

## **The Influence of Food Availability on Burrowing Activities The Crab *Sesarma boulengeri* (Calman)**

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### **Abstract**

*Sesarma boulengeri* (Calman) crab populations were tested for food limitation in an intertidal flat in Shatt Al-Arab River. Food supply was artificially increased by adding thin - cut plants. This resulted in a relative increase in the crabs population density, recruitment and organic content. Crabs dig more burrows than they require for their protection and their physiological needs; some time they may dig burrows in excess even when empty burrows are available in response to their food supply. The hypothesis was examined by comparing burrow and crab densities in an intertidal flat, then manipulating the burrow density and food availability in the laboratory. Furthermore, females were assumed to be more sensitive to the food availability than males and small crabs more sensitive than large crabs and the numbers of burrows were more than crabs. Smaller crabs of both sexes burrow faster and to lesser depths. New burrows despite the presence of unoccupied burrows and burrowing activity of smaller crabs of both sexes varied with food availability. The final results showed that the small crabs may be more sensitive to food availability and may be more capable of adjusting their burrowing activity to their food supply.

**Key words:** *Sesarma*; Crabs ; Burrow; Tidal flat; Food availability

### **Introduction:**

Large numbers of terrestrial and aquatic animals burrow and modify the environment by constructing semi-permanent or permanent burrows or by producing temporary subsurface trails (1). Burrowing animals were found in wide range of environments including freshwater, seawater and terrestrial soils. Most of them live in aquatic sediment or in terrestrial soils, (2,3). Salt marshes have very high primary production (4). Nevertheless, many salt marsh consumers may be food limited, for example *Sesarma* crabs may be food limited in spite of the large amount of detritus present both the amount of ingestible food per consumer and its quality may be limiting (5). Crabs feed by collecting bits of mud with their small claws and sift through the mud for detritus. Detritus is decaying plant and animal matters. They are released into the water from marsh plant and animals that have died. This decaying matter is full of the nutrients that plant and animals stored while they were alive. Eating detritus is an easy way for crabs to collect the nutrients they need (6).

Crabs are known to adjust their burrowing activity to a variety of conditions, such as stem density, root mat density, substratum water, ground temperature tidal and diurnal activity (7,8). *Sesarma Boulengeri* (Calman) a species of crabs common in tidal flat of Shatt Al-Arab river used in this study. These crabs like to live near water on the mud or sand. They dig burrows with a half inch wide and go almost straight down in the mud. The burrows can reach a 25 cm deep. Most crabs search for food at low tide and stay near their burrows. The paper examines the effect of food availability and burrow density on burrowing activity of crabs.

### **Methods:**

Crabs are sampled during summer 2004 in an intertidal flat at Shatt Al-Arab river the sediment is muddy sand. *Sesarma boulengeri* is by far the dominant consumer species in this area. To investigate whether burrow: Crab ratios and to provide information on natural burrow densities and population structure to be used in setting up laboratory experiments depending on the sampling techniques described by (9). An area 10 X 10 m, apparently homogeneous in *Halocnemum strobilaceum* plants height and density, crab density and physical factors, was divided into 0.5 X 0.5 m quadrates and marked permanently with dowels. 15 quadrates were chosen by the simple random method. Each quadrate was enclosed with corrugated fiberglass while water covered the substratum and most crabs in their burrows. To characterize the study site and to measure association of burrows with structure, grass shoots within the quadrate were clipped near the substratum at low tide. To determine the characteristics of each burrow and identify resident crab, burrow opening were marked with numbered sticks and burrow casts were taken with paraffin wax. The sex was noted and their carapace breadth was measured to the nearest 0.05 mm with vernier calipers because some burrows are kept plugged by resident crabs, this procedure was repeated on next 2 days with newly opened burrows.

On the 3rd day, burrow casts were removed and their depth, angle from the substratum surface, diameter and configuration were noted. To sample root mat density, water and organic content, a deep sediment core was taken with 6 cm in diameter PVC tube; sieved through a 0.5 mm mesh and the roots were dried for 48 hours at 70°C and 110°C weighed to determine the water and organic content respectively.

