

Burrow-orientated activity in the ocypodid crab, *Dotilla fenestrata*, living in a mangrove swamp

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The behavioural repertoire of the Scopimerinae crab, *Dotilla fenestrata*, is the result of a juxtaposition of rigid and plastic patterns, as an adaptation to the intertidal habitat. On the one hand, the activity of *D. fenestrata* can be classified in a number of stereotyped behavioural patterns, the occurrence of which may change throughout the low water or on the basis of the crabs' relative size, according to an expected schedule. For example, digging is more pronounced in larger individuals and mostly occurs when the crab emerges or just before it seals itself inside the burrow at the flooding tide. In contrast, maintenance of the burrow is a constant behaviour. Feeding rate, estimated from the number of pseudofaecal pellets emitted, is constant both throughout low water, with the exception of noon when it decreases, and with the feeding crab's size. The behavioural patterns that assure water uptake and temperature regulation (sponging and visits inside the burrow) are more frequently performed around noon. Agonistic patterns are mostly performed by larger individuals; the rate of aggression by resident crabs, against neighbours but mostly against smaller passers-by, increases with the flooding tide. On the other hand, for a surface deposit-feeder like *D. fenestrata*, plastic behaviour is mainly caused by the unpredictable distribution of food over the emerged platform. The result is a number of adaptive flexible behaviours, like: (1) the presence within the same population of both burrow-centred crabs and wanderers; (2) the construction by the former subpopulation of two types of burrows (feeding-trench burrows and igloos); and (3) significant differences in the behavioural budgets of the inhabitants of the two burrows. The ability to 'switch' modes of activity allows responses to both the predictable and unpredictable elements of intertidal environments, the mangrove swamp included.

INTRODUCTION

Dotilla fenestrata (Hilgendorf) is the only East African representative of the subfamily Scopimerinae (Brachyura: Ocypodidae). It is a common inhabitant of tropical sandy and muddy shores (Hartnoll, 1973), including mangrove swamps. Like other ocypodid and mictyrid crabs, it shows a range of morphological and behavioural adaptations to intertidal life. The two main aspects of these adaptations are a semi-terrestrial habit and feeding on surface deposits left by the receding tides (Ansell, 1988).

The adaptations for a semi-terrestrial habit include tympani or gas windows on the meral segments of the legs (Maitland, 1986), tufts or rows of setae (Hartnoll, 1973) for water uptake by capillarity when the crab stops its activity and flattens itself against the sand surface by a behaviour called 'sponging' (Fielder, 1970), and grooves on the exoskeleton where the water streams along the carapace from exhalant to inhalant openings, which serve for oxygenation as well as for cooling of the body by evaporation (Fishelson, 1983).

The adaptation for feeding on surface deposits consists of a flotation feeding mechanism similar to that of other ocypodid crabs (Fielder, 1970). Water, originally stored in the gill chambers, is used to separate suspended organic

material from sand (Miller, 1961; Fielder, 1970; Wolcott, 1976; Quinn, 1980; Robertson & Newell, 1982); the particulate organics (mostly diatom cells, but also bacteria, protozoa, blue-green algae, nematodes and detritus) adhere to 'spoon-shaped' setae on the second maxillipeds (Bigalke, 1921; Vogel, 1984) and are then ingested. Spherical pellets of rejected inorganic materials (pseudofaecal pellets) accumulate in the dorsal buccal region, where they are periodically removed by the chelae, swept underneath the body and kicked to the rear by the animal (Zimmer-Faust, 1987).

These adaptations set intertidal limits to Scopimerinae distribution. As air-breathers they need an area that is regularly uncovered to provide time for feeding during the (mostly diurnal) low waters. As surface deposit-feeders they need an area that is regularly covered by the tide to renew the surface food supply. Subsidiary requirements are for sediment types (particle size and water content) suitable for burrowing (Ansell, 1988), the third behavioural adaptation of the species.

Burrows have diverse functions; they provide refuges from disturbance, predation and thermal extremes, but also assure the renewal of moisture loss, by accessing interstitial water through capillarity, and mark the centre of the crab's feeding range (Ansell, 1988). Gherardi et al. (1999) provided a detailed description of

the architecture of *D. fenestrata* burrows, distinguishing between the feeding-trench burrow dug on sandy substrates (a rectilinear trench where the crab feeds, walled on one or both sides by a row of pseudofaecal pellets) and the igloo built usually (but not always) on muddy substrates (a 2-cm enlarged chamber covered by a dome made of 2–6 superimposed rows of bricks). In *D. myctiroides* (H. Milne-Edwards), Takeda et al. (1996) distinguished vertical burrows, constructed in well-drained and firm sand, and igloos, that crabs build in semi-fluid, unstable sand.

However, in most species, including *D. fenestrata*, such burrow-orientated activity is abandoned by a large part of the population in favour of wandering, generally beyond the confines of the normal zone (Ansell, 1988). With the flooding tide, wanderer crabs recede to the burrow quarters, either stealing burrows from residents or building igloos in loose moist sand or in the waterlogged area at the edge of the approaching tide.

The present paper analyses the behaviour of the burrow-orientated component of a population of *D. fenestrata* inhabiting a Kenyan mangrove swamp.

MATERIALS AND METHODS

The study was carried out in the mangrove swamp of Mida Creek (20 km south of Malindi, Kenya) in

November, 1995 and March–April, 1997. A small gulf was chosen facing the village of Sita because its banks of sand were inhabited by a large population of *Dotilla fenestrata*. Figure 1 shows our experimental intervention in that area. A transect (36 m long) was laid to evaluate the general activity of the crabs around their burrows. The transect was inspected, by a researcher using binoculars at a distance of 2 m, at regular intervals seven times for each diurnal low water, on 7 November (spring tide) and 15 November (neap tide) 1995. Fixed quadrats are represented by 1–9, measuring 60 × 60 cm. Their locations (from the HWN level) were: 1, 5 m; 2, 15 m; 3, 30 m; 4, 15 m; 5, 25 m; 6, 10 m; 7, 17 m; 8, 22 m; 9, 27 m.

At quadrats 1, 2 and 3, an observer recorded the behaviour of *D. fenestrata* both occasionally (using the technique of the focal animal, that is the behaviour of one single crab was followed *ad libitum*) and during the entire low waters on 21, 23 and 24 November 1995, respectively. On the last date, the temperature at the substrate level was recorded every hour of observation. Behavioural observation was possible because individuals rapidly habituate to the presence of an observer. Each crab was observed *in continuum* for 10 min; the behaviours analysed were related to the construction and maintenance of the burrow, to feeding, to the uptake of water and to agonism. At quadrats 4–9, the crabs' behavioural budgets were studied: at

