

Feeding and burrowing ecology of two East African mangrove crabs

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Abstract. The behavior and ecology of two mangrove crabs, *Sesarma meinerti* De Man, 1887 and *Cardisoma carnifex* (Herbst, 1794) were investigated at the beginning of the rainy season (October–November 1988) at Mida Creek, Kenya. Both species occupy upper intertidal levels, above mean high-water neap, and completely overlap in their zonation. Each burrow lasts ca. 3 wk, with no significant difference between the species. Both are more active around dusk and dawn and also follow a similar trend in their foraging activity, but differ in that burrowing is mainly diurnal in *C. carnifex* and nocturnal in *S. meinerti*. A hierarchy of food preference, established by offering *C. carnifex* and *S. meinerti* leaves of five mangrove species, proved similar for both, with *Bruguiera gymnorhiza* ranking first and *Avicennia marina* last, but significant only for *C. carnifex*. A rough estimate of the amount of litter consumed by these two species and of the soil mixed up by their burrowing activity indicates that they play a role of primary importance in the ecology of East African mangroves.

Introduction

To date, ecological work on East African mangrove crabs has been surprisingly scant. Extensive studies conducted over the last 20 yr on the mangrove ecology of the Caribbean (Odum and Heald 1975) and, more recently, of Southeast Asia (Malley 1978, Nakasone et al. 1982, Leh and Sasekumar 1985, Lee 1989) and Australia (Robertson 1986, Robertson and Daniel 1989), have pointed out that mangrove crabs (mainly Sesarmidae, Grapsidae, Ocypodidae and Gecarcinidae) play a central role in the energy flow of these coastal ecosystems and have a considerable impact on the soil structure and chemistry. The burrowing activity of crabs in mangroves and salt marshes may strongly affect the substratum topography, granulometry (Warren and Underwood 1986) and soil chemistry (Daiber 1977, Montague 1980, 1982, Jones 1984, Bertness 1985).

Grazing on fresh mangrove litter is typical of most Sesarmidae and Gecarcinidae. In Queensland, Sesarmidae remove up to 80% of the annual leaf fall (Robertson and Daniel 1989) and 75% of the propagules (Smith 1987 a) from the forest floor, while in Florida and Panama, crabs have been indicated as minor consumers of the forest primary production (leaves: Odum and Heald 1972, 1975; propagules: Smith et al. 1989).

A list of crab species is available for most East African countries, but only a few notes are given on their ecology (Somalia: Vannini and Valmori 1981 a, b; Madagascar: Crosnier 1965; Tanzania: Hartnoll 1975; South Africa: Barnard 1950), with the exception of South Africa (Macnae 1963) and Mocambique (Macnae and Kalk 1969) where the subject has been treated extensively. Few studies have dealt with *Cardisoma carnifex* and *Sesarma meinerti*, two of the most common African mangrove crabs (*C. carnifex* in Aldabra: Grubb 1971, Alexander 1979; *S. meinerti* in Mocambique: Cott 1929; both species in Kenya: Hogue and Bright 1971). The aim of the present paper is to give a preliminary assessment of their ecological role in Kenyan mangroves, particularly their litter consumption and impact on the soil. Three questions were addressed: (1) Do habitat use and/or activity patterns of the two most abundant crab species differ? (2) How is the soil affected by their burrowing activity? (3) Are leaves of different mangrove species removed at different rates?

Materials and methods

Species

Sesarma meinerti De Man, 1887 (family: Sesarmidae, according to Guinot's classification 1978) is widely distributed in the Indo-Pacific, from the coasts of Africa (from Somalia to Natal) to Madagascar and Australia (Vannini and Valmori 1981 a). This medium-sized crab (maximum carapace width 4 cm) digs straight, non-branched holes whose depth has been recorded as possibly more than 1 m (Hogue and Bright 1971), and 3 to 4 ft (ca. 0.9 to 1.2 m), based on one burrow only (Cott 1929). *S. meinerti* is, according to

a stomach content examination, almost entirely herbivorous (Cott 1929, M. Giuggioli personal communication).

Cardisoma carnifex (Herbst, 1794) (family: Gecarcinidae) is a large (9 cm carapace width) terrestrial crab, ranging from the Red Sea to Natal, Aldabra, Andamans, Japan, Formosa, Celebes and Polynesia, and is the only species of Gecarcinidae found in East Africa (Vannini and Valmori 1981 b). The burrow of this species, described by Hogue and Bright (1971), has a single entrance, like that of *Sesarma meinerti*. Burrows can be as long as 2 m, generally reaching the water table and ending in an enlarged chamber. The crab feeds on a variety of organic materials, mainly plant parts (Grubb 1971, Alexander 1979, Lee 1988).