The arenas were filled with sandy mud (collected from the Shatt Al-Arab tidal flat) 45 cm deep, with an upper diameter of 50 cm and surface area 25 m<sup>2</sup>. This sediment was maintained wet by adding 50 % water. It was changed for each trial to prevent accumulation of salt by evaporation. Results from the field study were used to determine the initial conditions used in the arenas. At the beginning of each trial, complete randomization of different factors was used in assigning each arena and experiments were replicated in (17) trials, between May and September 2004. Food treatment consisted of 0 – 11 grams of fly larvae medium added to each arena. Crabs were captured at the intertidal flat and 45 individuals were distributed into each arena. The sex ratio and size class distribution were similar to those observed in the sampling study, with the exception that no crab < 5 mm in carapace breadth were used, because of the difficulty of surveying their burrows. The following size classes were used, as determined by carapace breadth 5-8, 8-12, 12-16, > 16 mm. Because competition for burrows of adequate size may be stronger for larger crabs (10), the diameter of initial burrows was varied to match crab carapace length (crabs enter burrows sideways). Crabs were left in the arenas 4- 7 days. The laboratory was equipped with windows and with fluorescent light set on timer simulating the sunrise – sunset rhythm. Thus, the natural photoperiod was supplemented by an artificial photoperiod. Arenas were separated by blinds from the rest of the laboratory. Halfway through each trial, and again at the end of each trial, newly excavated burrows were marked and excavated material was collected, dried for 48 hours at 70°C, and weighed to the nearest 0.01 g. Excavation pellets were not trampled by the crabs and could be collected. Their sex and carapace breadth were noted. This procedure was repeated with newly opened burrows on the next 2 days burrow casts were removed and their depth, diameter and configuration were noted. Association of burrows with structural elements (grass stems) was estimated as described for the field study. Counts of new unbranched and branched burrows and measurements of excavated sediment were divided by the duration of each trial in days. To investigate time allocation to different activities, including burrowing, crabs were marked individually with numbered plastic tags affixed with glue to the carapace. The observer watched an individual for 10 seconds before going on the next one. This procedure was repeated one four times on different days; near mid-day during seven of the trials. Comparisons of the fraction of time allocated to each activity levels were made on arcsinetrans formed data. An index of relative activity at the surface for crabs of each sex or size class was calculated from the frequency of sighting observed and expected from the sex ratio and size class distribution in the arenas. Comparisons of responses to initial burrow density and to food availability were also made

across sexes and size classes, for the variables branching ratio, burrow depth and time allocated to burrowing. All activities variables have been analyzed and studied using the Fractional ANOVA for all crabs and for each sex and size class

### **Results:**

The study site sediment, water and burrows characteristics that used to set up the experimental arenas were summarized in table 1.

In arenas, results showed that, females were significantly less active at the surface than males, spent significantly more time burrowing and burrowed less deeply. Males allocated significantly more time to agonism and to display. There was no difference between sexes in the branching ratio of burrows (table 2).

Crabs of the smallest size class were less active at the surface than larger crabs (table 3); all pairwise comparisons were significant at  $P < 0.05$  except between class 3 and 4. Smaller crabs burrowed less deeply. There was no overall significant difference between size classes in burrow branching ratio and in burrowing time. Pair wise comparisons between size classes, though indicated that smaller crabs allocated more time. Comparisons between classes 1 and 3 and between classes 1 and 4 were significant ( $P < 0.05$ ), larger crabs allocated time significantly more to agonism and display.

In arenas with a lower initial burrow density, there were significantly more newly excavated burrows and the branching ratio was significantly higher (table 4). There were no differences between treatments in the number of maintained burrows. The number of branches added to initial burrows and branches of new burrows, the amount of excavated sediment, and burrow depth or fraction of time allocated to burrowing. The effect of initial burrow density did not differ between males and females. This is suggested by a qualitative comparison between the two sexes (table 5) and by the non significant interaction between sex and burrow density for all variables examined.