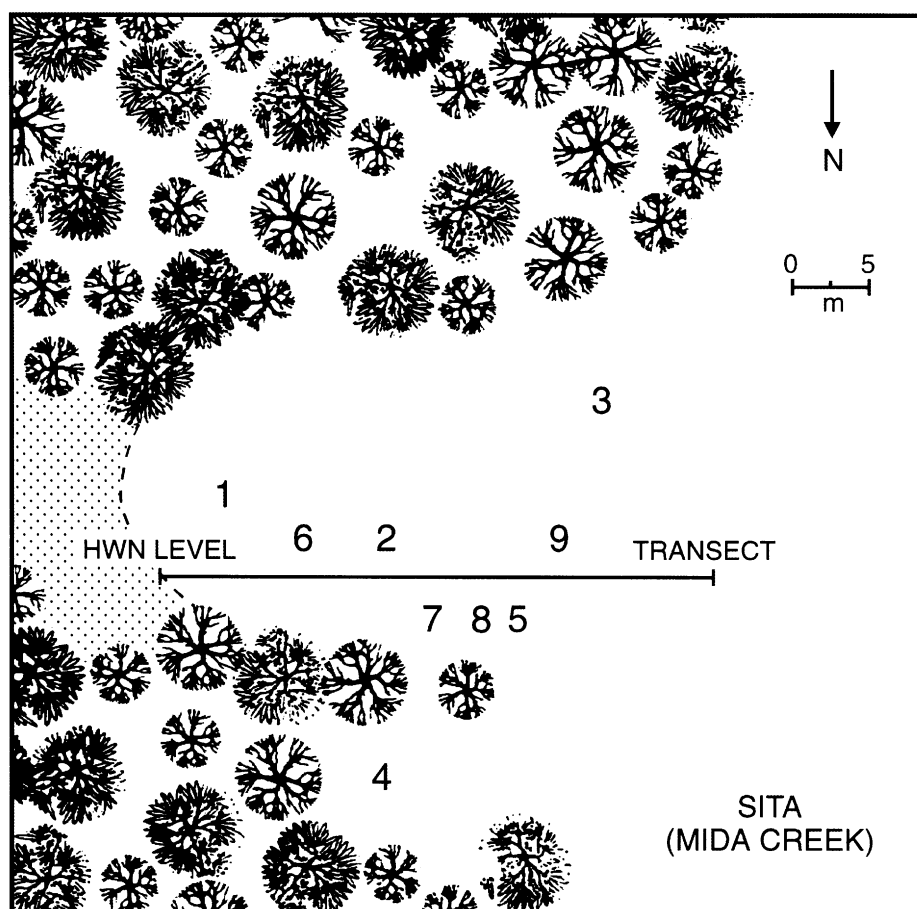


Figure 1. The study area at Mida Creek, showing our experimental interventions. A 36-m long transect was laid orthogonal to the coastline starting at the HWN level to evaluate the crabs' general activity. Numbers represent fixed quadrats, measuring 60 × 60 cm.

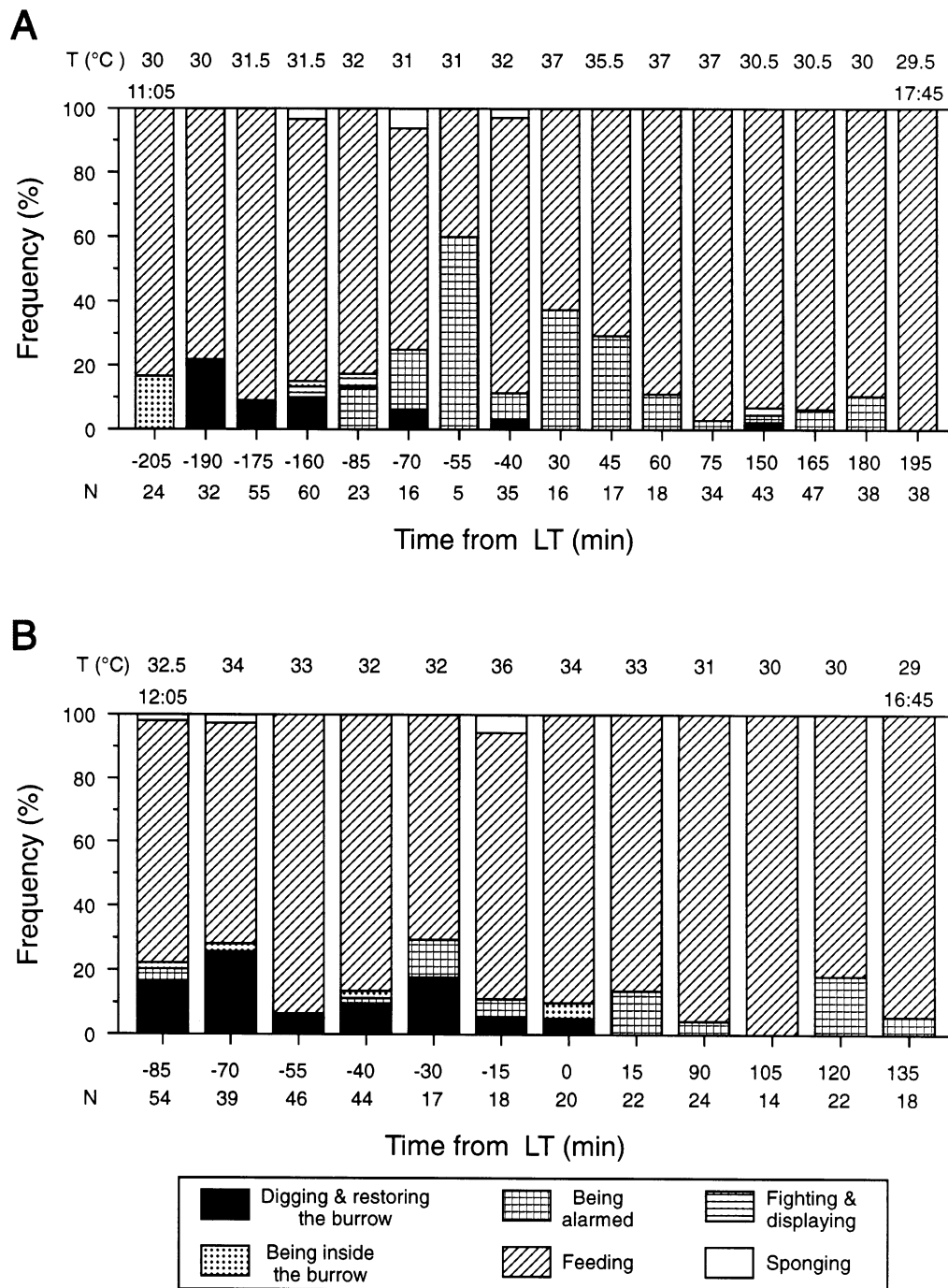


Figure 2. The behavioural budget of *Dotilla fenestrata* analysed in 60 × 60-cm quadrats at (A) 10 m and (B) 17 m from the HWN level on 29 March 1997 (LT 1430 hours) throughout the low water in an area where crabs inhabited feeding-trench burrows. N, sample size; T, temperature.

quadrat 4 on 7 November (spring tide) and 15 November (neap tide) 1995 and compared with the activity at quadrat 5; at quadrats 6–9 on 29 March 1997. Behaviour was grouped into six patterns (digging and restoring the burrow, being alarmed—the crab abruptly stopped its previous activity moving around or flattening its body onto the substrate, fighting and displaying, being inside the burrow, feeding, and sponging) and was recorded once every 15 min, with one hour of interruption. Contemporaneously, in 1997 the temperature at the substrate level was recorded.

Crab size was estimated by measurement of the ALW (antero-lateral angle width) with an ocular micrometer (to the nearest 0.1 mm) (Clayton & Al-Kindi, 1998). Three classes of crab size were arbitrarily distinguished: small, 1.7–4.4 mm ALW; medium, 4.4–7.1 mm ALW; and large, 7.1–9.8 mm ALW.

