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The East African Decapod Crab *Neosarmatium meinerti* (de Man) Sweeps Mangrove Floors Clean of Leaf Litter

Leaf litter removal by the abundant mangrove decapod crab *Neosarmatium meinerti* was studied in series of field and laboratory experiments in East Africa. In the high intertidal *Avicennia marina* zone crabs buried all leaves placed on the forest floor and consumed on average 67% of them within 2 hrs. High shore crabs in Kenya buried 4 g m⁻² leaf-litter in 1 hr, i.e. approx. twice the daily litter fall. In contrast, in the low shore *Sonneratia alba* zone, where typical leaf-eating crabs were absent, none of the offered leaves showed signs of herbivory. Leaf choice experiments in the laboratory showed that *N. meinerti* preferred some species to others. Leaf consumption per gram crab was higher in females than males. The laboratory studies also indicated that crabs could consume substantially more than the average daily litter fall. Video recordings documented frequent fights to gain or retain fallen leaves, suggesting strong competition for leaf litter. Earlier studies indicating that *N. meinerti* may sweep mangrove forest floors clean of leaf litter are confirmed. In high shore mangroves of East and South Africa where *N. meinerti* is common, energy flow appears unique: virtually all litter production is retained

INTRODUCTION

Mangrove ecosystems fringe tropical and subtropical coastlines throughout the world and function as nurseries for a wide variety of vertebrate and invertebrate marine species. Mangroves range among the most productive ecosystems in the world (1), primarily because of a high turnover of leaves and seeds (2). Based on the seminal works of Odum (3) and Heald (4), in the Caribbean the great majority of mangrove production was until recently believed to be exported to adjacent ecosystems (e.g. tropical lagoons and coral reefs) in the form of leaves. However, recent work by Robertson and colleagues has documented the importance of mangrove crabs in burying and consuming leaf litter within Australian mangrove forests (5–7). Robertson (5) and Robertson and Daniel (6) found that leaf-burial by crabs resulted in the retention of 28% of the leaf fall in low- and mid-intertidal forests, and 71–79% of leaf fall in high intertidal forests. This contrasts with the Caribbean where total herbivory rarely exceeds 10% of mangrove primary production (1). Robertson (8) hypothesized that the food webs of Indo-West Pacific mangroves may be different from those of the Caribbean because of differences in the decapod fauna. Robertson's hypothesis was corroborated by McIvor and Smith (9) who found almost no loss of leaf material due to grazing in Florida, supposedly because the crab fauna was dominated by carnivorous and deposit-feeding crabs.

The majority of East African mangrove decapod crabs are members of the 2 families Grapsidae and Ocypodidae (10, 11). Grapsid crabs, such as the sesarmids *Neosarmatium meinerti*, *N. smithi* and *Sesarma guttatum*, are avid leaf and propagule eaters (12–16). *N. meinerti* is one of the largest (adult carapace width 2.5–4.5 cm) most abundant and widespread crab species of East African mangroves. It occupies mainly high intertidal

areas, where it digs deep burrows (1–2m) under the canopy, and forage on sediment detritus and leaves (12).

Although litter production in tropical East Africa is high—up to 17 tonnes (t) ha⁻¹yr⁻¹, of which 80% are leaves (17)—the fate of mangrove leaf litter is poorly understood. Three previous studies have indicated that litter removal by crabs may be higher in Africa than anywhere else in the world. Steinke et al. (18) found that *Neosarmatium meinerti* removed practically all leaf litter from a subtropical mangrove in South Africa, and that 64% of the litter was consumed within 6 hrs. Rough estimates by Micheli et al. (14) suggested that *Cardisoma carnifex* (Brachyura, Gecarcinidae) and *N. meinerti* could consume considerably more than the daily litter fall in high intertidal areas in tropical Kenya. Unfortunately, methods employed by Micheli et al. (14) did not reflect a natural situation: crabs were offered large quantities of leaves (10 per crab) immediately next to burrows. Skov (19) estimated that *N. meinerti* removed 95% of the litter fall from 2 top-shore stands in tropical Zanzibar. Crab removal was calculated according to Robertson and Daniel (6) as the difference between the litter fall (excluding litter fallen during tidal flooding) and the amount of litter found on the ground (19). This method assumes that all litter not removed by the tide is taken by crabs. This assumption could be questioned: other animals, for instance, could be removing leaves (19). In Zanzibar Machiwa and Hallberg (20) also noted that where large grapsids crabs were present the forest floor was normally clear of leaf litter.

