

Aggregations of the sandy-beach isopod, *Tylos granulatus*: adaptation or incidental-effect?

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Spatial aggregations of organisms are common in nature. Aggregations have often been thought to play important roles in mate-finding, predator avoidance, reduction of water loss, or the acquisition of food and other resources, yet few empirical studies have been done on the processes that lead to aggregation. We studied aggregations of the giant isopod *Tylos granulatus*, which lives as a scavenger in the intertidal zone of sandy beaches on the west coast of South Africa. Individuals emerge with the receding tide leaving exit holes, then forage for about two hours before returning to the vicinity of the high-water mark where they aggregate to bury themselves, leaving behind cone-shaped mounds. Our observations showed there was no correlation between aggregations and the availability of food, and that manipulating the position of food had no effect on the aggregations. Reproduction, which is seasonal and synchronous, also seems unlikely to explain the year-round aggregations. Experiments showed *T. granulatus* preferentially burrows in existing holes or mounds rather than creating new ones. The advantages of this are analysed in terms of energy conservation, and as a means of reducing risks of exposure to predators or being swept away by the incoming tide. Whatever the benefit, the preferential use of existing holes can incidentally lead to aggregation, which may not itself have any adaptive function.

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Introduction

Aggregations of organisms are frequently observed in nature, and are commonly thought to play a role in mate-finding, predator avoidance, avoidance of water loss, or the acquisition of food or other resources (for reviews see Takeda 1984; Turchin 1989; Morris, Wiser & Klepetka 1992). From a theoretical standpoint aggregations have far-reaching influences on both intraspecific and interspecific interactions (e.g. De Jong 1982; Atkinson & Shorrocks 1981; Hanski 1981; Linsenmair 1984; Ives & May 1985; Turchin 1989). Curiously, most theoretical studies assume the clumped distribution of organisms from the outset, and few empirical studies have attempted to explain precisely why and how aggregations form (Turchin 1989). Such studies may yield surprising results that are contrary to prevailing views on why aggregations exist. For instance, males of many insect species aggregate and it has often been thought that this increases their mating success. However, in the case of the nymphalid butterfly *Euphydryas editha*, Ehrlich and Wheye (1986) demonstrated that males within hilltop aggregations actually have a lower mating success than males outside aggregations. Later Odendaal, Turchin & Stermitz (1988) showed that aggregation of males of *Euphydryas anicia* is an incidental effect arising from their tendency to chase flying objects indiscriminately, including other males, to try to mate with them.

To explain why a particular aggregation exists is often difficult. The reason is that spatial patterns are usually influenced by other confounding factors as well. It may be easier to tease apart confounding factors where there are short-term fluctuations of both the spatial distribution of key resources and other factors that influence an organism's distribution. Such an environment is the intertidal zone on sandy beaches. Not

only does food arrive in a patchy and unpredictable fashion, but other factors influencing spatial patterns, such as the tidal water movements and humidity, also fluctuate through time. Sandy beaches also have other attributes that can aid studies of aggregation, including good visibility, even topography and the presence of visible clues to recent changes in the positions of organisms, such as holes or tracks (e.g. Hamner, Smythe & Mulford 1969; Hayes 1970; Kensley 1972).

The distribution of sandy-beach macrofaunal species is often patchy (Brown & McLachlan 1990). Many species form aggregations, the causes of which have been variously explained. One view is that aggregations are simply due to passive dispersal controlled by water movements (McLachlan & Hesp 1984). Both Cubitt (1969) and Dillery & Knapp (1969) believe this is true of *Emerita analoga*, although its aggregations reach a peak during reproduction (Perry 1980) and may thus have a reproductive function. Aggregations of *Donax incarnatus* and *D. spiculum* are also probably caused by water movements (Ansell, Sividas, Narayanan, & Trevalion 1972). However, clumping of both *Bullia digitalis* and *Donax serra* can be correlated with food availability (Brown, Stenton-Dozey & Trueman 1989). Dispersion of the rove beetle *Psammathobledius punctatissima* is related to the penetrability of the sand (Griffiths & Griffiths 1982). Aggregation is thus common among sandy-beach animals, although there are some such as the crab *Ocypode ryderi* that are territorial and widely spaced as a consequence (Vannini 1980). Land isopods regularly form aggregations (Allee 1926; Edney 1954; Friedlander 1965; Linsenmair 1984), the main function of which seems to be to reduce water loss, although increased growth rates and decreased metabolic rates are elicited by aggregation (Takeda 1984).

The sandy-beach isopod *Tylos* contains several species that are ideal for the study of aggregations. The genus is widespread on mid-latitude sandy beaches around the world (Giordani-Soika 1954; Holanov & Hendrickson 1980; Brown & Odendaal 1994), and various species are dominant members of the fauna on sandy beaches and can achieve enormous populations (e.g., Hamner, Smythe & Mulford 1969; Kensley 1972; Imafuku 1976; Hayes 1977). The biology of the genus has been reviewed by Brown & Odendaal (1994). *Tylos* feed for a few hours at night, but spend most of their time concealed under debris or buried in sand during the day, at or near the high-water mark. During each fortnightly tidal cycle, their position on the shore moves cyclically toward and then away from the sea. It is therefore not surprising that their distribution perpendicular to the land-sea axis has been explained in terms of the changing high-water mark and physical factors such as slope and humidity (e.g. Hamner *et al.* 1969; Hayes 1970; Kensley 1972; Imafuku 1976). However, although several studies mention aggregations in the longshore distribution of *Tylos* (Kensley 1974, Hayes 1977; Holanov & Hendrickson 1980), this aspect of the animal's distribution has remained unexplained.