Study sites

The work was conducted in October–November 1988 at Mida Creek, Kenya. Five species of mangrove are present in this area (*Avicennia marina*, *Rhizophora mucronata*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, and *Sonneratia alba*). A map and description of this area is given by Lumsden (1955). Zonation, burrow turnover and activity rhythms were studied in a grove (Site 1) where *A. marina* is the dominant species, with the occasional presence of *R. mucronata* and *C. tagal*. Leaf preference experiments were carried out at an adjacent site (Site 2), harboring all the mangrove species listed above. In both groves *S. meinerti* and *C. carnifex* were the dominant crab species at the high intertidal level. *Sesarma ortmanni* and *S. eulimene*, the other sesarmids reported in this area (Hogue and Bright 1971, Bright and Hogue 1972), were never found at the study site. At lower levels, species of Ocypodidae prevailed: fiddler crabs [mostly *Uca lactea annulipes* (H. Milne Edwards, 1837)], and ghost crabs (*Ocypode ceratophthalmus* Pallas, 1972). Several species of Xanthoidea and Portunidae were found in the subtidal environment.

Zonation

Burrow density and zonation were studied along a 4-m-wide transect running across the mangrove belt, from high-water neap tide level (HWN) to the landward limit of the mangrove trees. Burrows belonging to different crab species were counted in each 4 × 4 m quadrat of the transect.

Burrows were attributed to one of the two species according to the size of the entrance hole and other external features. *Cardisoma carnifex* burrows have large (usually 8 to 12 cm in diameter), round, well-defined entrances, hooded by a semicircular mound of dried mud. *Sesarma meinerti* burrows are smaller (4 to 6 cm in diameter), more irregular in shape, and are never hooded. As pointed out by Hogue and Bright (1971), feeding pellets – round in *S. meinerti* and rod-shaped in *C. carnifex* – often surround the entrances, and constitute an additional criterion for discrimination. There was a risk that small *C. carnifex* burrows were confused with large *S. meinerti* ones, but small specimens of the former species (the less common) were rarely seen, and thus such confusion would be minimal.

Burrow turnover

Burrows were counted every 3 d, from 20 October to 8 November 1988, in six permanent circles (2 m in diameter) traced on the ground, far apart, in a zone where crab density was about the highest recorded for both species. On each visit a map of the circle was drawn, recording the appearance of new burrows and the disappearance of old ones. The duration of randomly selected burrows was monitored over a 3 wk period by marking their entrances with numbered pegs.

Foraging and digging rhythms

Ca. 50 burrows bordering a 100 m path were chosen at random and marked. The burrows were checked hourly for 24 h on three occasions (new moon, 1st quarter, full moon), and burrowing and walking activity was recorded by observing the round pellets (residue of digging) and ground surface marks. After every record, the ground was carefully smoothed and the pellets removed. Air temperature was measured hourly.

Leaf preference

Leaf choice experiments were performed in the field by offering each crab ten leaves, arranged symmetrically around the burrow entrance at a distance of 20 cm and kept in place by a wire grid. Two series of leaves of five mangrove species were used each time, with the species always arranged in a different sequence.

Tests were performed early in the morning, when crab foraging was most intense. Each crab was tested once. During a single test, leaves taken by the crab were replaced every 10 to 15 min from two to eleven times, according to the crab's voracity. Leaves of approx. the same age (yellow leaves, just-fallen or easily abscised, i.e., ready to fall) were used. In order to test the influence, if any, of leaf size on crab preference, the length, width and weight (after oven drying for 3 d at 65°C) of ca. 20 randomly selected leaves of each species were measured.

Results

Zonation

The burrow zonation of *Cardisoma carnifex* and *Sesarma meinerti* was quite similar, both overlapping with the *Avicennia marina* distribution (Fig. 1). The density of *C. carnifex* was reduced only in those areas where pneumatophore density was high (40 to 55 m from HWN), probably because the large size of this crab species makes digging among pneumatophores difficult. The range of *Ocypode ceratophthalmus* was limited to the seaward fringe of the *Avicennia* belt, barely overlapping the other crab species, while *Uca annulipes* was found in the lower intertidal zone, limited to a narrow belt beyond the trees, with just a few pneumatophores. The highest recorded densities (number of burrows m⁻²) were 0.25 for *C. carnifex*, 11.64 for *S. meinerti*, 0.81 for *O. ceratophthalmus* and 0.81 for *U. annulipes*.

Burrow turnover

During the study period, the burrow density of both crab species varied significantly between observation areas but not with time (Table 1).