Crabs of different size, however, were affected differently by initial burrow density as suggested by qualitative comparison between size classes in table 6. In arenas with a lower initial burrow density for crabs of the smallest size class, branching ratio and burrow depth were significantly lower; the time allocated to burrowing was not affected by the treatment. For larger crabs, no differences occurred for branching ratio, depth and time allocation. The interaction between initial burrow density and food availability was not significant for any of the variables. The three- level interactions between food, burrow density and sex or size, and the two – level interactions between pairs of these variables, were not significant either.

In arenas receiving no food addition crabs added significantly more branches to initial burrows and branches of new burrows , the branching ratio was higher and the average between depth was lower (table 5 ). In addition , time allocation to various activities was significantly affected by the treatment. In low food arenas , crabs spent less time eating .There was no difference between treatments in the number of newly excavated burrows, the total number of maintained burrows, the amount of excavated sediment , are the fraction of time allocated to burrowing . The effect of food availability did not differ between males and females . This is suggested by a qualitative comparison between the tow sexes in table 7, and by the non significant interaction between sex and food for all variables examined.

Crabs of different size are affected differently by food availability. Smaller crabs showed a stronger response than large crabs (Table 9). In arenas with lower food availability, burrow depth was lower for crabs of all size. Moreover, for size class 1, branching ratio was higher and time allocation to burrowing was lower. Size class 2 also adjusted the branching ratio. For all variables, the interaction between size and food availability was not significant. For all tables (<sup>1</sup>Log-transformed data; <sup>2</sup>Arcsine-transformed data; <sup>3</sup>Divided by the duration of each trail in days).

**Table 1: (A) Summary of environmental and population characteristics observed in the study area and used as initial conditions in experimental arenas;**

Variable	Field study	Arenas
Sediment type	Sandy mud	Sandy mud
Sediment water	60%	62%
Burrow density	90m <sup>2</sup>	High 180 m <sup>2</sup> Low 95 m <sup>2</sup>
Crab density	85 m <sup>2</sup>	104 m <sup>2</sup>
Burrow : crab ratio	1.5	High 1.6 Low 1.1
Burrow angle	60% 50-90°	50 – 90 °
Burrow configuration	80% J shaped	Straight
Crab sex ratio ( M / F )	0.70	0.70
Crab size – class distribution by sex		
CB 5 – 8 mm	19% F 15% M	
CB 8 – 12 mm	12% 11%	
CB 12 – 16 mm	18% 11%	
CB > 16 mm	6% 7.5%	

**Table 1: (B) Matching of initial burrow diameter with crab size. CB. Carapace breadth.**

Size class	Carapace length <sup>2</sup>	Burrow diameter
CB 5 – 8 mm	6.2 mm	7.5 mm
CB 8 – 12 mm	8.3 mm	10 mm
CB 12 – 16 mm	10 mm	13 mm
CB > 16 mm	12.4 mm	16.7 mm

**Table 2: Comparison of activities between crabs of two sexes.**

Variable	Females	Males	n	Test	df	Significance
Activity of surface	0.8±0.05	1.2 ± 0.06	50	F=50.4	1	P<0.0001 <sup>1</sup>
Branching ratio	1.5±0.01	1.5 ± 0.01	50	F=0.5	1	Ns <sup>1</sup>
Burrow depth (cm)	14±0.01	13 ± 0.06	50	F=12.8	1	P<0.0001 <sup>1</sup>
%time burrowing	9.8 ± 1.3	5.2 ± 1.3	50	F=10.9	1	P<0.0006 <sup>2</sup>
%time agonism	0.5 ± 1.5	5.1 ± 1.5	50	F=27.4	1	P<0.0002 <sup>2</sup>
% time displaying	0.2 ± 0.7	2.1 ± 0.7	50	F=71	1	P<0.01 <sup>2</sup>