The present article focuses on longshore aggregations of *Tylos granulatus* at Groenrivier, on the West Coast of South Africa. The animals live at or above the high-tide mark and occur in a dense band about 5 to 10 meters wide that runs along the beach. They spend most of their time about 30 cm under the surface of the sand to emerge only at night for about two hours with the receding tide. During this period they forage below the high-tide mark. Afterward they return to a position above the next high-water mark where they again bury themselves. The band in which *T. granulatus* is distributed during the day consequently shifts seaward from spring to neap tide and back up again towards spring tide. Inside the band the animals tend to occur in large, dense clusters separated from one another by low-density areas (see Kensley 1972, 1974; also pers. obs. by authors).

The longshore distribution of *T. granulatus* provides a good case study for ecologists who are interested in explaining the distribution and abundance of animals dependent on ephemeral resources. Littoral-zone marine scavengers are dependent on whatever organic matter washes ashore, the amount and type of which may vary considerably through time. In the case of *T. granulatus*, aggregations could form when food arrives in a large clump or tends to be deposited at the same spot. We studied the relationship between spatial patterns of *T. granulatus* distribution and its food, first by monitoring the position of various types of food as well as that of the animals and, later, by manipulating the distribution and abundance of food to test if the animals would respond. We also monitored the movement trajectories of *T. granulatus* to determine how far and fast they are capable of dispersing while feeding.

During the course of the study an alternative hypothesis was developed to explain *T. granulatus* spatial patterns, based on the knowledge that non-random movement with respect to conspecifics will, under certain circumstances, incidentally result in aggregation (Odendaal *et al.* 1988; Turchin 1989). *T. granulatus* returns to the vicinity of the high-water mark after foraging, and tends to re-use existing holes vacated at the start of the activity period, or to burrow at surface irregularities

such as the cone-shaped mounds caused by the digging of other individuals. We tested the hypothesis that these tendencies might incidentally cause spatial aggregation, and discuss the potential adaptive significance of these behaviours for *T. granulatus*.

Specifically, we ask the following questions. (1) Are aggregations of *T. granulatus* correlated with the availability of food? (2) Can the distribution of aggregations be altered by manipulating the position of food? (3) Can aggregation be explained by the tendency of animals to re-use existing holes or mounds when burrowing? To answer these questions, we use three approaches: field observations of patterns of distribution, behavioural observations and manipulative field experiments.

Materials and methods

Study site and organism

Research was based at Groenrivier (30°45'S, 17°28'E) in Namaqualand on the west coast of South Africa. The beach there is 500 m long and bounded by rocky headlands at either end. The mouth of the Groenrivier estuary enters at the southern end, but the estuary is closed for prolonged periods and was not open for four years prior to the research.

After emergence from the sand, *Tylos* leaves distinctive round holes about 1.5 cm in diameter. When individuals burrow again, they rotate in a circle, throwing up sand and leaving mounds about 2 cm tall and 6 cm wide. Exit and entry holes are thus readily distinguishable. The correlation between numbers of mounds and density of animals was tight ($r = 0.787$, $p < 0.0001$ for 25 random 0.5m² quadrats) but, because more than one animal can burrow in a single hole, densities were close to twice hole counts. At the time of research, *T. granulatus* occurred at high densities in areas where it aggregated (76.96.m⁻² ±85.16 s.d.). Average depth to which animals burrowed was 32.9 cm (±8.77 s.d.; n = 30).

Spatial distribution on the shore

Twenty one parallel transects were laid out at right angles to the shore so that they covered the band in which *T. granulatus* occurred. The transects were 20 m long by 20 cm wide and 5 m apart, and positioned so that the high-water mark of the first night of observations (a spring tide) was at their mid-points. Transects were monitored at the end of the foraging period, when all the *T. granulatus* that were active that night had again buried themselves, and before the high tide erased the holes and mounds from that night. For each transect the exact positions of holes, mounds and food items were recorded to the nearest centimetre. At Groenrivier by far the largest proportion of food available for *T. granulatus* consists of stranded kelp (*Laminaria pallida* and *Ecklonia maxima*). Food items were divided into recently deposited kelp, vintage kelp and 'other' algae, as *T. granulatus* shows a preference for other algae over kelp (Kensley 1972) and because kelp becomes more nutritious as it matures (Duggins & Eckman 1994). The transects were monitored on 9 out of 10 successive nights.

Counts of holes, mounds and food items in each transect were totalled to give their longshore distributions. The distribution of mounds along the shore was tested for randomness by comparing their observed frequency-of-occurrence with

an expected Poisson distribution, following Zar (1984). This was done separately for each tide. To quantify the degree of aggregation, Lloyd's (1967) Index of Patchiness, m^*/m , gave a ratio of mean crowding to mean density. This measure was applied to the distribution of mounds each day. To estimate the precision of the m^*/m values, we calculated their standard deviations with the jackknife method (Reed 1983) by re-sampling the data 1000 times. The m^*/m means for each day were compared to 1 (the Poisson distribution), as well as to one another, by t-test (Zar 1984).