Text and figures give mean values and standard error. When the scores appeared to be drawn from a normally distributed population, parametric statistical techniques were used (Zar, 1984). Otherwise, statistical inference was made through nonparametric tests, following Siegel

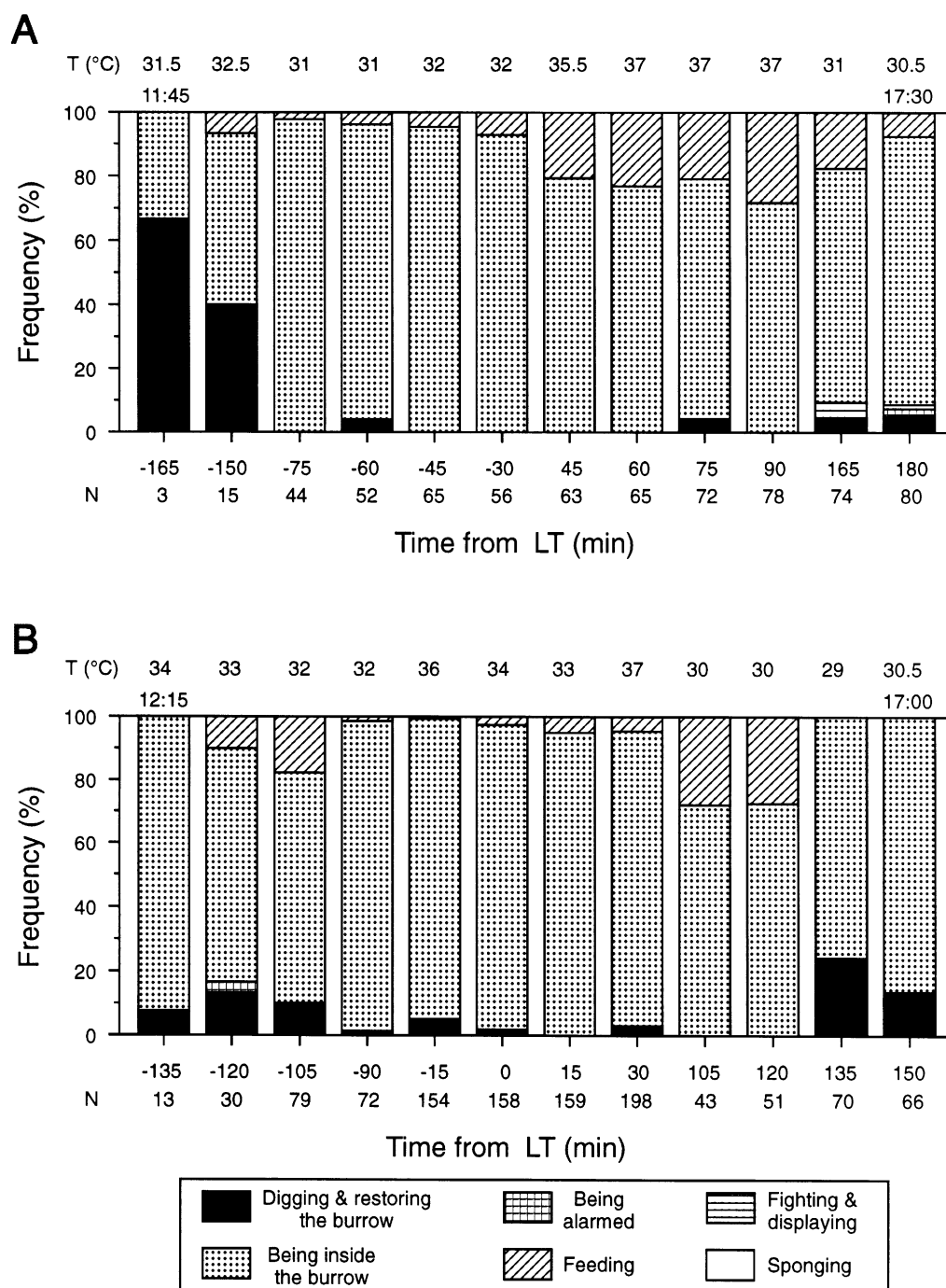


Figure 3. The behavioural budget of *Dotilla fenestrata* analysed in 60 × 60-cm quadrats at (A) 22 m and (B) 27 m from the HWN level on 29 March 1997 (LT 1430 hours) throughout the low water in an area where crabs inhabited igloos. N, sample size; T, temperature.

(1956). The level of significance under which the null hypothesis is rejected is $\alpha=0.05$.

RESULTS

Behavioural budget at the burrows

Comparison between feeding-trench burrows and igloos

At quadrats 6 and 7, located in an area where sand prevailed, *Dotilla fenestrata* inhabited feeding-trench burrows, whereas at quadrats 8 and 9, placed in muddy

sand, they were mainly in igloos (these two burrows' architecture has been sketched elsewhere (Gherardi et al., 1999)). Comparison of Figures 2 & 3 reveals that the behavioural budgets of crabs inhabiting the two burrow types strongly differed. If the comparison is limited to the two prevailing behaviours (being inside the burrow and feeding) and if three classes of time with respect to low tide (LT) (<60 min before LT, between 60 min before and 60 min after LT, >60 min after LT) are distinguished for both behaviours, the activity at quadrat 6 did not differ from that at quadrat 7 (being inside the