**Table 3 : Comparison of activities between different size.**

Variable	Size1	Size2	Size3	Size4	n	Test	df	significance
Active of surface	0.81 $\pm$ 0.5	1.2 $\pm$ 0.1	1.0 $\pm$ 0.05	1.1 $\pm$ 0.1	50	F= 2.6	1	P< 0.0001 <sup>1</sup>
Branching ratio	1.4 $\pm$ 0.06	1.6 $\pm$ 0.04	1.5 $\pm$ 0.04	1.6 $\pm$ 0.03	50	F= 0.7	1	Ns <sup>1</sup>
Burrow depth (cm)	6.3 $\pm$ 0.1	7.5 $\pm$ 1.3	9.1 $\pm$ 1.5	12.6 $\pm$ 1.7	50	F= 80	1	P<0.0001 <sup>1</sup>
%time burrowing	12.3 $\pm$ 5.0	8.0 $\pm$ 3.0	5.2 $\pm$ 1.0	6.3 $\pm$ 1.8	50	F= 4.2	1	P<0.001 <sup>1</sup>
%time agonism	0.5 $\pm$ 0.2	2.0 $\pm$ 1.4	3.1 $\pm$ 1.0	4.4 $\pm$ 2.0	50	F= 8.1	1	P<0.0001 <sup>2</sup>
%time displaying	0.2	0.4 $\pm$ 0.1	1.5 $\pm$ 1.7	2.0 $\pm$ 1.3	50	F= 50	1	Ns <sup>2</sup>

**Table 4 : Effect of initial burrow density on burrowing activity of crab and collapsed for two level of burrow density treatment .**

Variable	Low density	High density	n	Test	df	significance
Excavated ediment <sup>3</sup>	71.8 $\pm$ 7.1	70.2 $\pm$ 10.0	25	F=0.1	1	NS
All new burrows	40.3 $\pm$ 4.0	28 $\pm$ 12.3	25	F=10.8	1	P>0.001
New un branched burrows	30 $\pm$ 3.5	18.7 $\pm$ 4.0	25	F=20.1	1	P>0.0001
Maintained burrow <sup>3</sup>	9.1 $\pm$ 0.5	9.0 $\pm$ 0.5	25	F=2.6	1	NS <sup>1</sup>
New branches to initial burrow <sup>3</sup>	2.6 $\pm$ 0.3	2.5 $\pm$ 0.3	25	F=0.04	1	NS <sup>1</sup>
Maintained branches <sup>3</sup>	10.7 $\pm$ 0.4	10.8 $\pm$ 0.4	25	F=1.7	1	NS <sup>1</sup>
Branching ratio	1.2 $\pm$ 0.05	1.1 $\pm$ 0.05	25	F=9.0	1	P<0.002
Burrow depth (cm)	11.0 $\pm$ 0.8	11.5 $\pm$ 0.8	25	F=1.3	1	NS <sup>1</sup>
%time burrowing	8.2 $\pm$ 2.2	6.4 $\pm$ 1.2	25	F=25	1	NS <sup>1</sup>

**Table 5: Response of burrowing activity by each sex of crabs to initial burrow density**

Variable	Low density	High density	n	Test	df	significance
(A) females						
Branching ratio	1.3 $\pm$ 0.1	1.3 $\pm$ 0.1	25	F= 0.3	1	NS <sup>1</sup>
Burrow depth (cm)	12.2 $\pm$ 0.9	13.0 $\pm$ 1.1	25	F= 0.3	1	NS <sup>1</sup>
% time burrowing	10.2 $\pm$ 3.5	7.3 $\pm$ 2.9	25	F=2.4	1	NS <sup>1</sup>
(B) Males						
Branching ratio	1.3 $\pm$ 0.1	1.3 $\pm$ 0.1	25	F= 1.5	1	NS <sup>1</sup>
Burrow depth (cm)	13.7 $\pm$ 1.0	12.5 $\pm$ 0.8	25	F= 3.0	1	NS <sup>1</sup>
% time burrowing	7.8 $\pm$ 2.3	4.5 $\pm$ 1.4	25	F=2.6	1	NS <sup>2</sup>