For each night the distribution of food items was regressed on that of mounds along all transects. Food was grouped as 'other' algae only, vintage kelp only, or all food types together (algae + vintage kelp + fresh kelp). Lastly, we considered the possibility that the potential influence of food might be masked because the animals are restricted to a narrower band across the transects than that in which the food is found. To counter this effect we created a fourth category for food, including only those food items that were located within the band in which the mounds were found.

Experimental manipulation of the distribution and abundance of food

To test the responses of *T. granulatus* to food availability, all the wrack on the northern half of the beach was gathered and deposited into four large, round heaps concentrated at the far northern end of the beach in the *Tylos* zone. The heaps measured several meters across and were about twenty meters apart. Any wrack that was washed up during the following three days and nights was added to the heaps. The intention of the experiment was to test whether the distribution of *Tylos* could be manipulated by concentrating all the food in four patches. Each morning the mounds marking the distribution of *Tylos* were monitored.

Night observations on the movement trajectories of *Tylos*

T. granulatus was observed during the nocturnal activity period, using night-vision equipment to avoid disturbance. When active, individuals frequently stop when they encounter depressions or food items, or sometimes without any visible stimuli. Their movement trajectories therefore approximate a series of individual moves joined by straight lines. Eight individuals were located during the activity period and subsequently followed. A hand-held TRS-80 computer was used to record the time and type of all visible behavioural events, and the positions of all stopping points in the trajectory were marked with numbered wire flags. The eight trajectories were used to calculate the speed of an average *T. granulatus* as well as the distance moved during an activity period.

Tendency to burrow into existing holes

We conducted two experiments to evaluate the number and types of holes re-used by *Tylos* when burrowing. In the first experiment, three types of holes were made available to returning *Tylos*: (1) holes vacated by *Tylos* at the start of the activity period; (2) holes vacated at the start of the period by individuals that were then removed from the population; and (3) artificial holes about 10 cm deep made with a stick approximately as wide as adult animals, thus creating holes

virtually indistinguishable from exit holes made by *T. granulatus*. On three consecutive nights, thirty-nine holes of each of the three types were monitored in a low-density part of the *Tylos* zone, and twenty of each type in a high-density area. The proportions of the different types of holes used by *Tylos* to burrow were arcsine transformed and analysed by ANOVA.

In the second experiment 65 holes vacated on the first of seven successive nights were marked with wire flags and monitored for re-usage over five of the next six nights. Many of the holes became mounds after they were re-used. These data allowed calculation of percentages of different types of holes that were re-used, and the average amount of time that a *T. granulatus* spends under the surface. During these experiments, we also timed the speed it took individuals to bury themselves when they created a new hole *versus* using an existing hole.

Testing if existing holes influence the dispersion of *Tylos*

To test whether the presence of previously-made holes and mounds influence where *T. granulatus* burrows, and hence its dispersion pattern, six circles of 1.5 m radius were prepared in the *Tylos* zone. Inside the circles the surface of the sand was smoothed with a broom. In three of the circles more or less evenly spaced holes were made in the outer half of the circle. The three circles contained 400 holes, 200 holes, and 2 holes respectively. The other three circles contained the same numbers of made-by-hand mounds resembling those of *T. granulatus*, but no holes.

Towards the end of a night's activity period adult animals were collected, and groups of 20 individuals released in the centre of each of the six circles. After ten minutes the circles were examined and the number of animals buried inside them counted. Six trials were conducted for each of the six circles over a period of several nights. In several trials one or two animals burrowed where they were released in the centre of the circles. These individuals were ignored in subsequent analyses of the data. ANOVA analyses of the data were based on arcsine transformations of proportions.

Results

Spatial distribution of *Tylos* and food on the beach

T. granulatus occurred in a narrow band on the shore (Figure 1). Along the long-shore axis of the beach its distribution was clearly non-random, and the position, shape and intensity of aggregations differed from night to night (Figure 1, Table 1), as did the density and position of food items which were distributed over a wider zone than *Tylos* (Figure 2). Chi-square tests comparing *Tylos* distributions against the Poisson distribution showed that mounds were significantly aggregated on all nights (Table 1). T-test comparisons of the means of Lloyd's Index of Patchiness (m^*/m) with 1, and comparisons of m^*/m means between different nights revealed significant differences at a level of $p < 0.001$ (Table 1).

For the nine nights, 36 regressions were calculated relating the availability of each of the four food categories to the distribution of *Tylos*. Only six were significant. On one night each there were significant correlations for 'other' algae ($r = 0.57$, $p < 0.01$), vintage kelp ($r = 0.53$, $p < 0.05$) and total food items ($r = 0.66$, $p < 0.001$). For three of the nine nights the

Table 1 The mean density of *Tylos* mounds in all transects along the shore for each day, and chi-square values for tests of the distribution of mounds along the shore against the Poisson distribution using the method outlined by Zar (1984), and Lloyd's Index of Patchiness m^*/m of *Tylos* mounds. All m^*/m means differed from 1, and from one another, at $p < 0.001$. Altogether 21 transects were read each night except on night 9, when 16 were read

Night	Mean density	<i>N</i> _a	<i>df</i>	Chi-square	$m^*/m \pm sd$
1	14.28	300	6	92.69*	1.50 ± 0.44
2	22.57	474	7	97.95*	1.66 ± 0.62
3	28.23	593	7	30.52*	1.36 ± 0.24
4	34.57	726	8	44.88*	1.14 ± 0.69
5	27.23	572	7	39.87*	1.42 ± 0.33
6	38.00	798	8	30.71*	1.21 ± 0.11
7	19.76	416	6	27.13*	1.29 ± 0.19
8	71.66	1505	10	31.42*	1.20 ± 0.93
9	39.75	636	9	32.78*	1.36 ± 0.33

*N*_a, the number of holes in all transects for each day

* $p < 0.001$

correlations were significant for food within the *Tylos* band ($r = 0.84$, $p < 0.001$, $r = 0.43$, $p < 0.05$ and $r = 0.51$, $p < 0.05$).