The leaves of mangrove trees are characterized by a high concentration of polyphenolic compounds/tannins, which have shown to deter herbivory by mangrove crabs (21, 22). Leaf tannin and energy content varies between tree species, and differs between fresh (green), senescent (yellow) and decaying leaves (8, 18, 22). Leaf characteristics may influence the leaf preference of crabs. Choice situations may arise when several tree species concur, or when leaves that fell elsewhere in the mangrove are imported on the tide.

Male and female crabs are likely to have different energy requirements, due to differences in the energetic costs of producing eggs or sperm (22). A study conducted on the sesarmid crab *Sesarma intermedia* showed that females were more specialized in their feeding habits and had higher assimilation rates than males (23).

This study addresses 4 questions: *i*) Do crabs of high shore mangroves in East Africa, *Neosarmatium meinerti* in particular, play an important ecological role by burrowing and consuming leaf litter? *ii*) Does *N. meinerti* show a preference for leaves of any particular tree species? *iii*) Does feeding rate or leaf preference differ between males and females of *N. meinerti*? *iv*) Is there any behavioral evidence of leaf litter competition among the crabs?

METHODS

Study sites: The study was carried out at 3 locations in East Africa:

Gazi Bay (4° 25'S, 39° 30'E), Kenya. Mangrove forest of ca 600 ha. The study site was located in a high intertidal zone

(> 3 m above chart datum) characterized by a pure stand (ca 0.5 km²) of *Avicennia marina* trees in fine to medium sandy sediments. This habitat is flooded during spring high tides only. *Neosarmatium meinerti* was abundant (ca 5–10 individuals m⁻²).

Maruhubi (6° 09'S, 39° 12'E), Zanzibar, Tanzania. Small mangrove forest, ca 100 ha, in the vicinity of Zanzibar town. Two study sites were chosen: *i*) High intertidal zone dominated by *A. marina* trees, with relatively firm, muddy sediments, flooded on spring high tides only. The density of *N. meinerti* was ~5 individuals m⁻². *ii*) Low intertidal zone with pure stand of *S. alba* trees in sandy sediments. The zone is flooded on every high tide. Larger leaf eating crabs, including *N. meinerti* were absent. A few individuals of the smaller genus *Metopograpsus*, which may eat leaves (16), were observed.

Chwaka Bay (6° 11'S, 39° 26'E) Zanzibar, Tanzania. Largest mangrove stand in Zanzibar ca 3000 ha. The study site was in a high intertidal *Rhizophora mucronata* zone where sediments were a firm mixture of sand and mud. *N. meinerti* was found at densities ca 3–5 individuals m⁻².

Leaf Area to Leaf Dry Weight Conversion

Crabs were given leaves of known surface area. All leaves employed had their outline drawn on paper prior to and following crab feeding. The areas of leaf drawings were measured using an image analyzer. The leaf matter removed by crabs was then calculated using a leaf area to dry weight conversion: for each tree species a series of leaves were collected and their outline drawn on paper. Leaves were then dried in the oven (48 hrs, 70°C), and weighed. Conversions employed 50 leaves of *A. marina* and 30 leaves of *R. mucronata*.

FIELD EXPERIMENTS

Leaf Burial and Leaf Consumption at Maruhubi

In order to assess how quickly crabs could remove and consume leaves, 2 experiments were performed: in the first leaves were left in plots for 24 hrs once and twice per *A. marina* and *S. alba* zone, respectively. In the second experiment leaves were left for 2 hrs in the *A. marina* zone on 4 consecutive days.