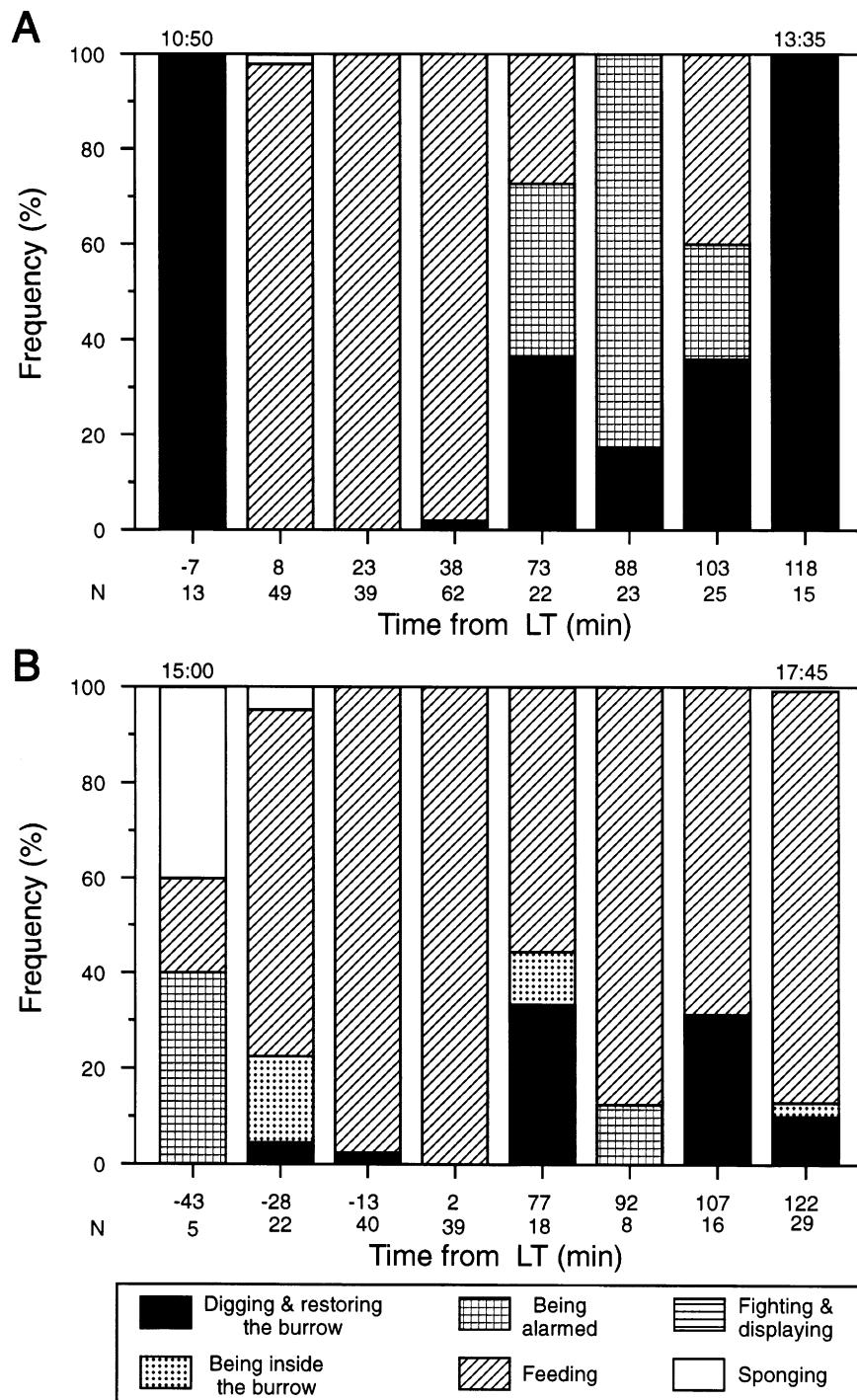


Figure 4. The behavioural budget of *Dotilla fenestrata* analysed in 60 × 60-cm quadrats at 15 m from the HWN level (A) on 7 November 1995 (spring tide, LT 1057 hours) and (B) on 15 November 1995 (neap tide, LT 1543 hours) throughout the low water in an area where crabs inhabited feeding-trench burrows.

burrow: $F=0.44$, $df=1$, 22, ns; feeding: $F=1.1$, $df=1$, 22, ns) and quadrat 8 was not different from quadrat 9 (being inside the burrow: $F=2.18$, $df=2$, 18, ns; feeding: $F=1.74$, $df=2$, 18, ns). Thus the data of quadrats 6 and 7 were pooled, as were those of quadrats 8 and 9, and the comparison was made between crabs living inside feeding-trench burrows and those in igloos. During low water, the crabs inhabiting igloos spent significantly more time inside the burrow (mean ± SE acts in %:

$80.98 \pm 3.14\%$, $N=24$ vs $1.61 \pm 2.48\%$, $N=28$; $F=930.57$, $df=1$, 46, $P<0.001$) and less time feeding in the open (mean ± SE acts in %: $9.98 \pm 2.04\%$, $N=24$ vs $83.34 \pm 2.48\%$, $N=28$; $F=324.58$, $df=1$, 46, $P<0.001$).

Feeding also differed among temporal classes, being more frequent at the end of low water (mean ± SE acts in %, < -60 min: $42.03 \pm 9.64\%$, $N=16$; -60/+60 min: $48.74 \pm 8.61\%$, $N=19$; > +60 min: $57.34 \pm 9.94\%$, $N=17$; $F=3.87$, $df=2$, 46, $P<0.05$).

Table 1. Mean \pm SE number of behavioural acts (or products of them) performed by residents every 10 min: comparison among *Dotilla fenestrata* size-classes.

Behavioural acts	Size-classes						<i>H</i>	df	<i>P</i>
	Small mean \pm SE	N	Medium mean \pm SE	N	Large mean \pm SE	N			
Excavated pellets	1.37 \pm 0.65	49	1.50 \pm 0.61	56	2.63 \pm 0.83	35	6.042	2	<0.05
Restoring acts	0.78 \pm 0.20	49	0.80 \pm 0.16	56	0.54 \pm 0.17	35	1.527	2	>0.05
Pseudofaecal pellets	43 \pm 8.25	43	42.72 \pm 3.90	40	36.54 \pm 6.61	13	1.842	2	>0.05
Visits of the burrow	1.37 \pm 0.29	49	0.71 \pm 0.19	35	1.04 \pm 0.20	56	2.875	2	>0.05
Sponging acts	2.78 \pm 0.59	49	1.25 \pm 0.28	56	1.74 \pm 0.55	35	2.707	2	>0.05
Agonistic acts	0.35 \pm 0.15	49	1.25 \pm 0.41	56	1.80 \pm 0.45	35	10.192	2	<0.01

N, sample size; *H*, output of Kruskal–Wallis one way ANOVA by ranks.

Table 2. Mean \pm SE number of behavioural acts (or products of them) performed by residents every 10 min: comparison among phases of the semilunar cycle.

Behavioural acts	Phases of the semilunar cycle						<i>H</i>	df	<i>P</i>
	Spring mean \pm SE	N	Spring/Neap mean \pm SE	N	Neap mean \pm SE	N			
Excavated pellets	1.32 \pm 0.42	91	3.37 \pm 1.09	40	1.04 \pm 0.41	25	3.692	2	>0.05
Restoring acts	0.79 \pm 0.13	91	0.45 \pm 0.10	40	1.24 \pm 0.31	25	4.946	2	~0.05
Pseudofaecal pellets	50.34 \pm 5.84	41	35.15 \pm 4.53	27	41.41 \pm 5.60	22	2.569	2	>0.05
Visits of the burrow	1.31 \pm 0.20	91	0.85 \pm 0.19	40	0.8 \pm 0.36	25	2.897	2	>0.05
Sponging acts	2.70 \pm 0.39	91	0.40 \pm 0.24	40	1.04 \pm 0.34	25	19.013	2	<0.01
Agonistic patterns	0.78 \pm 0.24	91	1.92 \pm 0.48	40	0.8 \pm 0.31	25	10.271	2	<0.01

N, sample size; *H*, output of Kruskal–Wallis one way ANOVA by ranks.

Table 3. Mean \pm SE number of behavioural acts (or products of them) performed by residents every 10 min: comparison among times from the LT (in min).

Behavioural acts	Time from the LT								<i>H</i>	df	<i>P</i>
	< -60 mean \pm SE	N	-60/+60 mean \pm SE	N	+60/+180 mean \pm SE	N	> +180 mean \pm SE	N			
Excavated pellets	4.80 \pm 1.95	15	1.05 \pm 0.50	42	0.85 \pm 0.41	46	2.38 \pm 0.80	53	8.214	3	<0.05
Restoring acts	0.93 \pm 0.32	15	0.62 \pm 0.20	42	0.85 \pm 0.18	46	0.79 \pm 0.17	53	2.98	3	>0.05
Pseudofaecal pellets	35.44 \pm 5.30	18	50.64 \pm 8.24	25	46.77 \pm 6.44	22	39.64 \pm 5.34	25	1.385	3	>0.05
Visits of the burrow	0.27 \pm 0.12	15	0.60 \pm 0.11	42	1.41 \pm 0.25	46	1.49 \pm 0.32	53	9.576	3	<0.05
Sponging acts	0.80 \pm 0.47	15	0.98 \pm 0.37	42	3.48 \pm 0.63	46	1.41 \pm 0.32	53	19.135	3	<0.001
Agonistic patterns	1.60 \pm 0.48	15	0.50 \pm 0.18	42	1.30 \pm 0.37	46	1.19 \pm 0.43	53	7.622	3	>0.05

N, sample size; *H*, output of Kruskal–Wallis one way ANOVA by ranks.

No correlation was found between soil temperature and the percentages of either feeding (after arcsine square transformation, feeding-trench burrows: $r = -0.229$, $df = 26$, ns; igloos: $r = 0.104$, $df = 22$, ns) or being inside the burrow (feeding-trench burrows: $r = -0.072$, $df = 26$, ns; igloos: $r = 0.168$, $df = 22$, ns).