During one spring (new moon) and one neap tide, the volume of all the excavated material that was scattered around ca. 20 burrows of each species was evaluated at 1 h intervals for 24 h. The ground pellets were assigned to a diameter class of 1, 1.5 or 2 cm. Diameters were converted to volumes (in cm³), assuming that the pellets were spherical in shape. The total per burrow volume of material excavated over 24 h was calculated (Table 2).

Table 1. *Sesarma meinerti* and *Cardisoma carnifex*. Number of burrows of each crab species monitored on six occasions, in six areas (a to f; 3.14 m² of surface each) marked on the forest floor at distances varying between 10 and 22 m from high-water neap tide level. NS: not significant

Date	<i>S. meinerti</i>							<i>C. carnifex</i>						
	a	b	c	d	e	f	Avg.	a	b	c	d	e	f	Avg.
23 Oct.	4	6	8	16	18	14	11.0	1	0	1	0	0	1	0.5
26 Oct.	3	2	18	18	16	12	11.5	1	1	0	1	1	2	1.0
29 Oct.	2	2	12	15	13	20	10.7	1	1	1	0	0	3	1.0
1 Nov.	3	7	14	15	17	22	13.0	1	1	0	0	0	0	0.3
3 Nov.	4	9	13	21	18	17	13.7	1	1	0	0	0	0	0.3
8 Nov.	4	4	12	9	14	7	8.3	1	1	0	0	0	0	0.3
Avg.	3.3	5.0	12.8	15.7	16	15.3	11.4	1.0	0.8	0.3	0.2	0.2	1.0	0.6

ANOVA (after square root transformation):

	Among days (df=5,25)	Among areas (df=5,25)
<i>S. meinerti</i>	F=2.17, NS	F=25.23, p<0.01
<i>C. carnifex</i>	F=1.96, NS	F= 3.36, p<0.05

Table 2. *Sesarma meinerti* and *Cardisoma carnifex*. Average volume (in cm³) of excavated matter per burrow over a 24 h period, in different tidal periods, compared between species. NS: not significant

Tidal period	No. of burrows	cm ³ of matter	
		Avg.	SE
Neap tide			
<i>S. meinerti</i>	22	14.7	4.10
<i>C. carnifex</i>	18	2.4	1.44
Spring tide			
<i>S. meinerti</i>	27	40.0	10.33
<i>C. carnifex</i>	19	27.7	14.95

ANOVA (after square root transformation):

F(species) = 4.71 (df=1,82), p<0.05
 F(periods) = 6.00 (df=1,82), p<0.05
 F(interaction) = 0.01 (df=1,82), NS

The amount of soil dug proved to be significantly different between both species and tidal periods. *Sesarma meinerti* was more active than *Cardisoma carnifex*, and both species were more active at spring tide than at neap tide. The average combined volume excavated during the two tidal periods by both crab species was measured in two areas of the transect where they were densest. The amount of soil excavated per m² over 24 h varied from roughly 210 cm³ (at spring) to 80 cm³ (at neap).

Together with burrow density, the numbers of collapsed and freshly dug burrows were recorded on six observation dates (from 20 October to 8 November in the six circles). The average daily turnover, excluding records immediately after extreme high spring tide when most burrows collapsed and were dug again, was about 9% (average=8.7%; confidence limits: 5.8 to 11.6%).

If it is assumed that only the oldest burrows are destroyed, then the average burrow life is 100/8.7=11.5 d. The pattern differs if burrows are destroyed at random, in which case, as shown by a simple simulation, 95% of the burrows are destroyed after 32 d (confidence limits: 23 to 42 d; Fig. 2). The simulation was carried out adopt-

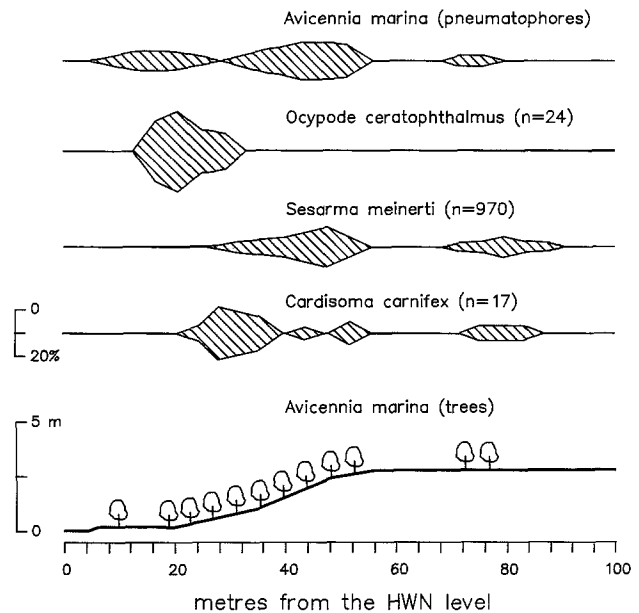


Fig. 1. *Ocyropsis ceratophthalmus*, *Sesarma meinerti* and *Cardisoma carnifex*. Mida Creek, Site 1. Schematic forest profile and crab burrow zonation. Vertical scale represents percentage of burrows of each crab species over the total number of burrows counted in the transect. Tree and pneumatophore densities established using arbitrary units. *Uca annulipes* burrows (distribution not shown) occupied a narrow band at the seaward limit of the section of forest represented in diagram. n = total number of burrows; HWN = high-water neap tide level