Seven senescent leaves of known surface area were introduced in 8 plots 2 by 2 m, within both *A. marina* and *S. alba* zones. Leaves were tethered by attaching one end of a 1.5 m string to

the petiole and the other end to a peg placed centrally in the plot. Strings had numbers attached so single leaves could be identified. The dry weight (dw) of the 7 leaves was on average 0.4 g m⁻² corresponding to 20% of the daily average leaf fall, estimated to be 2 g dw m⁻² d⁻¹ (17). (NB Plots were not cleared of naturally fallen leaves before the addition of experimental leaves). Leaf material eaten should therefore be considered as additional to the normal daily crab consumption. At the end of experiments, leaves were recovered and the remaining surface area noted. Leaves taken into burrows were extracted by gently pulling the string.

Leaf Removal at Gazi Bay

Senescent leaves were placed within 12 plots 2 x 2 m at densities of either 10, 20 or 40 leaves. This corresponded to ~1, 2 or 4 g dw m⁻², which was equivalent to a low, medium or high daily leaf litter fall, respectively. The plots were checked for remaining leaves after 1 hr. Leaves were not tethered, so the quantity eaten was not assessed.

Feeding Behavior

Ten senescent leaves of *A. marina* were added to a 1 m² plot gently outlined in the mud within the *A. marina* zone at Maruhubi. Leaves were monitored for 15 minutes using a video camera mounted on a tripod. This was repeated at 4 different stations ca 20–50 m apart on two consecutive days, between 8.00 and 10.00 hrs. The method was replicated at Chwaka, but using 8 and 6 pairs of green and senescent leaves of *R. mucronata* per plot. A further 4 plots were observed at Chwaka between 20.00 and 22.00 hrs. Only 0.5 m² could be observed at night because of low resolution when using infrared lamps.

Laboratory Leaf-choice Experiments

Specimens of *N. meinerti* were caught in the high intertidal *A. marina* zone in Maruhubi, weighed, measured (carapace width) and placed individually within laboratory microcosms. Microcosms consisted of 50 L plastic bins which were half-filled with sediment derived from the area of crab capture. Bins were flooded with seawater at times corresponding to tidal cover of capture areas. A hole was drilled at the bottom of bins to permit drainage. Bins were covered with metal mosquito net to prevent escape and induce shade. Crabs were given 24 hrs to acclimatize before the experiment started. Each experiment employed 3 blocks of 6 bins (Σ 18 crabs) placed under a half-roof behind the Institute of Marine Sciences, Zanzibar. A total of 7 leaf choice experiments were conducted, during which crabs were replaced 3 times, employing a total of 54 crabs. Crabs that were used in 2 consecutive experiments had a minimum of 24 hrs to purge their stomachs.

Crabs were offered tethered leaves of known surface area and allowed 24 hrs to consume these. Remaining leaves were extracted after 24 hrs, and crab burrows were excavated to retrieve small pieces of leaves lost due to 'sloppy' feeding, after which the total surface area of uneaten leaves was recorded. Each crab was presented with a choice of 2 different leaf types, apart from experiment 1 (Table 2). In order to test if the feeding rates or leaf preferences differed between the sexes of *N. meinerti*, 9 female and 9 male crabs were used in each experiment and placed randomly within each block.

RESULTS

Leaf Burial and Leaf Consumption in the Field

In the *A. marina* zone at Maruhubi all leaves left for 24 hrs (8 plots) had been taken into *N. meinerti* burrows and eaten. This corresponded to a crab consumption of 2.4 g dw m⁻² d⁻¹, which was 20% in excess of the average daily litter fall at the stand. In the same stand, all leaves left for 2 hrs had been taken into

Figure 1. Leaf consumption of *A. marina* leaves by crabs over 4 days in 8 plots each day.