The experimental rearrangement of the kelp wrack on the beach into four patches had no apparent effect on the *Tylos* distribution. Although the distribution of holes was not formally measured, there was no visible concentration of holes near the patches of wrack and the experiment was discontinued after four days.

Nocturnal observations on the movement of *Tylos*

The activity of *T. granulatus* was highly synchronised. Individuals all emerged within minutes of each other. About two hours later they returned to the *Tylos* zone and burrowed under the surface in a matter of minutes. Trajectories of the eight animals we followed consisted of a series of individual moves that were approximated by straight lines drawn between stopping points (Figure 3). The eight trajectories yielded a total of 59 moves, with an average of 7.34 ± 2.97 moves per trajectory. The average length of a move was 1.35 ± 1.73 meters. Using the times it took to complete trajectories of specific lengths, we calculated that the average speed at which a *T. granulatus* moved on the beach was 0.014 ± 0.011 m/s (including frequent stops). On this basis, over a two-hour activity period, an individual *T. granulatus* could therefore travel about 80 m. While the animals were actually moving, they achieved an average cruising speed of 0.130 ± 0.061 m/s. If a *Tylos* travelled at this speed without stopping, it would cover 936 m in 2 h.

Quantifying the tendency to burrow in existing holes

We first determined whether the frequency at which *Tylos* will burrow into existing holes is influenced by the nature of the holes available. Table 2 shows that there was no significant difference between the frequency at which the different

types of hole were used, although significantly more holes were used in high-density (about 87%) versus low-density (about 39%) areas.

In a second experiment, we recorded the frequency with which natural holes created on one night were re-used over the next eight nights. (The vacant holes persisted for several nights because the tides progressed from springs to neaps, so the high-water mark shifted further down the beach each night.) When a hole was used again, a mound appeared in its place as a result of the sand dug out by the animal. Of the initial 65 vacant holes that were monitored, only 9 (or 14%) were used the same night. By the end of the second night 36 (or 55%) had been used again, and this figure rose to 49 (or 75%) by the end of the third night.

Of the 27 holes that became mounds on the second night, 5 became holes again on the third night, indicating that about 19% of the *Tylos* were active two nights in a row. By the fourth night a further 4 of these mounds became holes again, indicating that about 18% of *Tylos* skipped a night. By the seventh night 18 of the original 27 mounds had become holes again, indicating that at least 66% of the population is active at least once a week. Only 3 out of 27 mounds did not become holes after eight days, indicating that about 11% of *Tylos* surfaced less often than once per week.

When individuals dug new holes, they took on average 28 sec ($n = 12$, range 10–41) to bury themselves (see also Brown & Trueman 1996). Those making use of existing holes took only 15 sec ($n = 11$, range 2–41) to disappear.

Testing if the presence of existing holes influences the dispersion of *Tylos*

Table 3 shows that in the circle experiment the dispersion of *Tylos* was significantly affected by the number of artificial holes or mounds, and by whether holes rather than mounds were available. Dispersion was greatest when hole and mound numbers were low, and roughly twice as much in the presence of mounds rather than holes. Of the 39 animals that buried themselves in the circles with experimental mounds, 35 (or 95%) burrowed into or contiguous to these mounds. Of the 81 *Tylos* that burrowed in the circles with experimental holes, only 1 made a new hole.

Discussion

The aim of the study was to elucidate the processes that lead to longshore aggregations of *T. granulatus*. Table 1 confirms that *T. granulatus* is extremely patchy and that its distribution does consistently depart from that of a Poisson distribution. One potential explanation for the aggregation of *T. granulatus* is that it relates to reproduction. We consider that unlikely, however, because aggregations occur year-round whereas reproduction occurs about once a year (Kensley 1974) and breeding is synchronous (Hayes 1977). Furthermore, the rates of movement recorded from the trajectories have the potential to disrupt aggregations from night to night. It is thus hard to imagine aggregations persisting if their sole purpose is for reproduction once a year.