ing a burrow density equal to 11.6 burrows m⁻², assuming that 8.7% (varying this value between its confidence limits: 5.8 to 11.6%) of the burrows were abandoned daily and dug anew, regardless of their "age". The procedure was reiterated for a total of 5000 d, and burrow durations were averaged for each turnover rate considered.

We marked 107 *Sesarma meinerti* burrows and checked for 25 d (Fig. 3), by which time about 95% of the marked burrows had been destroyed. A similar pattern was found for 45 burrows of *Cardisoma carnifex*.

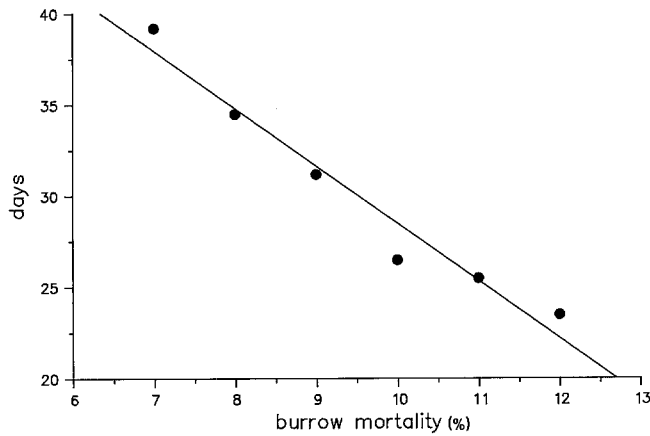


Fig. 2. *Sesarma meinerti* and *Cardisoma carnifex*. Relationship between percentage daily burrow destruction ("mortality") and number of days necessary for 95% burrow turnover. Actual value of daily burrow destruction (averaging densities of new and caved-in burrows) measured at Site 1 was ca. 9%. Simulation involved 5000 trials for each point

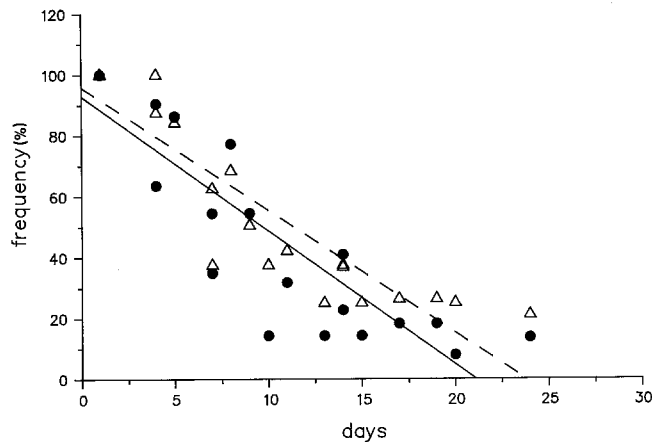


Fig. 3. *Sesarma meinerti* and *Cardisoma carnifex*. Burrow disappearance rate of 152 burrows (107 belonging to *S. meinerti* and 45 to *C. carnifex*) marked and individually checked for 25 d. Frequency = % of marked burrow openings still present. (●) *S. Meinerti*; (Δ) *C. carnifex*

Foraging and digging rhythms

Within the new moon spring tide and the neap tide observation cycles, both species' activity was concentrated around dawn and dusk. In *Cardisoma carnifex* this was true for both digging and foraging activity, while in *Sesarma meinerti* digging activity continued throughout the night (Fig. 4). *C. carnifex* activity started well before dusk and ended after dawn, while *S. meinerti* activity peaks were sharper and the individuals rarely left their burrows during the day. The activity of *S. meinerti* did not differ between neap and new moon spring tides, whereas in *C. carnifex* evening activity at neap tide was strongly reduced. Both species were active during the full moon spring tide, with no apparent periodicity. On this date an extremely (equinoctial) high tide occurred, together with heavy rainfall.