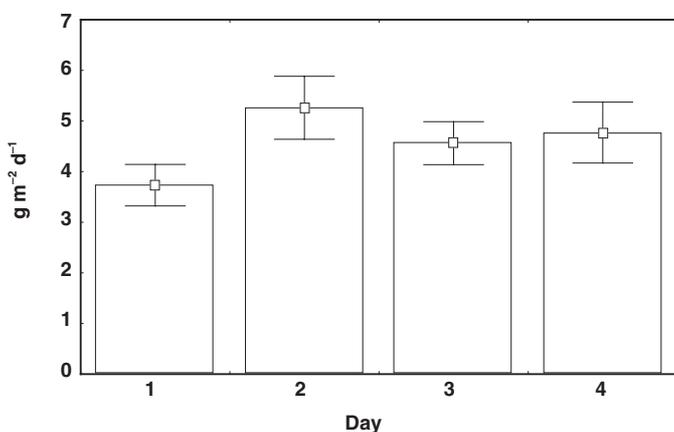


Table 1. Summary of the leaf choice experiments. Average dry weight (avg), standard error (se) and percentage (%) consumption of mangrove leaves by males and females (n = 9) in 7 experimental runs. The results of ANOVA are also presented (ns = not significant, *P < 0.05, **P < 0.001, M = males, F = females, A = *A. marina*, Agr = *A. marina* green leaves, B = *B. gymnorrhiza*, R = *R. mucronata*).

Leaves	Leaf consumption							Weight specific consumption							
	Males			Females			ANOVA		Males		Females		ANOVA		
	avg	se	%	avg	se	%	sex	species	avg	se	avg	se	sex	species	
Experiment 1	<i>A. marina</i>	1.0	0.1	85	1.1	0.1	96	ns		2.0	0.3	3.5	0.6	F>M*	
Experiment 2	<i>A. marina</i>	0.4	0.0	97	0.3	0.0	94	ns	ns	0.6	0.1	0.9	0.1	ns	ns
	<i>R. mucronata</i>	0.4	0.1	47	0.4	0.1	47			0.7	0.2	1.6	0.7		
Experiment 3	<i>R. mucronata</i>	0.6	0.2	54	0.2	0.1	17	M>F*		1.1	0.3	0.6	0.3	ns	
Experiment 4	<i>R. mucronata</i>	0.4	0.2	36	0.5	0.2	51	ns	B>R*	0.6	0.3	1.6	0.5	F>M**	B>R**
	<i>B. gymnorrhiza</i>	0.7	0.2	80	0.9	0.1	95			1.4	0.4	3.9	0.9		
Experiment 5	<i>A. marina</i>	0.4	0.0	100	0.4	0.0	95	ns	A>R**	0.8	0.1	1.6	0.3	ns	A>R***
	<i>R. mucronata</i>	0.2	0.1	19	0.2	0.1	18			0.4	0.2	0.6	0.4		
Experiment 6	<i>A. marina</i>	0.3	0.1	58	0.1	0.0	26	M>F*	ns	0.7	0.2	0.6	0.3	ns	ns
	<i>S. alba</i>	0.2	0.1	39	0.1	0.1	28			0.4	0.1	0.7	0.5		
Experiment 7	<i>A. marina</i>	0.2	0.1	56	0.1	0.0	19	ns	Ag r>A*	0.4	0.2	0.3	0.1	ns	Agr>A*
	<i>A. marina</i> , green	0.3	0.0	78	0.2	0.1	56			0.5	0.1	1.2	0.4		

Table 2. Summary of the behavioral studies (R.m = *Rhizophora mucronata*, B.g = *Bruguiera Gymnorrhiza*, A.m = *Avicennia marina*).