Terrestrial isopods are well known for their tendency to aggregate, and the behaviour is triggered by an active principle contained in their faeces. They benefit by reducing water loss (see Takeda 1984 for a review). In the case of *Tylos*,

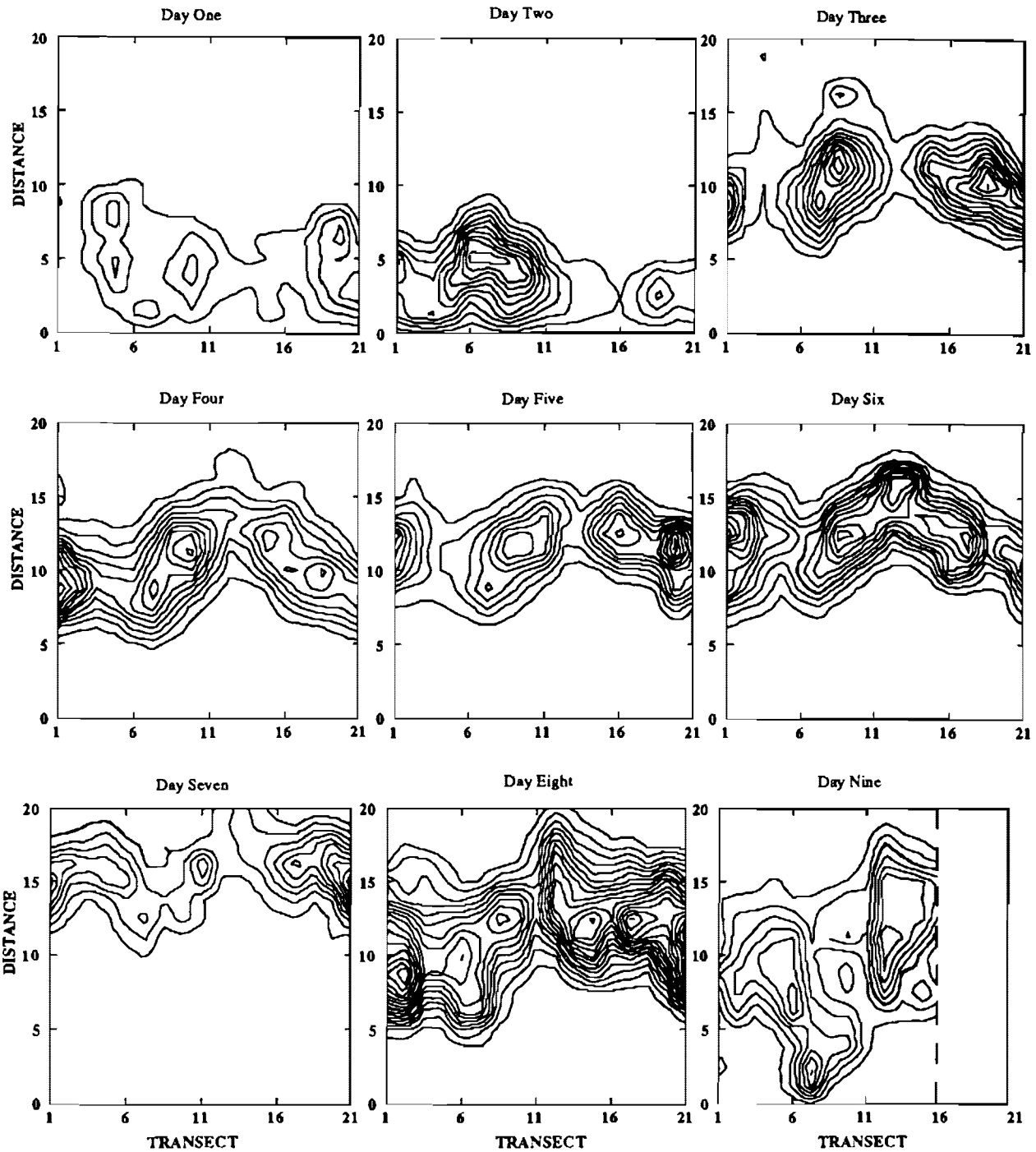


Figure 1 Contour distribution map of *T. granulatus* mounds along the 21 transects over nine days (*Tylos* density-interval value between contours is 2, lowest values being the outermost of the contours.). Distance down shore (0 = bottom of shore) in metres. Sampling on day 9 curtailed by the rising tide

aggregation is highly unlikely to achieve this end. During their activity period, when any desiccation stress is likely to peak, they move individually.

Pheromones are involved in the aggregation of terrestrial isopods, and appear to be concentrated in the animals' faeces (Takeda 1980, 1984). Our experiments showed that *Tylos* aggregates in the presence of its own holes and mounds, raising the possibility that they are attracted by pheromones left behind by the animals when emerging or burrowing. How-

ever, an equivalent rate of aggregation was induced by creating artificial holes and mounds (Table 2). As these would not have been exposed to any pheromones, we are sure that pheromones are not responsible for aggregation. *Tylos* seems to be reacting to the presence of physical structures rather than chemical cues when burrowing in aggregations.

Tylos does cluster around items of food. This leads to an obvious alternative hypothesis, that is, that the aggregations result from the patchy distribution of food items, as well as