**Table 6 : Response of burrowing by crabs of different size to initial burrow density .**

Variable	Low density	High density	n	Test	df	significance
(A) size class 1						
Branching ratio	1.3 $\pm$ 0.2	1.3 $\pm$ 0.2	25	F=4.5	1	P<0.05 <sup>1</sup>
Burrow depth (cm)	5.8 $\pm$ 0.3	6.0 $\pm$ 0.1	25	F=8.3	1	P<0.006 <sup>1</sup>
% time burrowing	11.0 $\pm$ 4.0	13 $\pm$ 1.5	25	F=1.0	1	NS <sup>2</sup>
(B) size class 2						
Branching ratio	1.3 $\pm$ 0.1	1.3 $\pm$ 0.1	25	F=0.7	1	NS <sup>1</sup>
Burrow depth (cm)	7.3 $\pm$ 0.8	7.2 $\pm$ 0.7	25	F=0.5	1	NS <sup>1</sup>
% time burrowing	4.2 $\pm$ 1.5	5.8 $\pm$ 1.9	25	F=4.1	1	NS <sup>2</sup>
(C) size class 3						
Branching ratio	1.4 $\pm$ 0.1	1.4 $\pm$ 0.1	25	F=0.1	1	NS <sup>1</sup>
Burrow depth (cm)	9.1 $\pm$ 0.9	8.0 $\pm$ 0.9	25	F=1.4	1	NS <sup>1</sup>
% time burrowing	4.2 $\pm$ 1.5	5.8 $\pm$ 1.9	25	F=0.04	1	NS <sup>2</sup>
(D) size class 4						
Branching ratio	1.4 $\pm$ 0.1	1.4 $\pm$ 0.1	25	F=0.6	1	NS <sup>1</sup>
Burrow depth (cm)	10.8 $\pm$ 0.4	11.7 $\pm$ 0.5	25	F=0.6	1	NS <sup>1</sup>
% time burrowing	6.6 $\pm$ 3.0	4.1 $\pm$ 2.0	25	F=1.7	1	NS <sup>2</sup>

**Table 7 :Response of burrowing activity by each sex of crabs to food availability .**

variable	Low food	High food	n	Test	df	Significance
(A) Females						
Branching ratio	1.6 $\pm$ 0.06	1.4 $\pm$ 0.1	25	F=9.6	1	P<0.002 <sup>1</sup>
Burrow depth (cm)	9.1 $\pm$ 1.0	9.5 $\pm$ 1.2	25	F=9.5	1	P<0.002 <sup>1</sup>
% time burrowing	11.5 $\pm$ 4.2	10.6 $\pm$ 4.7	25	F=0.3	1	NS <sup>2</sup>
(B)Males						
Branching ratio	1.6 $\pm$ 0.05	1.4 $\pm$ 0.1	25	F=16.2	1	P<0.0001 <sup>1</sup>
Burrow depth (cm)	10 $\pm$ 1.2	10.7 $\pm$ 1.3	25	F=20.0	1	P<0.0001 <sup>1</sup>
% time burrowing	5.3 $\pm$ 2.2	5.3 $\pm$ 1.5	25	F=0.002	1	NS <sup>2</sup>