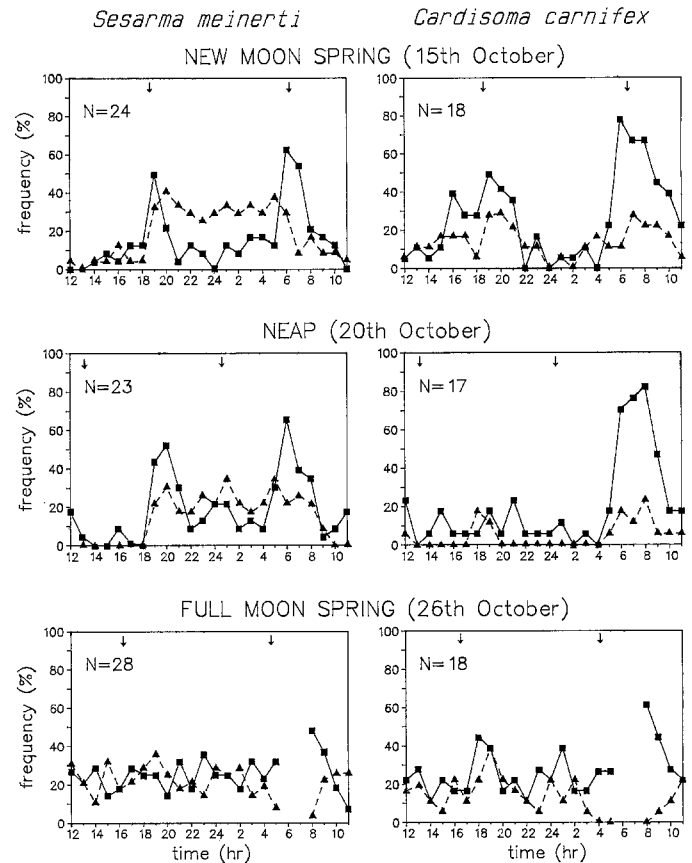


Fig. 4. *Sesarma meinerti* and *Cardisoma carnifex*. Daily foraging (■) and digging (▲) activity patterns at new moon, first quarter and full moon. Lack of data on 26 October from 5:00 to 7:00 hrs due to extensive tidal flooding of study area. N = number of burrows checked hourly. Frequency = % of burrows showing evidence of crab digging or walking. Arrows indicate the time of high tide

Table 3. *Sesarma meinerti* and *Cardisoma carnifex*. Spearman rank correlation test between relative frequency of active burrows (i.e., burrows with traces of digging or walking on total burrows) and intensity of such activities. In all cases the coefficient r_s is significant at least at the 99% level

Activity	New moon spring tide		Neap tide		Full moon spring tide	
	n	r_s	n	r_s	n	r_s
<i>S. meinerti</i>						
foraging	24	0.941	24	0.992	22	0.737
digging	24	0.926	24	0.936	22	0.742
<i>C. carnifex</i>						
foraging	24	0.933	24	0.925	22	0.892
digging	24	0.738	24	0.896	22	0.910

Activity intensity, evaluated (on a 1 to 4 scale) by the number of tracks and/or ground pellets at the burrow entrance, showed the same general trend (Table 3): the more burrows showing signs of activity, the greater the activity per burrow.

The duration of activity in each crab monitored, calculated as the percentage of observations in which signs

Table 4. *Sesarma meinerti* and *Cardisoma carnifex*. Hours of activity over a 24 h period (expressed as relative frequencies, %; SE in parentheses), at both spring (new moon) and neap tides. n = number of burrows monitored; NS: not significant

Species	Spring tide			Neap tide		
	n	foraging	digging	n	foraging	digging
<i>S. meinerti</i>	23	16.4 (2.1)	20.8 (2.6)	23	18.6 (2.7)	14.4 (2.9)
<i>C. carnifex</i>	18	28.2 (3.8)	13.9 (2.9)	17	19.1 (2.8)	3.8 (0.9)

ANOVA (on arcsin transformed data):

	Foraging			Digging		
	F	df	p	F	df	p
Crab species	4.53	1,77	<0.05	9.79	1,77	<0.01
Tidal period	1.17	1,77	NS	11.22	1,77	<0.01
Interaction	2.29	1,77	NS	0.19	1,77	NS

of activity were detected over 24 h, revealed that walking activity lasted longer in *Cardisoma carnifex*, but did not differ between spring and neap tides in either species (Table 4). Digging activity differed significantly between both species and tidal periods, lasting longer in *Sesarma meinerti* and at spring rather than at neap tide, confirming the findings for the amount of soil dug out of burrows.

Air temperature did not vary significantly between the observation dates but was significantly lower at night (ANOVA on non-transformed data; dates: $F=0.34$, $df=2,65$, NS; day-night: $F=71.64$, $df=1,65$, $p \ll 0.01$; interaction: $F=2.56$, $df=2,65$, NS). Diurnal temperature (averaging all hourly values for the three dates) was $28.2 \pm 0.4^\circ\text{C}$, nocturnal temperature $25.0 \pm 0.2^\circ\text{C}$.