Comparison between spring and neap tides in feeding-trench burrows

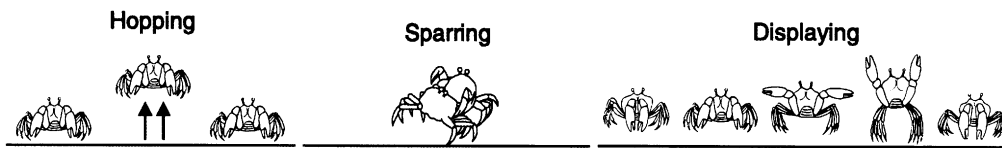
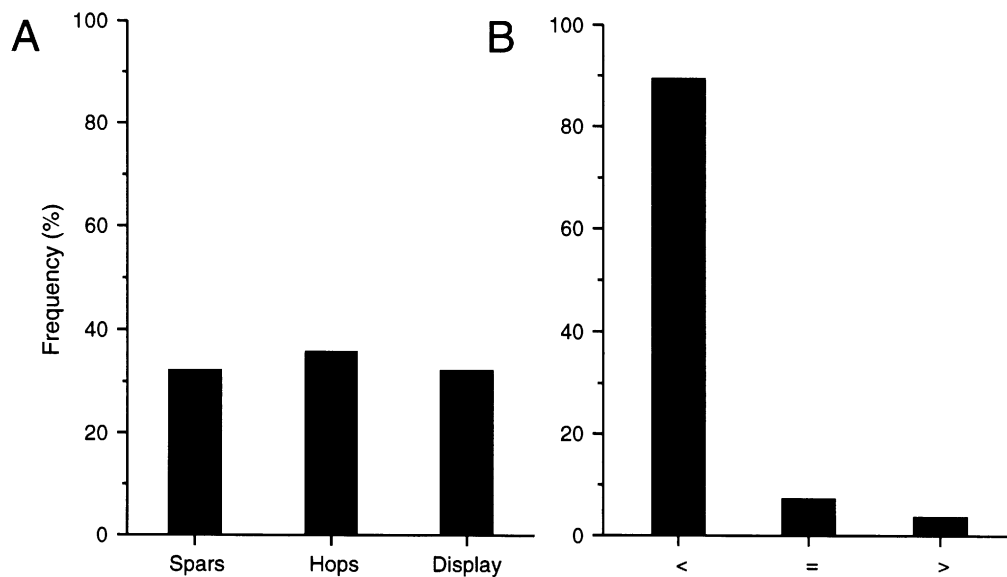
At quadrat 4, crabs exclusively inhabited feeding-trench burrows. The behavioural budgets at spring and

neap tides differed markedly (Figure 4). We compared only the two prevailing behavioural patterns, digging/restoring the burrow and feeding. For both behaviours, there was a difference in the semilunar cycle (ANOVA after arcsine square transformation, spring vs neap tides, mean \pm SE acts in %, digging and restoring: 36.47 \pm 14.81%, $N = 8$ vs 10.20 \pm 4.97%, $N = 8$, $F = 10.64$, $df = 1, 10$, $P < 0.01$; feeding: 45.45 \pm 16.42%, $N = 8$ vs 72.91 \pm 9.09%, $N = 8$, $F = 16.39$, $df = 1, 10$, $P < 0.01$) and in the time with respect to LT (three classes: before LT, between LT and 60 min after, >60 min after; digging

Table 4. Mean \pm SE number of behavioural acts (or products of them) performed by residents every 10 min: comparison among times from noon (in min).

Behavioural acts	Time from noon										<i>H</i>	df	<i>P</i>
	< -180 mean \pm SE	N	-180/-60 mean \pm SE	N	-60/+60 mean \pm SE	N	+60/+180 mean \pm SE	N	> +180 mean \pm SE	N			
Excavated pellets	8.12 \pm 3.24	8	0.44 \pm 0.33	16	0.38 \pm 0.20	34	0.87 \pm 0.39	55	3.44 \pm 1.02	43	23.254	4	<0.0001
Restoring acts	0.50 \pm 0.19	8	1.06 \pm 0.47	16	1.08 \pm 0.25	36	0.51 \pm 0.12	55	0.77 \pm 0.16	43	4.353	4	>0.05
Pseudofaecal pellets	36.29 \pm 11.55	7	64.25 \pm 14.57	12	60.41 \pm 7.65	17	32.88 \pm 4.54	25	36.79 \pm 3.94	28	11.5	4	<0.05
Visits of the burrow	0 \pm 0	9	0.31 \pm 0.12	16	0.97 \pm 0.28	34	1.51 \pm 0.25	55	1.21 \pm 0.29	43	16.053	4	<0.01
Sponging acts	0 \pm 0	9	2.67 \pm 0.90	15	2.21 \pm 0.69	34	2.34 \pm 0.46	55	1.02 \pm 0.30	43	10.217	4	<0.05
Agonistic patterns	0.56 \pm 0.38	9	0.5 \pm 0.39	16	0.06 \pm 0.59	34	1.22 \pm 0.41	55	2.00 \pm 0.41	43	24.764	4	<0.001

N, sample size; *H*, output of Kruskal–Wallis one way ANOVA by ranks.

**Figure 5.** Agonistic patterns displayed by *Dotilla fenestrata*.**Figure 6.** Aggression of residents against passers-by: (A) behaviour performed by residents and (B) relative size of passers-by (N=28).

and restoring: $F=9.48$, $df=2$, 10 , $P<0.01$, with 0/+60 significantly different from >60 after, Tukey test, q : 5.23 vs 3.88; feeding: $F=16.39$, $df=1$, 10 , $P<0.01$, with 0/+60 significantly different from >60 after, Tukey test, q : 4.30 vs 3.88).

Burrow-orientated activity in time and space

The activity around the burrow (the number of crabs outside their burrow aperture along the transect related

to the time from LT) decreased during low water in both spring (Spearman rank correlation: $r_s = -0.634$, $t = -3.847$, $df=22$, $P<0.001$) and neap tides ($r_s = -0.463$, $t = -2.089$, $df=16$, $P \sim 0.05$).

The distance from the HWN level seems not to condition the general activity of *D. fenestrata* at neap tide (at quadrat 4, 15 m from the HWN level: mean \pm SE number of active crabs = 31.66 ± 6.04 , $N=8$; at quadrat 5, 25 m from the HWN level: mean \pm SE number of active crabs = 25.4 ± 7.71 , $N=10$; Mann–Whitney *U*-test:

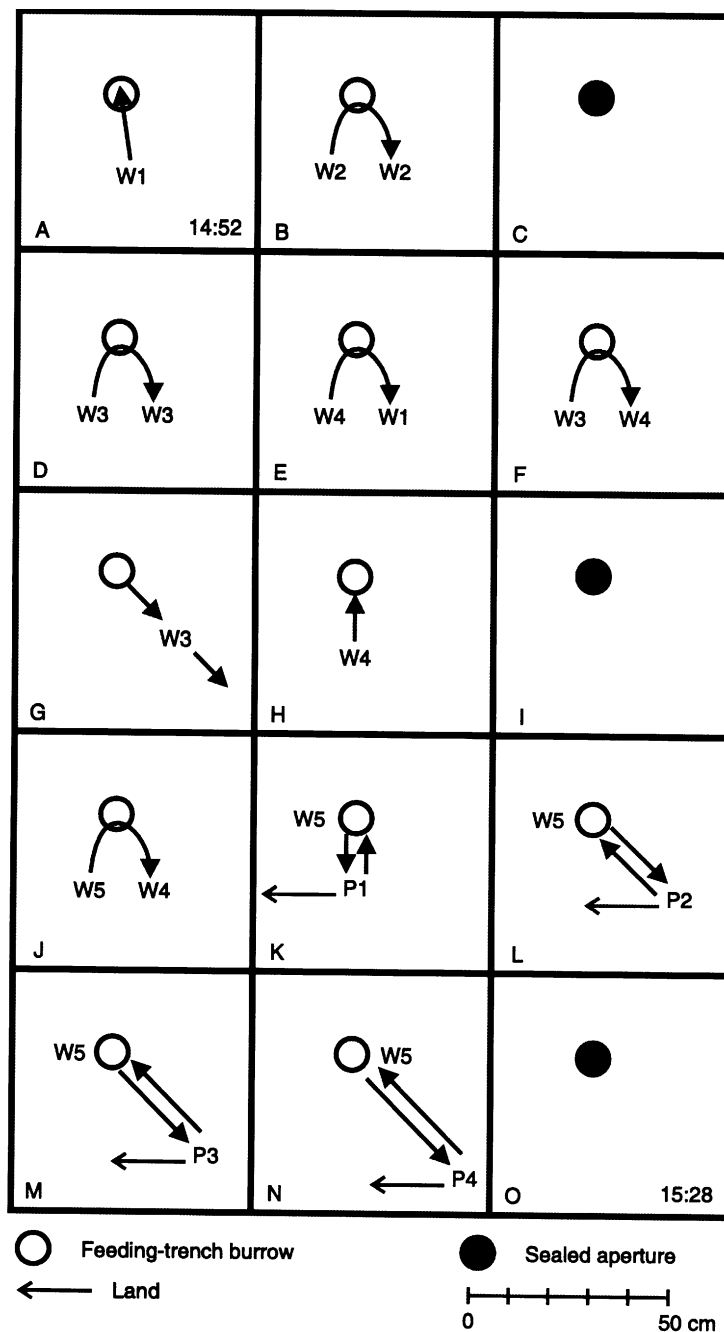


Figure 7. Sketch of the switch of burrows displayed by wanderers (W) and of their aggression towards passers-by (P) during the flooding tide period (8 November 1995, LT 1128 hours, 25 m from HWN level). Sequence of events is represented with letters at one lower corner of each quadrat. Curved arrows indicate the entering of the burrow by the crab at the tail of the curve and the exiting from the burrow by the crab at the head of the curve. Double arrows mean the outward displacement by one *Dotilla* towards either other residents or passers-by, with whom it fights, and then its return displacement to the home burrow. Single arrows indicate the direction followed by either passers-by or wanderers.

$U=28.5$, $N=10$ and 8, ns). By contrast, at spring tide, general activity was significantly higher at 25 m (at 15 m: mean \pm SE number of active crabs = 15.08 ± 4.32 , $N=12$; at 25 m: mean \pm SE number of active crabs = 39.83 ± 5.83 , $N=12$; $U=12$ and 12, $P < 0.01$).

Behavioural patterns

Digging and maintenance of the burrow

Digging was quantified on the basis of the number of pellets excavated every 10 min per crab during the

observations at quadrats 1, 2 and 3. Large individuals excavated more pellets than the other two size-classes (Table 1). By contrast, no difference was found within the semilunar cycle (Table 2). If the number of pellets is plotted with the time from both LT and from noon, a significant variation is seen in both cases (Tables 3 & 4); digging is obviously more pronounced after emergence and just before the sealing of the burrow at the flooding tide, but also in proximity to noon.

Maintenance of the burrow, including clearing the trench, was independent of crab size (Table 1), of the

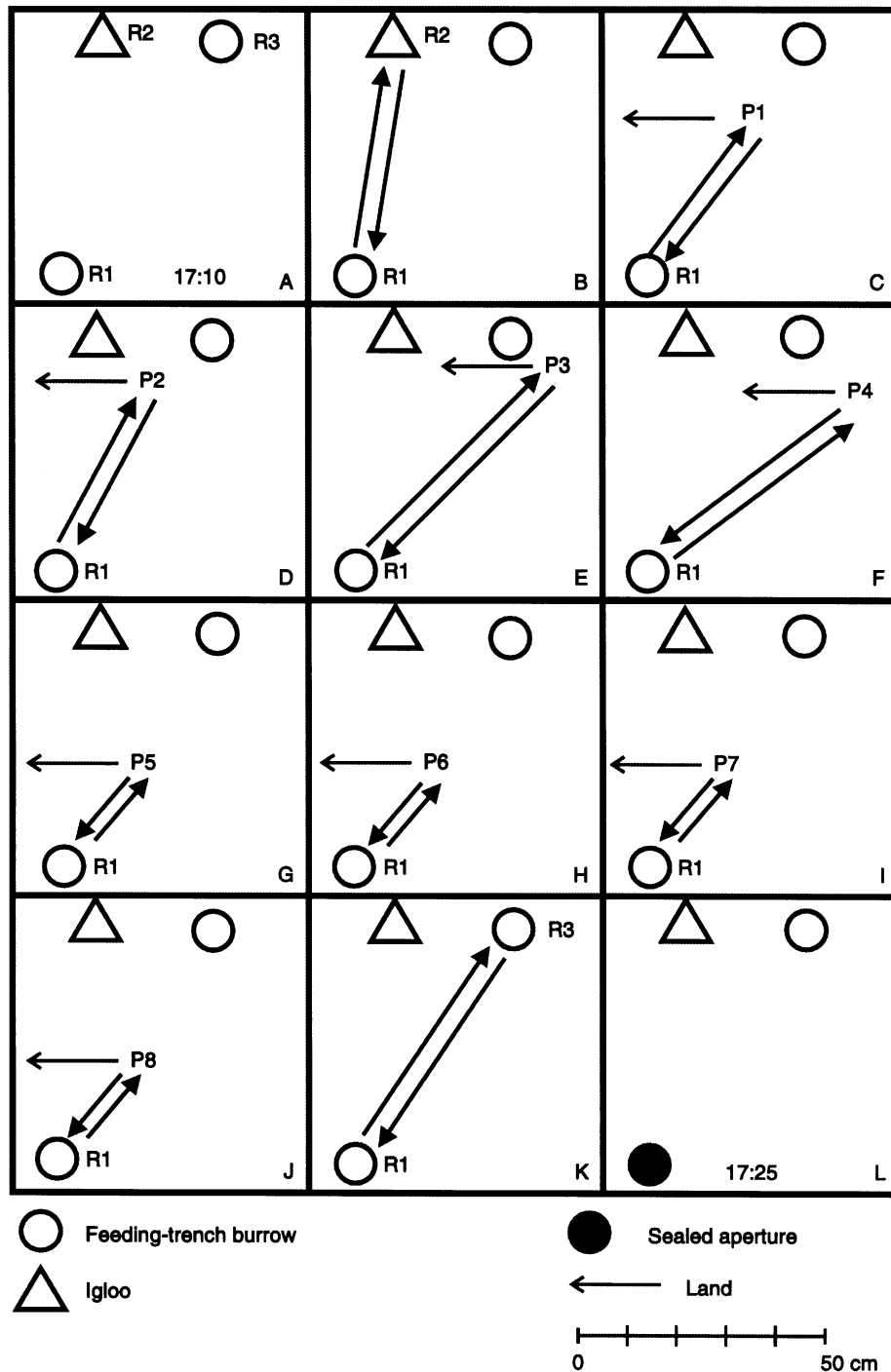


Figure 8. Sketch of the agonistic behaviour displayed by residents (R) against other residents and passers-by (P) during the flooding tide period (11 November 1995, LT 1257 hours, 25 m from HWN level). Sequence of events is represented with letters at one lower corner of each quadrat. Curved arrows indicate the entering of the burrow by the crab at the tail of the curve and the exiting from the burrow by the crab at the head of the curve. Double arrows mean the outward displacement by one *Dotilla* towards either other residents or passers-by, with whom it fights, and then its return displacement to the home burrow. Single arrows indicate the direction followed by either passers-by or wanderers.

semilunar cycle (Table 2), of the time from LT (Table 3) and of the time from noon (Table 4).