**Table 8 : Effect of food availability on burrowing activity of crabs (all)**

variable	Low food	High food	n	Test	df	Significance
Excavated sediment <sup>3</sup>	70.1 $\pm$ 6.2	73.5 $\pm$ 6.2	25	F=1.3	1	Ns
All new burrows	40.2 $\pm$ 5.1	33.8 $\pm$ 4.0	25	F=9.2	1	P< 0.003 <sup>1</sup>
New unbranched burrows <sup>3</sup>	22 $\pm$ 4.1	20 $\pm$ 4.2	25	F=0.9	1	Ns
Maintained burrow <sup>3</sup>	9.1 $\pm$ 0.5	9.0 $\pm$ 0.4	25	F=0.3	1	NS <sup>1</sup>
New branches initial Burrow <sup>3</sup>	3.2 $\pm$ 0.3	2.1 $\pm$ 0.4		F=18.8	1	P<0.0001 <sup>1</sup>
Maintained branches <sup>3</sup>	12.3 $\pm$ 0.7	11.7 $\pm$ 0.6	25	F=8.7	1	P<0.005 <sup>1</sup>
Branching ratio	1.7 $\pm$ 0.03	1.5 $\pm$ 0.02	25	F=64.2	1	P<0.0001
Burrow depth (cm)	12.3 $\pm$ 1.0	1.34 $\pm$ 0.2	25	F=53.0	1	P<0.0001 <sup>1</sup>
% time burrowing	6.3 $\pm$ 2.0	6.0 $\pm$ 1.7	25	F=0.5	1	NS <sup>2</sup>

**Table 9: Response of burrowing by crabs of different size to food availability**

Variable	Low food	High food	n	Test	df	Significance
(A) Size class 1						
branching ratio	1.6 $\pm$ 0.05	1.5 $\pm$ 0.05	25	F=21.0	1	P<0.0001 <sup>1</sup>
burrow depth ( cm )	5.1 $\pm$ 0.2	6.2 $\pm$ 0.6	25	F=10.4	1	P<0.002 <sup>1</sup>
% time burrowing	6.0 $\pm$ 0.2	6.2 $\pm$ 0.6	25	F=10	1	P<0.03 <sup>2</sup>
( B )size class 2						
Branching ratio			25	F=8.7	1	P<0.004 <sup>1</sup>
Burrow depth ( cm )	1.6 $\pm$ 0.05	1.3 $\pm$ 0.07	25	F=5.0	1	P<0.03 <sup>1</sup>
% time burrowing	6.8 $\pm$ 0.7	7.2 $\pm$ 1.0	25	F=1.4	1	Ns <sup>2</sup>
( c ) size class 3	10.3 $\pm$ 7.3	6.7 $\pm$ 3.5				
Branching ratio			25	F=2.0	1	Ns <sup>1</sup>
Burrow depth ( cm )	1.6 $\pm$ 0.7	1.4 $\pm$ 0.2	25	F=6.7	1	P<0.03 <sup>1</sup>
% time burrowing	8.2 $\pm$ 0.9	8.6 $\pm$ 1.0	25	F=0.4	1	Ns <sup>2</sup>
(d) size class 4	4.2 $\pm$ 2.1	5.1 $\pm$ 2.3				
Branching ratio			25	F=1.5	1	Ns <sup>1</sup>
Burrow depth (cm)	1.5 $\pm$ 0.6	1.3 $\pm$ 0.5	25	F=10	1	P<0.003 <sup>1</sup>
% time burrowing	11.2 $\pm$ 0.5	13 $\pm$ 1.3	25	F=0.3	1	Ns <sup>1</sup>
	6.4 $\pm$ 2.8	6.2 $\pm$ 3.9				

**Value of F is main effect of food in factorial ANOVA.**

### **Discussion:**

The burrow / crab numbers ratio which is found to be > 1 is acceptable according to the observations in previous studies. The crabs may dig new burrows with each tidal cycle which relatively stable in muddy substrate with a root mat

Crabs of each sex or different size may not be equally sensitive to food supply, because of differences in foraging efficiencies, in food assimilation or in food requirements (11) .Sex ratios were not modified by food treatment, though males have disadvantage in food gathering by having feeding chela . They compensate for this by feeding for longer periods of time (12). The sex ratio of crabs (males / females) generally found to be greater 1:1, in this experiment that the sex ratios greater than 1:1 and possibly due to differential mortality .