Station		Leaf		No. crabs involved	Max per crab	No. leaves stolen	2 leaves taken simultaneously
		Species	Given				
Chwaka 1	day	R.m	16	16	12	3	4
Chwaka 2	day	R.m	12	0			
Chwaka 3	day	R.m	12	8	8	1	1
Chwaka 4	day	R.m	12	7	9	2	4
Chwaka 6	night	R.m	5	3	3	1	0
Chwaka 7	night	R.m	6	3	2	3	1
Chwaka 8	night	R.m	4	3	3	3	1
Chwaka 9	night	R.m	5	0			
Marahubi 1	day 1	A.m	10	2	2	1	0
Marahubi 2	day 1	A.m	10	3	3	1	0
Marahubi 3	day 1	A.m	10	5	7	1	2
Marahubi 4	day 1	A.m	10	10	4	4,3,2	0
Marahubi 1	day 2	A.m	10	5	4	2	0
Marahubi 2	day 2	A.m	10	7	5	2,2	1
Marahubi 3	day 2	A.m	10	10	4	2,2	1
Marahubi 4	day 2	A.m	10	9	4	4,2,2	0

crab burrows (8 plots x 4 trials). Overall, 50% of 2-hr leaves had been completely eaten, 38% showed a varying degree of herbivory, whilst 12% had not been touched. On average, the crabs consumed 60 to 75% of added leaves, within 2 hrs (Fig. 1), with no significant difference in consumption between days (ANOVA, $p > 0.05$). Overall, the mean leaf consumption was on average $4.6 \text{ g dw m}^{-2} \text{ d}^{-1}$, corresponding to > 3 times the mean daily litter fall.

In the *S. alba* zone at Marahubi, none of the tethered leaves ($n = 112$) showed any sign of herbivory irrespective of whether they were left for 2 or 24 hrs.

In Gazi Bay, all leaves placed in the plots ($n = 280$) were buried within the hour.

Feeding Behavior

The result of video recordings of *N. meinerti* feeding behavior are shown in Table 1. In Marahubi the crabs took 50 and 78% of the leaves offered within 15 minutes on day 1 and 2, respectively, which is close to what is deposited during 24 hrs on the forest floor. In 2 plots the crabs cleared all leaves within 15 minutes, which is about 20% more than that deposited during 24 hrs. When all recordings are pooled the crabs in Chwaka took 56% of leaves offered to them within 15 minutes corresponding to > 2 times the daily litter fall in the area. In 2 of a total of 16 recordings no leaves were taken. On both these occasions no crab activity was documented. Several crabs buried more than one

leaf during recording. On 2 occasions a leaf was recorded falling from a tree, only to be taken within seconds by *N. meinerti*. Larger crabs often robbed smaller crabs of captured leaves, but 'theft' also took place between equal-sized animals. The number of stolen leaves per video recording was positively correlated with the number of crabs seen foraging on leaves (Table 1, $R^2 = 0.67$, $p < 0.001$). Crabs that buried a leaf normally resurfaced from burrows within 1–2 minutes, seemingly to look for more leaves. Crabs resurfacing after burrowing a leaf often had to defend their burrows against other crabs trying to enter, and fights typically occurred close to burrows. On several occasions, crabs were seen entering into neighboring burrows only to be chased out.

Laboratory Leaf-choice Experiments

The results of the leaf-choice experiments are shown in Table 2. *N. meinerti* consumed from 0.2 to 1.1 g dw leaves per day, equal to 10% and 55% of the daily litter fall m^{-2} . The highest weight-specific consumption ($\text{g dw leaves g}^{-1} \text{ dw crab d}^{-1}$) of males and females combined was when only senescent *A. marina* leaves (the dominant tree at the crabs home location) were offered (Table 2, exp. 1), and the lowest when only *Rhizophora* leaves were offered (Table 2, exp. 3). When given the choice, crabs ate 2.3 (males) to 2.4 (females) times more *Bruguiera* than *Rhizophora* leaves (Table 2, exp. 4: $P < 0.01$), and 2 (males) to 2.7 (females) times more *Avicennia* than *Rhizophora* leaves (Ta-

ble 2, exp. 5: $P < 0.001$). *Rhizophora* was therefore, overall, the least attractive species. When given a choice between green or senescent *A. marina* leaves (Table 2, exp. 7), crabs ate 1.3 (males) to 4 (females) times more green leaves ($P < 0.05$). Females had higher weight-specific consumption rates than males on 2 occasions (Table 2, exp. 1: $P < 0.05$. Exp. 4: $P < 0.01$). When all experiments were combined females had an almost double weight-specific consumption rate compared to males (Fig. 2, $p < 0.001$).