Feeding

A good estimate of feeding activity is the number of pseudofaecal pellets produced in 10 min by each crab. We did not observe a significant difference in the number of pellets among size-classes (Table 1), phases of the semi-lunar cycle (Table 2) or the times from LT (Table 3). In

contrast, there was a significant reduction after at least one hour from noon (Table 4).

No correlation was found between the substrate temperature and the number of pseudofaecal pellets (averaged among animals observed contemporaneously) (Spearman rank correlation: $r_s = 0.643$, $N = 6$, ns).

In a sample of 53 crabs, the average time for each animal to produce ten pseudofaecal pellets was measured with a chronometer. There was no difference among size-

classes (one-way ANOVA: $F=1.19$, $df=2$, 50, ns), the mean \pm SE time being 5.90 ± 0.52 s ($N=23$) for small crabs, 7.24 ± 0.83 s ($N=18$) for medium ones and 6.25 ± 0.57 s ($N=12$) for large specimens.

We observed no functional difference in the use of one chela (either right or left) by the animals. For each of 63 specimens we recorded (10 min) which chela was used to remove pseudofaecal pellets from the mouth and then assessed (using either the Wilk's or binomial test) whether one chela was used more than the other. Crabs removing pseudofaecal pellets with the chelae of both sides (47.62%) were significantly more numerous than prevalently right-handed (31.75%) and prevalently left-handed (20.63%) specimens (Wilk's test: $G=6.907$, $df=2$, $P<0.05$).

Water uptake and temperature regulation

The number of visits inside the burrow did not differ among size-classes (Table 1) or within the semilunar cycle (Table 2), but was significantly higher at the end of the low water (Table 3) and around and after noon (Table 4).

Sponging was performed equally by differently-sized crabs (Table 1), but mostly occurred at spring tide (Table 2), after 1–2 h from LT (Table 3) and around noon (Table 4).

Aggression

With few exceptions, the objects of aggression are burrows and feeding areas (feeding-trenches).

Three main behavioural patterns have been distinguished in the agonistic repertoire of *Dotilla fenestrata* (Figure 5).

(1) Hopping (the 'agitation' described by Fielder (1970) in *Scopimera inflata* (H. Milne Edwards)). The crab raises and lowers itself rapidly on the tips of its walking legs by straightening and bending them, jumping up and down on the spot. The chelae are held slightly extended so that the inertia of each jump makes them flap as though attached to a sloping hinge. This behaviour is often repeated up to five times and lasts a few seconds.

(2) Sparring (Fielder, 1970). The two crabs circle facing each other with their chelae outstretched towards the opponent. The sparring ends abruptly when the chelae are interlocked, each combatant attempting to grasp the opponent's chelipeds near their bases. A brief 'tug-of-war' then follows which ends with the retreat of one crab, actively pursued by the other.

(3) Displaying. The defender straightens its walking so that its legs are nearly vertical, thus raising its body maximally. Simultaneously the chelae are slowly raised so they are at their fullest extension above the body and are held in this position for a short period of time. The chelae are then dropped rapidly in front of the crab, their tips nearly touching the sand surface. As the chelae are lowered, the crab lowers its body to its initial position by bending its walking legs. This behaviour is often repeated up to three times and lasts a few seconds. Often, *D. fenestrata* was observed in this display without other crabs in proximity, and even on the top of the domes of igloos.

The frequency of agonistic patterns is higher in larger individuals (Table 1), during the phase between spring and neap tides (Table 2) and after noon (Table 4). In contrast, agonism is constant throughout low water (Table 3).

With the incoming of flood tide, at the return to the burrow quarters of some wanderer crabs, we observed strong agonistic behaviour performed by residents against passers-by (Figure 6). While the exhibited pattern did not significantly differ (hopping vs sparring vs displaying: $G=0.069$, $df=2$, ns), attacks occurred mostly against the passers-by that were smaller than the resident (smaller- vs equal- vs larger-sized crabs: $G=37.737$, $df=2$, $P<0.001$). Figures 7 & 8 schematically represent the aggressive behaviour that large crabs exhibited at the end of the feeding periods towards other resident crabs but especially towards passers-by.

DISCUSSION

Species inhabiting the intertidal zone are subject to a wide range of environmental fluctuations arising from tidal and diel changes. Some of these changes, e.g. tidal immersion and emersion and daily changes in light intensity, are predictable cyclical phenomena. Others, e.g. those dependent on the weather or interactions with other organisms, are not at all predictable (or only to a limited extent).

Thus, the behavioural responses of intertidal organisms fall into two categories. Some are the necessary outcome of morphological and physiological adaptations which enable the organism to exploit the intertidal environment and help to define a particular environmental niche; these relate mainly to the more predictable changes, e.g. the endogenous rhythms which control the tidal and diel activities of organisms and the main components of those activities, particularly feeding. Other behavioural responses provide the flexibility to survive the more extreme and unpredictable fluctuations affecting that particular niche; these include responses which fine-tune the endogenous rhythms and allow the organism flexibility with respect to short-term changes (Ansell, 1988).

Rigidity in the behaviour of Dotilla fenestrata

A juxtaposition of rigidity and plasticity characterizes the behaviour of *Dotilla fenestrata* inhabiting the mangrove swamp of Mida Creek. On the one hand, light–dark, tidal and semilunar cycles condition its phase of activity. Like most Ocypodidae, the species is active almost exclusively during diurnal low waters (at nocturnal low waters, a number of *Dotilla* open their burrows but do not display any activity outside of it) (Gherardi et al., 1999).

The activity of *D. fenestrata* can be classified in a number of stereotyped behavioural patterns, the occurrence of which may change either throughout the low water or on the basis of the behaving crab's size, according to an expected schedule.

Thus, digging is more pronounced in larger individuals (which have to excavate larger tunnels) and mostly occurs when the crab emerges or just before it seals itself inside the burrow at the flooding tide. On the other hand, maintenance of the burrow is a constant behaviour. The trench especially must be kept clear because it is an easy

way to escape towards the burrow mouth at the approach of a potential predator.

Feeding rate, estimated from the number of pseudo-faecal pellets emitted, is constant both throughout low water (with the exception of noon when it decreases) and with the feeding crab's size, and is not related to the variation in temperature (contradicting Fishelson, 1983). Weissburg (1992), discussing male fiddler crabs their potential handicap in foraging caused by the master chela, distinguished the scoop rate (the rate at which the chela delivers substratum to the mouth) and the extraction rate (the rate at which food is extracted from the inorganic matrix), as parts of the intake rate (food biomass ingested/time); he invoked a more complete understanding of the relationships between scoop and extraction rates and food abundance.

The behavioural patterns that assure water uptake and temperature regulation (sponging and visits inside the burrow) are more frequently performed around noon and, especially sponging, during spring tides when the platform is emerged for longer lengths of time.