Differences in burrowing activity were apparent between sexes and size females spent less time outside their burrows than males. This observation may be partly due to an artifact of the visual sampling technique as females are actually more involved in burrowing which make them not easily seen. Also they are less involved in agonistic and courtship activities and when gravid protect their brood. A higher burrow turnover rate may be expected for females, because they have an increased food requirement and they may be dislodged by large males which are less able to burrow because their large claw (3) and they allocate less time to agonistic and courtship activities and non receptive females dig more if forced to interact with displaying males an artifact of the arenas . Males burrowed more deeply which agrees with finding of (13)and is consistent with the presumed lower burrow turnover of males . The smaller crabs were less active outside the burrows. This may be partly due to an artifact of the visual sampling technique; small crabs are more involved in burrowing. The being visible less frequently and were less involved in agonistic and courtship activities. The large number of burrows for smaller crabs, because they have a higher need for food, they lose their burrows more often to larger competitively dominant crabs, and they do not all have activity. They burrow longevity was lower for smaller burrows when there was no root mat (10) and the smaller may dig more if forced to interact with displaying males an artifact of the arenas . Larger crabs burrowed more deeply and smaller crabs even though they tended to allocate more time to burrowing than large crabs did, can excavate only small amounts of sediment at time. The crabs dug new burrows and branches even in arenas with a high initial burrow density. A lower initial burrow density, however, resulted in higher number of branched and unbranched burrows, with lower average depth. There was no difference in time allocation to

burrowing which suggests that time for burrowing was allocated to digging new burrow and branches rather than to making existing burrows deeper. Burrows were then more abandoned often in Lower density arenas than in high density arenas, and burrow turnover was higher. This sensitivity to existing burrow density may reflect attendance to dig burrows wherever possible. New burrows in a substratum with a low density may be less likely to collapse, thus making excavation of new burrows effective. A second reason may be a stronger competition for territories under higher burrow density.

Female and male crabs were not affected differently by initial burrow density, they may tend to dig burrows when a low burrow density makes this possible. This may be easier for females, which have a higher burrowing ability and are less involved in agonistic and courtship activities. Yet males defend display territories and breeding burrows (14).

Neither large nor small crabs allocated more time to burrowing in arenas with a lower initial burrow density. Smaller crabs already spend more time burrowing than larger crabs and may not be able to increase their burrowing time further. Rather, smaller crabs responded by burrowing less deeply and allocating their burrowing time to new burrows and branches. In addition sensitivity to burrow density may be particularly high in Small crabs because of their relatively high population density. Because small crabs are less involved in agonistic and courtship activities, they may respond to high population density by digging more unbranched and branched burrows and remaining more in their burrows rather than by reducing their time allocation to burrowing.

When food availability was lower, crabs excavated as much sediment and dug more burrows and burrow branches, while allocating as much time to burrowing. They did so by burrowing faster and to lesser depths. Digging burrow branches near the surface may bring more organic matter to the surface and better stimulate plants growth, than digging whole new deeper burrows for the following reasons. Firstly, there is more organic matter in the sediment near the surface than in deeper layer (15). Thus excavating short burrows should yield more organic matter per unit volume excavated. Second, the physio-chemical and nutrient requirements in the upper substratum layers may be most critical to plants growth, indeed in the upper layer there is a higher density of roots and rhizomes and nutrients may be more easily extracted from sediment. Furthermore, in the upper layer oxygenation by plants (metabolic oxidation and passive O<sub>2</sub> release), nutrient inputs or burrows are likely to betel stimulate the availability of these nutrients (16).

The increased investment in burrowing under low food supply may be cost – effective because of these direct and indirect benefits accruing to the crabs. In addition, digging branches near the surface may better enable a crab in a better way to keep control of the original burrow by reducing the risk of losing it to another crab or of being without a burrow should the new burrow collapse or encounter some construction obstacle. These constraints may be stronger when food is limited. In contrast in the low density situation both unbranched and branched burrows were excavated.