Leaf preference

Because of the different number of leaves offered to each crab (according to its voracity) and different number of leaves eaten, data analysis was simplified by determining the hierarchy of preference shown by each crab for the five leaf species, independent of the actual number of leaves taken underground. Applying the Kendall correlation test to 21 *Sesarma meinerti* and 24 *Cardisoma carnifex* revealed no preference in food choice by the former but a significant hierarchy was evident in the latter (Table 5).

The preference sequence of *Sesarma meinerti*, though not significant, was similar to that of the other species. The order in which the leaves were arranged was changed in each trial, so that the crab's choice was independent of the grid position occupied by each leaf species. Leaves in front of the burrow (regardless of leaf species) were not significantly preferred over the lateral ones ($\chi^2=16.73$, $df=9$, NS = not significant, for *S. meinerti*; $\chi^2=16.81$, $df=9$, NS, for *Cardisoma carnifex*).

The number of mangrove leaves eaten by the crabs did not correlate significantly with the average leaf surface area (calculated as the product of the leaf axes) for

Table 5. *Sesarma meinerti* and *Cardisoma carnifex*. Preference for leaves of five mangrove species [(A) *Bruguiera gymnorhiza*, (B) *Sonneratia alba*, (C) *Rhizophora mucronata*, (D) *Ceriops tagal*, (E) *Avicennia marina*], for 258 leaves eaten by 21 *S. meinerti* and 262 by 24 *C. carnifex*. Average ranks and Kendall correlation coefficient (W) indicated; NS: not significant

Average ranks of:	Mangrove species					W	df	χ^2	p
	A	B	C	D	E				
<i>S. meinerti</i>	2.7	2.7	2.9	3.1	3.6	0.05	4	4.35	NS
<i>C. carnifex</i>	2.0	2.7	2.8	3.2	4.2	0.32	4	30.76	<0.001

each mangrove leaf species, in either *Cardisoma carnifex* ($r=0.55$, $df=3$, NS) or *Sesarma meinerti* ($r=0.53$, $df=3$, NS). The same result was obtained considering leaf dry weights (*C. carnifex*: $r=0.19$, $df=3$, NS; *S. meinerti*: $r=0.25$, $df=3$, NS).

In the early morning, when foraging activity was most intense in both species, ca. 9 leaves h^{-1} were buried in each crab burrow (*S. meinerti*: average = 10.7, SE = 1.6; *C. carnifex*: average = 8.4, SE = 1.2), with no significant difference between crab species ($t=1.2$, $df=42$, NS).

Based on average burrow density (Table 1), average daily duration of foraging activity (Table 4), and average daily percentage of burrows showing signs of foraging excursions (from Fig. 4), the combined potential leaf burial (and presumably consumption) quota of the two crab species, when offered an excess quantity of litter, is about 30 leaves $\text{m}^{-2} \text{d}^{-1}$ (34.2 at neap and 26.2 at spring tide) or, converting this value into leaf dry weight (averaging the values for the five species), ca. 14 g dry wt of leaves $\text{m}^{-2} \text{d}^{-1}$.

Discussion

Zonation

Both *Cardisoma carnifex* and *Sesarma meinerti* occupy the landward fringe of East African mangals, though the latter occasionally ranges down to the seaward fringe (Macnae 1968, Bright and Hogue 1972, Hartnoll 1975, Jones 1984). At Mida Creek (Kenya) the two species extend throughout the high intertidal grove, completely overlapping in their range, but are densest in a belt between mean and extreme high-water spring tide. Vannini and Valmori (1981 a) observed a similar zonation of burrows for the two species in the Giuba river estuary in Somalia, while elsewhere (Mauritius, Aldabra, Rodriguez; Vannini personal observation) these species were observed only in the upper intertidal levels.

Zonation was measured in a single transect where the mangrove belt was ca. 50 m wide; in adjacent sites, where the slope was much steeper, the belt was reduced (and thus crab burrows as well) to 3–4 m. Only a few burrows of *Cardisoma carnifex* and none of *Sesarma meinerti* were seen where trees were absent (in spite of the hard mud substratum preferred by both species; Bright and Hogue 1982), but burrows of both species were often found,

mingled as usual, under the cover of trees other than mangroves. (This has also been observed elsewhere: under coconuts in Kenya, casuarinas on Mauritius, mango trees in Somalia; Vannini personal observation). Thus both species seem to seek a relatively dry substratum (possibly because it guarantees longer burrow duration) under plant cover, which need not be mangroves. Here they coexist with no apparent spatial segregation.