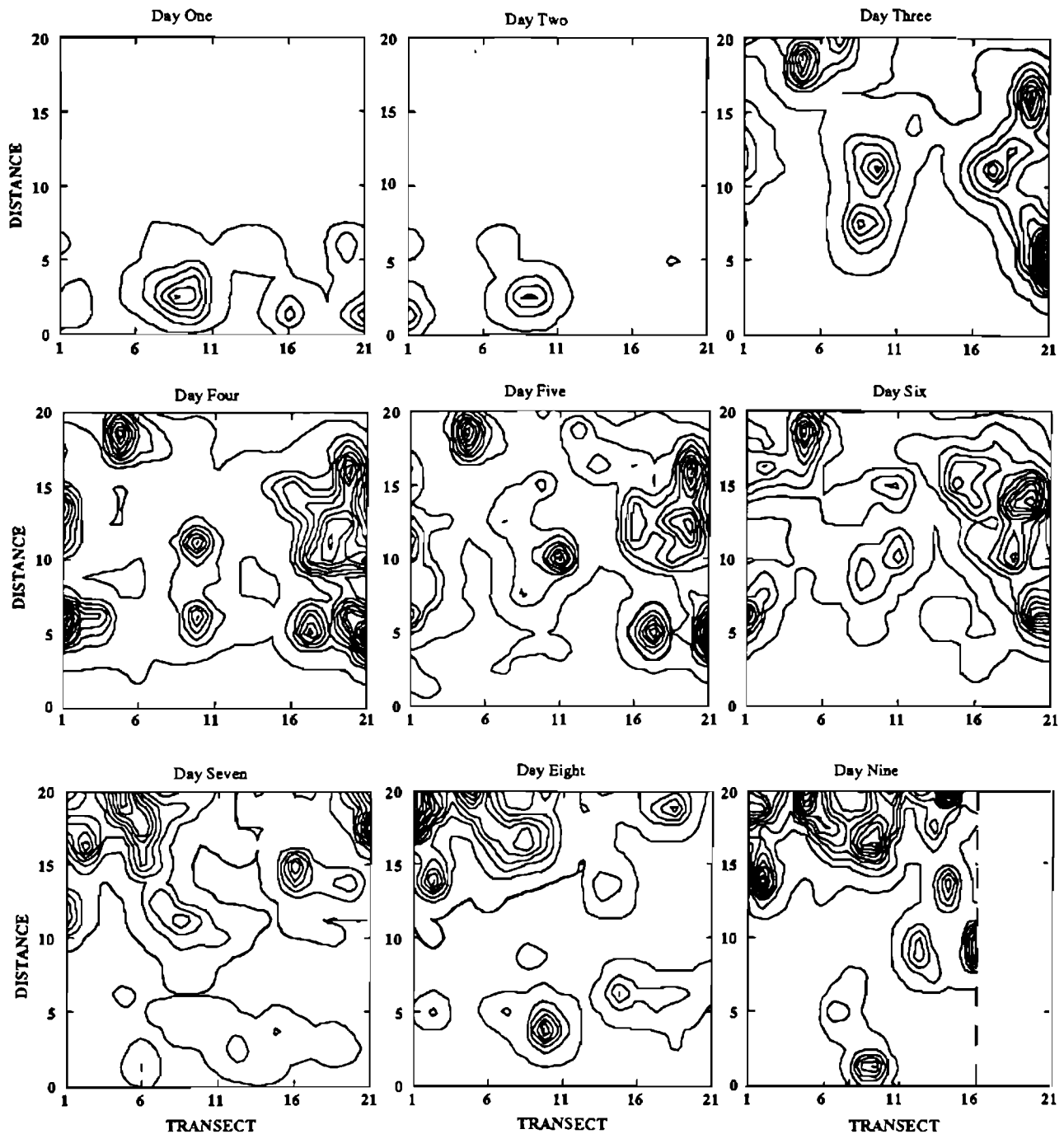


Figure 2 Contour distribution map of food availability (combining all types of food), along the 21 transects over nine days (food density-interval value between contours is 5). Distance down shore (0 = bottom of shore) in metres. Sampling on day 9 curtailed by the rising tide

the manner in which the animals search for them (see Turchin 1989 for review). Only six out of 36 potential regressions relating *Tylos* distribution to the availability of food were significant. However, testing the influence of food on the distribution of *Tylos* by regression is flawed to some extent because *Tylos* is restricted, for physiological reasons (Kensley 1974, Holanov & Hendrickson 1980, Garthwaite, Hochberg & Sassaman 1985), to a zone about 10 m wide, whereas food is deposited by the tide over a wider zone. To counter this problem, a food category was created that included only those food items that occurred within the band occupied by *Tylos*

for that particular day. Even so, regressions of *Tylos* abundance against this category were significant in only three out of nine days. These data, as well as the apparent failure to perturb the *Tylos* distribution by creating large food patches, indicate that the distribution of food in the beach plays at most a minor role in the formation of longshore aggregations. The high mobility of *T. granulatus* and the shape of its movement trajectories would soon erode any influence of food distribution on the distribution of the animals. Comparison of Figures 1 and 2 emphasises the lack of relationship between the distribution of food and that of *Tylos*.

