E. dentatus*, despite the fact that the number of suitable dens remained high.

Although *S. leptosoma* is by far the most common crab in the study area, the roots of *R. mucronata* are also densely populated by other species. For example, about five *M. thukuhar* and three *S. guttatum* A. Milne Edwards per m^2 were recorded in the same area (Cannicci *et al.*, 1996b; Vannini *et al.*, in press). No data are yet available to indicate a similar disappearance of these species from the dead tree roots. Thus, more work has to be done to determine whether or not *E. dentatus* is affected solely by the disappearance of *S. leptosoma* from the dead trees or by the eventual collapse of the whole decapod community.

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Addresses: (SC, MG) Dipartimento di Biologia Animale e Genetica "Leo Pardi," Università di Firenze, via Romana 17, I-50125 Firenze, Italy (e-mail: scann@eurorock.dbag.unifi.it); (RKR) Kenya Marine and Fisheries Research Institute, P.O. Box 81561, Mombasa, Kenya; (MV) Museo di Zoologia "La Specola," via Romana 17, I-50125, and Centro di Studio per la Faunistica ed Ecologia Tropicali del CNR, via Romana 17, I-50125 Firenze, Italy.