Burrow turnover

It is a general ecological trend for the genus *Sesarma* that the primarily terrestrial species inhabiting the supralittoral zones do not dig burrows but rather use crevices and abandoned burrows, while the eulittoral species construct elaborate burrows (see Seiple and Salmon 1982 for references). Though *S. meinerti* has been reported to belong to the first category (Cott 1929), our observations indicate that its burrow turnover is comparable to that of the gecarcinid *Cardisoma carnifex*, reported to be an efficient burrower by Powers and Bliss (1983), and that ca. 10% of the *S. meinerti* burrow openings at the study site were dug anew daily. In fact, this species devotes a considerable percentage of its activity time to burrow maintenance (significantly longer than *C. carnifex*).

The average burrow duration of 25 d observed in both species is far above the theoretical 11.5 d foreseen if only old burrows collapsed. Furthermore, it is close to the lower limit determined in the case of random abandonment of burrows (23 d). The value actually found probably represents a compromise between these two models and indicates that both mechanisms are operating.

Because of the dryness of the upper soil layers, burrow entrances frequently collapse and are dug again, while the deeper parts – which probably do not collapse as often as the entrances – continue to be inhabited by the crabs. Thus, only entrances are continuously rearranged and often repositioned. Seiple and Salmon (1982) report a similar observation for *Sesarma reticulatum* in *Spartina* spp. salt marshes and suggest that crabs shift burrow entrances in order to approach new plants to feed on.

If most of the digging activity is confined to the upper 20 cm of soil, then the crabs manipulate about 0.07% of the soil daily (considering the average volume of soil dug out of burrows during a spring and a neap tide), i.e., they displace and mix up ca. one quarter of the upper 20 cm of soil per year. This frequent digging may enrich the mud surface both by oxygenating the soil and by bringing organic material to the upper layers. The soil turnover achieved by burrowing is known to increase the productivity of *Spartina alterniflora* vegetation in salt marshes (Montague 1982, Bertness 1985), and it is likely that it has a similar effect in mangrove forests.

Activity pattern

With increasing distance from the intertidal zone, crabs usually exhibit an activity pattern dependent mainly on the light-dark cycle, rather than on changes in water level

(Barnwell 1968, Palmer 1973). This seems to be true for these two species since, at both spring and neap tides, the principal activity peaks occurred at the same times of the day (around sunset and sunrise). Nevertheless *Cardisoma carnifex*, which digs holes as deep as 2 m (Hogue and Bright 1971) compared to the average 1 m of *Sesarma meinerti* (Cott 1929, Hogue and Bright 1971), may be affected to some extent by variation in the water level inside its burrow. This could explain the lesser intensity of this species' activity during the neap evening low tide. Instead, well-defined activity peaks were detectable on 15 October, when dusk and dawn coincided with high tide. No relationship between the crab's daily activity pattern and tidal cycle has been found in *Cardisoma hirtipes* (Goshima et al. 1978) and *C. guanhumi* (Palmer 1971).

During the full moon spring tide on 26 October, the study area was subjected to both flooding and a nocturnal rain shower. The effect of such a high moisture level for both soil and air on the land crabs' activity was to make it more or less continuous. This has also been observed in other species of Gecarcinidae (Bliss 1968, Hogue and Bright 1971, Goshima et al. 1978).

Cardisoma guanhumi is mainly nocturnal (Gifford 1962, Chace and Hobbs 1969, Palmer 1971) but, like *C. carnifex*, its activity may start well before dusk and terminate well after dawn (Henning and Klaassen 1973, Henning 1975), particularly in shaded biotopes (Powers and Bliss 1983). The tendency shown by this species to burrow under trees may allow it to prolong activity during diurnal hours.

Although some studies have detected a tidal component in the activity pattern of the eulittoral sesarmid *Sesarma reticulatum* (Palmer 1967, Seiple 1981), the only entraining agent for *S. meinerti* and another supralittoral Sesarmidae, *S. cinereum* (Seiple 1981), seems to be the dark-light cycle.

While *Cardisoma carnifex* and *Sesarma meinerti* exhibited a significant neap-spring variation in digging activity, their foraging did not differ between dates. Throughout a lunar cycle, surface conditions do not change dramatically since the grove is not flooded by most spring tides. However, the rise in water table level at spring tide may either moisten the soil, thus facilitating digging, or cause the burrows to cave in, forcing the crabs to restore them.