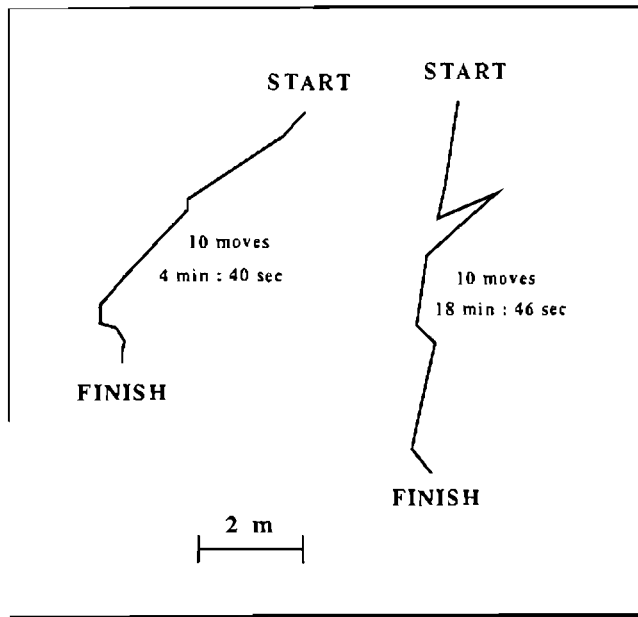


Figure 3 Two examples of the individual movement trajectories of the eight *Tylos* followed

The second hypothesis we examined was that *T. granulatus* aggregations are a consequence of the tendency for animals to burrow into existing holes or mounds made by other conspecifics. When individuals return to the vicinity of the high-water mark after foraging, they may encounter and burrow into existing exit holes, leaving behind a mound. Further returning *Tylos* come across the mounds made by other animals and burrow there, thereby intensifying aggregation in an area. Therefore, the tendency for *Tylos* to re-use old holes as

well as the tendency to burrow at resultant mounds will cause aggregations to occur. The circle experiment directly supports this 'hole-and-mound' hypothesis. The dispersion of *Tylos*, and its resultant distribution, were strongly affected by the presence and density of holes and mounds.

The hole-and-mound hypothesis implies that an area with a large number of exit holes and mounds would tend to 'capture' more *Tylos* than an area with few exit holes. This effect is evident in the results of the circle experiment. Furthermore, the experiment measuring usage of exit holes showed that significantly more holes are re-used in high-density than low-density areas. The higher the density of exit holes in an area the more likely that a returning *Tylos* will encounter a hole. A prerequisite for the hole-and-mound hypothesis would be that a fairly large proportion of exit holes be re-used, and that the tendency to burrow at a mound will be reasonably high. The exit hole experiment, as well as the monitoring of vacant holes showed that the re-usage of vacant holes is high, and in the circles experiment 90% of the animals that burrowed inside the circles with mounds did so contiguously to the experimental mounds.

The question arises as to why *T. granulatus* re-uses old exit holes and why the animals bury themselves at topographic irregularities such as mounds made by other animals. One potential reason for using existing holes would be to save energy. We attempted to calculate the energy saving that results from using a vacant hole as opposed to digging a new one. *T. granulatus* burrows at most once every two tidal cycles. In this respect it is intermediate between the sandy-beach whelk *Bullia digitalis* or the mole crab *Emerita*, which both burrow repeatedly with every tidal cycle (Brown 1982; Trueman 1970), and an infaunal bivalve such as *Donax serra* which, once buried as an adult, remains in the sand

Table 2 The proportion (and number, n) of the different types of holes re-used in a low-density and high-density area, and analysis of variance of their arcsine transformations. Holes were categorized as natural exit holes, natural holes from which the animal was removed, and artificial holes simulating exit holes

Type of holes available					
Area	Night	Removed (n)	Artificial (n)	Natural (n)	
Low	1	0.25 (12)	0.17 (12)	0.25 (12)	
Low	2	0.30 (10)	0.20 (10)	0.50 (10)	
Low	3	0.89 (9)	0.33 (9)	0.56 (9)	
Mean (SD)		0.48 (0.35)	0.23 (0.08)	0.44 (0.16)	
High	2	1.00 (6)	1.00 (5)	0.50 (6)	
High	3	0.93 (14)	0.87 (14)	0.93 (14)	
Mean (SD)		0.96 (0.05)	0.93 (0.09)	0.71 (0.30)	
Analysis of variance					
SOURCE	SS	df	Mean square	F-ratio	p
Main Effects	2.3351	3	0.7783	7.317	0087
Density	2.1344	1	2.1344	20.063	.0015
Type	0.2007	2	0.1003	0.943	4247
Density × Holes	0.2798	2	0.1399	1.315	3154
Residual	0.9574	9	0.1063		
Total (corr)	3.5724	14			

Table 3 Proportions of animals that burrowed within the perimeter of the circles, relative to the number (2, 200 or 400) and type (holes or mounds) of structures present. An ANOVA of their arc-sine proportions is given below. (*n*) is the number of animals used in each trial

	Number of holes or mounds				
	2 (<i>n</i>)	200 (<i>n</i>)	400 (<i>n</i>)		
Holes	0.00 (18)	0.47 (20)	0.30 (20)		
	0.00 (18)	0.26 (19)	0.58 (19)		
	0.00 (20)	0.20 (20)	0.30 (20)		
	0.00 (20)	0.20 (20)	0.40 (20)		
	0.00 (20)	0.42 (19)	0.45 (20)		
	0.00 (18)	0.58 (17)	0.50 (18)		
Mean (SD)	0.00 (0)	0.35 (0.17)	0.42 (0.11)		
Mounds	0.00 (20)	0.35 (17)	0.47 (19)		
	0.11 (18)	0.11 (18)	0.20 (19)		
	0.00 (20)	0.00 (20)	0.10 (19)		
	0.00 (20)	0.00 (20)	0.10 (19)		
	0.05 (20)	0.05 (20)	0.15 (20)		
	0.00 (18)	0.26 (19)	0.50 (20)		
Mean (SD)	0.03 (0.04)	0.13 (0.14)	0.25 (0.18)		
Analysis of variance					
Source	SS	df	Mean square	F-ratio	p
Main effects	0.6306	3	2.102	13.782	0.000
Number	0.5510	2	2.755	18.063	0.000
Type	0.0796	1	0.796	5.220	0.296
Number × type	0.1224	2	0.612	4.013	0.286
Residual	0.4576	30	0.152		
Total (corr)	1.2107	35			

permanently unless washed out by the waves (Brown, Stenton-Dozey & Trueman 1989). For *D. serra*, burrowing is very costly, whereas the opposite is true for *Bullia* and presumably for *Emerita*.