Agonistic patterns are mostly performed by larger individuals; the rate of aggression by resident crabs, against neighbours but mostly against smaller passers-by, increases with the flooding tide, a phenomenon already seen in *Scopimera inflata* by Fielder (1970) who called these aggressive crabs 'rogues'. Because smaller individuals are more often females (F. Gherardi, personal observation), the attacks of large individuals towards smaller ones cannot simply be explained as the expression of territorial behaviour; an alternative meaning might be the attempt to discover (and/or copulate with) a receptive female. In *Scopimera globosa* De Haan, Yamaguchi et al. (1979) and Wada (1981a,b) recognized two types of sexual behaviour: (i) a male chases a female and, when he captures her, they complete copulation on the substrate surface (this behaviour was also observed in *S. proxima* Kemp (Silas & Sankarankutty, 1967)); and (ii) copulation is not performed on the surface, but after having captured a female, the male carries her into his burrow and plugs it by scraping up the sand from around the entrance or from inside the burrow. *Dotilla fenestrata* also showed the latter behaviour (females were abducted by males and dragged inside their burrows). Similarly to fiddler crabs (Salmon, 1965; Crane, 1975; Salmon et al., 1978; Christy, 1980; Christy & Salmon, 1984), male *Ilyoplax pusillus* De Haan (Wada, 1981a), and large *D. fenestrata* (F. Gherardi, personal observations), may wave or display in intra-male combat and as signalling device to attract mates.

Plasticity in the behaviour of Dotilla fenestrata

For crabs that feed on surface deposits, the most unpredictable parameter in the mangrove swamp is the distribution of food over the emerged platform; this changes from tide to tide in such a complex way that crabs cannot efficiently sample or interpret food gradients. In *Scopimera inflata*, Zimmer-Faust (1987) observed that, given that the crab must contact substrates to assess its worth, selective grazing may be

too inefficient because of sampling costs and the neural investment needed to understand food quantity. *Scopimera* distinguished among organic and inorganic materials and showed, at least in the laboratory, a threshold concentration (60% food solutions) for substrate rejection, that was lower than that normally encountered in the natural habitat (Zimmer-Faust, 1987). This species may use visual cues to orientate feeding movements (Zimmer-Faust, 1987), while other ocypodid crabs rely entirely on chemoreception to direct foraging activities (in *Uca pugilator* (Bosc) and *Ocypode quadrata* (Fabricius), chemoreceptors are located on the dactyls (Robertson et al., 1981; Trott & Robertson, 1984)). In *Uca pugilator*, optimal conditions for feeding are found in organic sediment with organic content at or above 1.0% (by weight), which is however fully saturated with water (Reinsel & Rittschof, 1995); this allows the complete dactyl penetration with the highest number of chemoreceptors that can contact the stimuli.

In the mangrove swamp, the absence of spatial uniformity of feeding material and the *D. fenestrata*'s stereotyped all-or-nothing responses to feeding stimuli result in a number of adaptive flexible behaviours.

First, there are differences among individuals in the length of time devoted to burrow-centred activity (crabs that are 'full' avoid further dangers and seal themselves into their burrows largely prior to the flooding, about 20% of *D. fenestrata*), in the feeding activity between neap and spring tides (during neap tides, characterized by a slower current, fewer food items are deposited on the surface), and in the spatial distribution of burrows (mostly reflecting food availability).

Second, when the crabs emerge from their burrows with the receding tide, one part of the population (in *Scopimera inflata* <10% (Zimmer-Faust, 1987), while in *D. fenestrata* reaching a maximum of around 80% of the emerging crabs (F. Gherardi, personal observation)) wanders about forming dense aggregations or 'droves' that often move away from the normal residence zone. This behaviour was shown in Mictyridae (*Mictyris longicarpus* Latreille (Cameron, 1966) and Ocypodidae Macrophthalminae (*Macrophthalmus japonicus* (De Haan) (Wada, 1978; Henmi, 1984, 1989)), Ocypodinae (*U. annulipes* (Latreille) (M. Vannini, personal communication), *U. lactea* De Haan (Yamaguchi, 1971), *U. pugilator* (Crane, 1975), *U. vocans vocans* (Linnaeus) (Murai et al., 1982; Nakasone, 1983) and *U. tangeri* Eydoux (von Hagen, 1962; Crane, 1975)) and Scopimerinae (*Dotilla blanfordi* Alcock (Altevogt, 1957), *D. fenestrata* (Hartnoll, 1973; Gherardi & Russo, 1997), *D. myctiroides* (Tweedie, 1950; Altevogt, 1957), *D. sulcata* (Forskåll) (Fishelson, 1983), *Ilyoplax pusillus* (Wada, 1981a), *Scopimera globosa* (Yamaguchi & Tanaka, 1974; Wada, 1981a,b) and *S. inflata* (Zimmer-Faust, 1987)). Drove formation has been explained by reproductive functions (von Hagen, 1962; Yamaguchi, 1971; Crane, 1975; Wada, 1978, 1981a,b; Nakasone, 1983), by dry conditions in burrow areas (Wada 1981b; Murai et al. 1982; Henmi 1984, 1989; Reinsel & Rittschof, 1995), by high population densities (Ono, 1965; Yamaguchi & Tanaka, 1974; Wada, 1981a) and by poor food availability near burrows (Cameron, 1966; Crane, 1975; Robertson et al., 1980; Murai et al., 1982, 1983; Gherardi & Russo, 1997). The compactness, at least observed in *D. fenestrata*'s

aggregations, appears a passive mechanism against predation (Russo et al., 1998).

Third, the specimens that remain sedentary throughout most of, or the entire, low water construct burrows of different architectures (feeding-trench burrows and igloos), which are not necessarily related to the nature of the substrate (although usually sandy for the former and muddy for the latter). The type of burrow strongly conditions the inhabitant's behavioural budget. While the residents of feeding-trench burrows spend around 80% of their time feeding during low water (and stay only 2% of the time inside the burrow), crabs inhabiting igloos feed for around 10% of the available time, remaining below the domes for more than 80%. In addition, while the former feed constantly around low water, the latter concentrate their feeding activity with the incoming flood tide. No relation was found between behavioural budget and surface temperature. One possible explanation of the differences in behavioural budget is that the substrate where igloos are built is richer in organic matter than the substrate around feeding-trench burrows, allowing the residents to minimize the time devoted to feeding, while maximizing the energetic input. In this way, the inhabitants of igloos reduce their exposure to both predators and environmental extremes. At least in *D. myctiroides*, Takeda et al. (1996) found a small quantity of air together with the crab itself inside igloos. In these air-filled chambers beneath the sand surface, the crab continued to scoop up the sand from the lower surface of the chamber and attached the scooped pellets to the ceiling. Consequently, the crab, together with the chamber, continually moved deeper into the sand until it was below the water level.

CONCLUSION

Dotilla fenestrata and other Scopimerinae have evolved a semi-terrestrial, surface deposit feeding habit, with contrasting behavioural adaptations. Indeed, they exhibit a combination of stereotyped behaviours and flexible responses, which allow the efficient exploitation of tidally-replenished food resources under good conditions and the maintenance of some activity when conditions are less favourable. Thus, most Scopimerinae exhibit two different feeding modes, one orientated around a semi-permanent burrow, the other away from any burrow. In addition, the burrow-centred *D. fenestrata* specimens construct two types of burrows, the feeding-trench burrow and the igloo. The two burrow types are accompanied by specific behavioural repertoires, characterized by slight differences in the stereotyped behaviours.

The ability to 'switch' modes of activity allows responses to both the predictable and unpredictable elements of intertidal environments (Ansell, 1988), the mangrove swamp included.

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