The most interesting feature emerging from this part of the present study is the partial temporal segregation in activity of the two species: *Cardisoma carnifex* is active during the night and day (possibly because of its greater resistance to high temperature and low humidity), while *Sesarma meinerti* is strictly nocturnal. Foraging excursions were carried out mainly around sunset and sunrise by both species, and therefore peaks of locomotor activity largely overlap. On the contrary, digging activity was performed throughout the night by *S. meinerti*, but only in the evening and morning by *C. carnifex*, with little sign of activity between 22:00 and 4:00 hrs. However, since the two species largely overlap both in their distribution and activity periods, the slight segregation observed is more likely due to a differential resistance to environmental stress or to a different susceptibility to diurnal preda-

tors (such as ibises and egrets, quite common at the study site) rather than to interspecific competition.

Feeding preference

Measurements of average litterfall in mangrove forests yielded values ranging from $0.3 \text{ g m}^{-2} \text{ d}^{-1}$ for scrub mangroves in south Florida, USA (Pool et al. 1975), to $6.4 \text{ g m}^{-2} \text{ d}^{-1}$ in Malaysia (Ong et al. 1982). Data on litter production are available (all within these limits) for the east coast of America (mainly Florida) and for southeast Asia (See Twilley et al. 1986) but not for Africa, though it is reasonable to expect a similar order of magnitude. The quantity of leaves that crabs store in their burrows was not directly measured here but rather inferred on the assumption that, in our experiments, only the burrow owner was foraging on the leaves offered (since crab tracks leading to adjacent burrows were not detected on the ground) and that the foraging rhythm of each crab is fairly constant throughout its activity period. Our datum represents a theoretical maximum rather than a direct measurement of the actual litter consumption rates, considering that litter was given in excess during the experiment and that crabs did not spend any time searching for food since this was presented right at the burrow entrance.

Nevertheless the value of $14 \text{ g m}^{-2} \text{ d}^{-1}$ roughly calculated for crab leaf removal in the present study is much greater than any previous measurements of litterfall in mangrove environments and also than the average 1.6 to $2.2 \text{ g m}^{-2} \text{ d}^{-1}$ crab litter consumption given by Robertson and Daniel (1989) for high intertidal forests in northeast Australia, which represents 71 to 79% of the total annual litterfall in those mangals. Despite the high degree of approximation, our estimate of litter removal by these crabs suggests that they are capable of eating a major proportion of the forest primary production, thus explaining the surprisingly low litter standing stocks observed at the study site.

Although, in the present study, mangrove seeds were not used in the food preference experiments, crabs were occasionally observed consuming propagules, and the seeds found on the forest floor often showed evidence of grazing. Since studies conducted in Australia and southeast Asia showed that mangrove crabs, by consuming mangrove propagules, influence the forest tree species composition (Smith 1987a, b, Smith et al. 1989), a similar impact of mangrove crabs on the forest structure might be envisioned in East African mangals.

Avicennia marina leaves are reported to have a high nitrogen and low tannin content, factors considered to favour herbivory (Robertson 1988, Camilleri 1989, Micheli submitted). These leaves were ranked first in laboratory food choice experiments carried out with *Sesarma* species (*S. erythrodractyla*, Camilleri 1989; *S. messa*, Micheli 1991). In all our field trials *A. marina* was the least preferred species, even though significantly so only in *Cardisoma carnifex*, so that leaf chemical properties, as well as leaf dimensions, probably do not affect the crab's choice. The rather low water content of *A. marina* might explain the crabs' feeding behavior since in high

intertidal forests, such as the one where the present research was carried out, water could be scarce and may be acquired only from such food as succulent leaves. The lower selectivity exhibited by *S. meinerti* might depend on factors other than food quality, such as the limited time available for foraging activity (this species spends significantly less time foraging than the other species) or insufficient litter availability. In contrast, *C. carnifex* might have access to alternative food sources during its longer-lasting foraging excursions. In other studies as well, field experiments have failed to show a leaf species preference even though this was evident in the laboratory (*Sesarma messa* and *S. smithii* in North Queensland; Micheli submitted).

Conclusions

Cardisoma carnifex and *Sesarma meinerti* largely overlap in habitat and resource exploitation: they occupy the same position in the intertidal gradient; both feed on mangrove leaves and dig burrows at comparable rates, and both display maximum activity at dusk and dawn, though *S. meinerti* seems to be strictly nocturnal while *C. carnifex* extends its activity period to diurnal hours. A slight spatial segregation between the two species is probably due to the smaller body size of *S. meinerti*, which allows this species to burrow also in areas of the forest with a high pneumatophore density. *C. carnifex* exhibits greater selectivity in its food choice, but a better knowledge of the diet of both species is needed in order to ascertain which factors control their feeding behavior.

Our measurements of the intensity of burrowing and leaf consumption give a rough estimate of soil and litter turnover rates. These results obviously need replication at different times of the year and in more than one grove. Nevertheless, they provide a first indication of the importance of land crabs in Kenyan mangals, together with the first quantitative description of some aspects of the behavior of these species.

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