For an adult *T. granulatus* weighing 5.7 g wet weight, the energy cost of burrowing in slightly damp sand to a depth of 1 meter, has been estimated by Brown & Trueman (1996) to be 0.3 J. However, it must be stressed that this calculation gives the mechanical energy cost and takes no account of metabolic inefficiency and in particular heat loss. Assuming 20% efficiency, the mechanical energy cost should be multiplied by five to give total metabolic cost. On this basis, the cost to *Tylos* of burrowing 30 cm will be $0.3 \times 0.3 \times 5 = 0.45$ J. As the penetrability of the sand decreases with depth (Brown & Trueman 1991), the real cost may be double this.

This cost must be viewed against the total energy expenditure of the animal over a 24 h (or two tidal-cycle) period. Marsh & Branch (1979) have monitored the oxygen consumption of *T. granulatus* in the laboratory and have noted remarkable circadian and circatidal rhythms of oxygen uptake. From their results it can be calculated that the average oxygen consumption of an animal of 5.7 g (wet weight) is about 2.856 ml O₂ in 24 h (= 4.084 mg O₂). Assuming an oxycalorific value of 3.4 cal (14.2 J) per mg O₂ (Ivlev 1934; Crisp 1971;

Brown 1981), this gives an energy expenditure over the period of some 58 J, including metabolic heat losses (Brown 1979).

Thus the cost of burrowing to a depth of 30 cm over a 24 h period is likely to be only about 1–2% of the animal's total daily metabolic energy expenditure. Something less than this might be saved by using an existing burrow. This saving would appear rather little and is certainly no compelling justification for using an existing burrow rather than excavating a new one.

Exit holes may, however, assist *T. granulatus* in several other ways that are unrelated to the saving of energy. *T. granulatus* is active in the small window of time between the turning of the tide and the advance of the incoming tide. Their highly synchronized activity period confirms this tight schedule. Not only may an animal need to beat conspecifics to the food on nights when little is washed up, but they also need afterwards to locate proper burrowing sites which prevent them from being washed away during the next high tide yet also keep them within range of their food and moist sand (Kensley 1972). Much has been written about the danger and frequency of *Tylos* being swept out to sea (e.g. Menzies 1952; Hamner *et al.* 1969; Kensley 1972, 1974; Yuasa 1973; Imafuku 1976; Hayes 1977). The observation of *T. granulatus* in

the guts of fishes caught along the west coast underlines this danger. An animal that uses an existing hole will disappear more quickly below the surface and into safety from rampant waves or predators as it often takes several minutes to break the smooth beach surface when a new hole is dug. Digging into exit holes or at topographic irregularities such as the edges of other mounds provides the animals with a foothold. In our study the ability to disappear quickly under the surface did not appear very important as the animals had buried themselves long before the tide reached their burrowing sites. However, it should be noted that our study was conducted from springs to neaps and not the other way around, when escaping the incoming tide might be more important.

Existing holes may perhaps also decrease the vulnerability of *Tylos* to predators when they return to the zone in which they burrow. Although Kensley (1974) did not record any predation on *Tylos*, we observed the remains of *Tylos* where yellow mongoose (*Cynictis penicillata*) had been digging intertidally on the sandy beach where we worked, and remains of the isopods were also found in the scats of this predator. The fact that *Tylos* is inactive during the full moon cycle further supports the notion that predation may be an important factor regulating activity. When digging new holes, *Tylos* took about 28 seconds to disappear under the surface, whereas animals using existing holes took only 15 seconds. The difference of 13 seconds may sound trivial, but when thousands of *Tylos* are almost synchronously burying themselves it may critically alter the relative vulnerability of individuals exposed to predation.

Most previous studies on aggregation implicitly presumed the phenomenon to be adaptive and therefore focused on the consequences of aggregation at the level of individuals and the population. Theoretical models were based on attraction between individuals or processes that would increase an individual's ability to find food, mates or avoid predation. Our studies, as well as those by Odendaal *et al.* (1988) and Morris *et al.* (1992), suggest that aggregations may in fact sometimes be incidental effects of other adaptive processes. In other words, aggregation need not be an adaptive process in its own right; it may arise as a consequence of some other adaptive process. In the present case, *T. granulatus* does not aggregate in response to food, and we have no reason to suspect it does so for reproductive purposes. It does show a preference for burrowing in existing holes, and this may incidentally lead to aggregation. Why it prefers existing holes is not resolved. Our calculations suggest that this is not an energy saving device. It may decrease exposure time and reduce mortality from either predation or wave action, but even this is not proven. Whatever the underlying causes, aggregation does seem incidental to the fact that *Tylos* preferentially burrows into existing holes or mounds rather than creating new ones.

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