DISCUSSION

This study has documented the importance of the sesarmid crabs *N. meinerti* in the retention of primary production from tropical East African mangrove forests. Our results support previous findings with this species from Kenya, Zanzibar, and South Africa (14, 18, 19). The high shore mangrove forest studied at Maruhubi, Chwaka Bay (Zanzibar, Tanzania) and at Gazi

(Kenya) have the appearance of having been swept clear of leaves. The tide has a minimal influence on leaf removal, since high shore areas are covered for less than 5% of the time (19). Our results show that dense populations of *N. meinerti* clean the forest floor. Crabs on the high shore at Maruhubi consumed $> 50\%$ of offered leaves within 2 hrs and 100% within 24 hrs. Leaves were offered, in addition to those falling from trees in the stand. Taking into account that crabs ate both offered leaves and the mean daily leaf fall, crabs would have consumed > 4 times the mean daily litter fall. The capacity of *N. meinerti* to consume such amounts, suggests that leaves in the normal situation are a scarce food resource. Indeed, video recordings documented fierce competition for offered leaves, with fights and thefts of leaves increasing with increase in crab density.

In contrast to the high shore sites, none of the leaves offered were removed at a lower shore site where the abundance of herbivorous crabs was low and *N. meinerti* was absent. Similar results were recorded by McIvor and Smith (9), who found that sites in Florida dominated by carnivorous and deposit feeding crabs had low incidence of litter consumption, whereas consumption at sites in the Indo-Pacific where herbivorous sesarmid crabs were abundant was high. Leaf retention within the mangrove is likely to be further reduced at this low shore site due to tidal daily coverage.

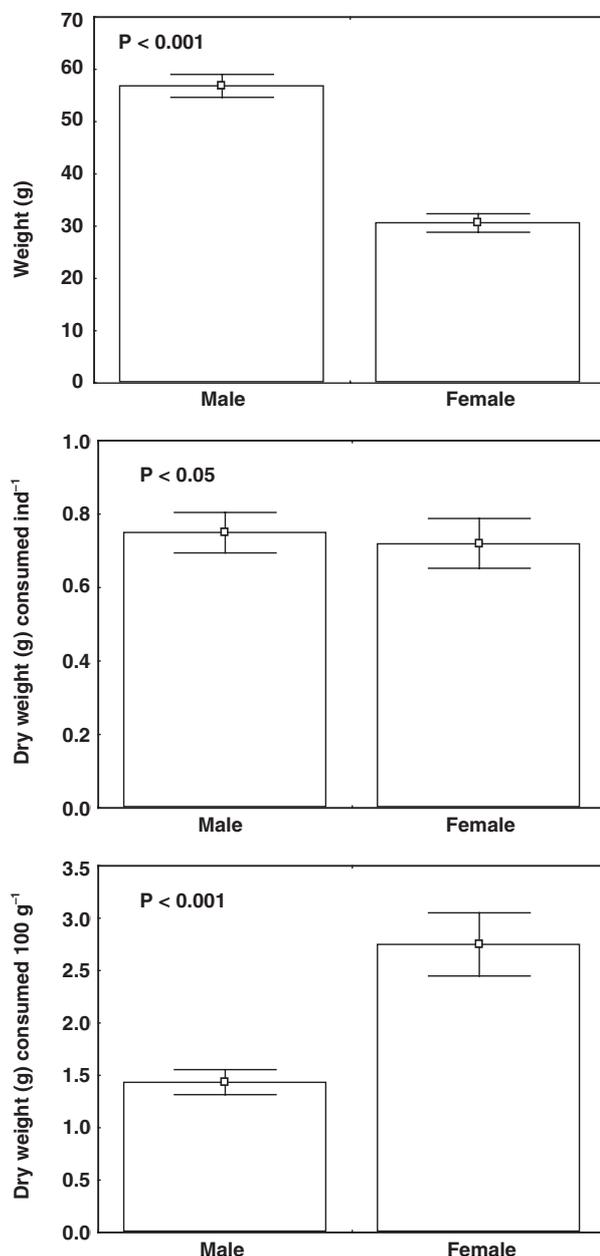
Laboratory experiments showed that *N. meinerti* leaf consumption was lowest when crabs were fed *R. mucronata* leaves. *Rhizophora* has a notoriously high tannin content (8), which may deter crab herbivory (21). The highest leaf consumption was observed when *N. meinerti* was fed on *A. marina* leaves and *Bruguiera gymnorrhiza*. This may be because *A. marina* was the tree species dominant in the area where crabs were caught, or because of the relatively low tannin, but high nitrogen content of this species (8, 14, 22, 24). Micheli (22) noted that *Bruguiera* spp. have soft leaves rich in water, and that this may improve palatability. Dahdouh-Guebas et al. (25) did not find preference for *N. meinerti* for any particular type of leaf, i.e. *R. mucronata*, *Ceriops tagal*, *B. gymnorrhiza* and *A. marina*, but their data set was small and not statistically tested.