The hypothesis of a selective value of burrowing for food enhancement was formulated with no assumptions about trait group size. Thus direct and indirect benefits of burrowing are assumed to be possible. An individual digging a burrow may directly benefit by eating the detritus it has excavated. Over a broader trait group size, crabs digging burrows may benefit indirectly via the increased production of plants detritus. Although crabs should remain in the vicinity to derive such a benefit from their burrowing and the food that excess burrowing grew as a result of the excess burrowing should remain localized in the vicinity, the scale of these constraints need not be that of the immediate vicinity of a single crab or small group of crabs. Differences in detritus availability occur over a scale of meters or more and demes (subpopulation characterized by the frequency of occurrence of genotype) might be kilometers or more in size (17).

There were no differences between sexes in the effect of food availability on burrowing activity. Females may not be as predicted more sensitive than males to food availability or larger females may rely more on dislodging smaller crabs when food supply is low to reduce their energetic expense for burrowing. There were on the other hand differences between size classes with smaller crabs of both sexes showing a stronger response to low food availability. The dug more branches while decreasing their time allocated for burrowing. Smaller crabs may be particularly sensitive to food availability because they may stand more chance of driving benefit from their investment during their lifetime they can invest more energy in



burrowing as opposed to display and agonism their burrowing ability may allow them to better adjust their burrowing to food availability and have a higher size-specific rate of metabolism. Early stages are presumed, in fact to be particularly sensitive to food availability megalops larva select a settling substratum partly on the basis of organic content and population density of early crab stage is limited by food supply (18), the small crabs dig small and shallow burrows which would affect especially the upper substratum layer because the layer is richest in organic matter. Small crabs constitute a large fraction of the population. Thus their burrowing may have a larger total effect on plant than that of large crabs. If small crabs are more sensitive to food limitation and respond to low food availability by increasing their burrowing then crab burrowing activity should be inversely proportional to crab nutritional state (e.g. as measured by crab organic content). Additionally, selective removal of large or of small crabs should have different effect on plant production (19).

As with many complex biological interactions the observed results might be attributable to secondary interactions or indirect cause and effect relationships. The observed differences cannot be explained by the increased agonism and by an extension of the foraging range in search of food. In order to reduce agonistic interactions crabs should remain in their burrows more than they would under high food supply, or use the vacant burrows if chased from the ones they are occupying, this would cost them less energy than digging new burrows and branches. Moreover adding branches is not likely to help an individual locate a better food patch, since differences in detritus availability occur over a scale of meters or more. Indeed crabs spent more time foraging; when food availability was low. Increased agonism might be a consequence of their more extensive wandering under these conditions. In light of what is known about crabs burrow dynamics, the effects of their burrows of plant growth and their limitation by food results suggest a response to food supply. Montague (5) proposed a model of the salt marsh in which fiddler crabs get on indirect benefit from their burrowing and foraging in terms of increased spartina litter. The fiddler crabs burrowing may reduce competition for food by increasing food availability, in addition to providing ( a ) shelter from predators tides and environmental extremes, ( b ) water for physiological needs , and ( c ) sites for reproduction (25) . This trait can be selected for if the fiddler crab population does not mix during most of the life cycle, thus allowing the deme bearing that particular trait to enjoy the benefits of an increased food supply (20). It would be interesting to know whether fiddler crabs dig more burrows than they require for other activities or physiological needs, thus obtaining an increased food supply.

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### الخلاصة

تناول البحث تأثير وفرة الغذاء على كثافة حفر السرطانات في مسطحات المد والجزر لضفاف شط العرب وقد اجريت الدراسة حقليا "ومختبريا" للحصول على نتائج اكثر دقة. بينت النتائج ان السرطانات تظهر حساسية تجاه نقص المتطلبات الغذائية وانها تقوم بالحفر بصورة اكثر واسرع عندما يقل الغذاء ، كما تقوم بحفر الحفر المتشعبة ونقل الرواسب بسرعة اكبر مما هي عليه في الظروف الاعتيادية. اظهرت النتائج بان الاناث اكثر حساسية من الذكور وان السرطانات اليافعة اكثر حساسية من السرطانات الكبيرة في هذا المجال. كما بينت النتائج بان كثافة الحفر تكون اكثر من كثافة السرطانات عندما يكون هنالك نقص في المتطلبات الغذائية.