Neosarmatium meinerti in the laboratory typically consumed $< 2\%$ of its body weight per day, and the average daily consumption when all experiments are taken together was $650 \text{ mg dw crab}^{-1} \text{ d}^{-1}$. This is lower than estimates of field consumptions at Maruhubi, but similar to previous laboratory trials (19). Machiwa and Hallberg (26) found much lower consumption or between 15 and $70 \text{ mg crab}^{-1} \text{ d}^{-1}$ depending on size for crabs collected from the same mangrove stand as ours. The discrepancy between our results and theirs might be in the experimental design. We used 50 L buckets with sediment where the crabs made burrows, while they used 10 L buckets without sediment. As *N. meinerti* is a very timid animal the absence of shelter and sediment may have reduced their consumption because of stress. Also our video recordings indicated that they eat their leaves inside burrows as crabs were never observed eating leaves on the sediment surface. Emmerson and McGwynne (15) found in their laboratory trials a consumption level between 73 and $460 \text{ mg crab}^{-1} \text{ d}^{-1}$, i.e. still considerably lower than our estimates but again they did not use sediment, instead they used artificial plastic tubes to imitate burrows.

Females had an overall higher leaf consumption per unit body weight than males. Females may have higher food energy requirements due to the higher energy loss to produce eggs compared to sperm. Females are also generally smaller than males, with a subsequent lower surface-volume ratio, and a higher potential for energy loss through, e.g. evaporative cooling.

Our results lend credit to Robertson's hypothesis (5) that herbivorous crabs of the Indo-Pacific are instrumental in retaining mangrove production. Burrowing crabs, such as *N. meinerti*, take mangrove leaves underground thus further reducing the risk of

Figure 2. Average weight of males and females ($n = 27$), consumption per individual and per crab.



tidal export (14). Burrowing of leaves is also likely to speed up remineralization, by encouraging decomposition by the soil microflora (27). Fragmentation and partial digestion of leaf matter by crabs may further accelerate microbial decay and nutrient uptake by soil microflora (see 12, and references therein). Species such as *N. meinerti* may therefore be instrumental in the recycling of essential mangrove nutrients such as nitrogen. Indeed, Smith et al. (28) found primary production in an Australian mangrove was significantly reduced when crabs were excluded. Sesarimid crabs may be heavily preyed upon by fish and other large predators and their production exported from mangrove ecosystems as a result of offshore migration by these fishes (29). Such a trophic link is unlikely to occur in the high intertidal areas of East African mangroves, because of infrequent inundation and lack of other large predators such as crocodiles.

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