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Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus.*

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SUMMARY: Aspects of the ecology and behaviour of *Ocypode cursor* were studied on the beaches of Northern Cyprus. The crabs were widely distributed around the north coast of the island, occurring on 68 of the 77 sandy beaches investigated. At the main study beach at Alagadi, crabs occupied a band approximately 12 m wide; starting approximately 3 m horizontally from the edge of the sea (tidal fluctuation was minimal). Most small burrows occurred near to the sea, with the burrows of larger crabs predominating higher up the beach. Burrow numbers varied during the summer which was mainly attributable to variations in the numbers of burrows of juveniles. The sex ratio of emergent crabs also varied during the summer, possibly reflecting burrow oriented behaviour of reproductive females. There were strong correlations between burrow diameters and carapace lengths of the occupant crabs. There was a positive correlation between the presence of crab burrows and the number of people using sections of beach. The crabs were principally nocturnal, benefitting from food discarded by tourists. They also scavenged animal carcasses and were active predators of turtle eggs and hatchlings. Crab burrows usually had a single opening oriented towards the sea and those cast were L- or J-shaped. Burrows did not penetrate to the water table. The water content of the sand at the bottom of burrows was around 14 % by weight. Their burrows in the well-sorted sand provided the crabs with a thermally stable environment.

Key words: Crustacea, Decapoda, *Ocypode cursor*, ecology, behaviour, Cyprus

INTRODUCTION

Semi-terrestrial crabs of the genus *Ocypode* Weber, 1795 are typical inhabitants of tropical and sub-tropical sandy beaches (Dahl, 1953; Hedgepeth, 1957) where they occupy conspicuous burrows (Vannini, 1980a). Many aspects of the ecology of *Ocypode* species have been investigated (see reviews of Vannini, 1976; 1980a, Little, 1983 Atkinson & Taylor, 1988), but comparatively few studies have been carried out on *O. cursor*. The distribution of *Ocypode cursor* (Linnaeus, 1758) extends from west Africa into the Mediterranean where its distribution appears to be expanding (Manning and Holthuis, 1981; Ziese, 1985; Glaubrecht, 1992). The only field studies on this species in the Mediterranean are those of Gilad-Shuchman and Warburg (1977), Shuchman and Warburg (1978) and Warburg and Shuchman (1979). These authors studied the shore distribution, population structure and burrow shape of *O. cursor* in north Atlit, Israel and demonstrated that the water content of the sand was the key factor determining burrow distribution.

Several aspects of the ecology of *O. cursor* were examined in the present study. Crab distribution around the northern coast of Cyprus was noted. On Alagadi beach, the spatial distribution of the crabs was closely monitored and factors which may have

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influenced crab distribution were investigated. Burrow morphology was examined and burrow microenvironment was inferred from measurements of sand column temperatures. Behavioural observations included observations of diel activity patterns and feeding behaviour, including predation on turtle eggs and hatchlings.

MATERIALS AND METHODS

The distribution of *O. cursor* in Northern Cyprus in 1994 was noted by observations made throughout the area at 77 sandy beaches. Detailed studies were carried out at one site, Alagadi, where there were two beaches. The west beach was approximately 1050 m in length, divided into three bays, and was more sheltered than the east beach which was 800 m long and consisted of a single embayment. These sites were easily accessible and supported a large population of ghost crabs. The beach was a popular nesting site for green turtles (*Chelonia mydas)* and loggerhead turtles (*Caretta caretta*) and was also a heavily-used recreational beach. Recreational use of the beach was prohibited at night to prevent disturbance of nesting turtles: this also protected the nocturnally-active crabs from human disturbance.

In 1994, an area extending 43 m from the waterline to the back of the shore, and 50 m in width was selected for study in the central part of the west beach. The beach was surveyed with station heights related to the lowest sea level recorded during the study (Reference Datum - RD). The study site was then divided into four zones for descriptive purposes. From RD shorewards, the first three zones were each 6 m wide and the fourth zone extended to the back of the beach and was 25 m wide. Zone 1 extended to a height of 0.65 m above RD, zone 2 was a horizontal platform, zone 3 extended to a height of 1.15 m above RD and zone 4 was virtually horizontal. The numbers and size distribution of burrows within zones were examined in July 1994. The total number of burrows within the study site was recorded for the months of July, August and September. During each month four counts of the total burrow number were taken, all the counts had a period of at least six days between them. The diameter of the opening of each burrow within each of the four zones was measured using Vernier callipers and was assigned to one of five size categories (<10 mm, 10-19 mm, 20-29 mm, 30-39 mm and 40-50 mm). Some burrows were cast by pouring a gypsum slurry into them. When the gypsum had set, the casts were carefully excavated by hand and their shape and dimensions noted. On several occasions, the burrow occupant was trapped inside the cast enabling the crab's size and sex to be determined.

In 1996, a further set of burrow diameter measurements was taken, this time the size categories were extended to up to 70 mm to accommodate burrows larger than those observed in 1994.

The depth of the water table was determined along the 1994 beach transect. Sand samples (200 g) were taken for the determination of sand moisture content. For the study of sand granulometry, 100 g sand samples were taken from a depth of 30 cm and sieved using graded Endecott sieves. Grain size analysis followed Folk (1974).

In order to investigate human impact on the crab population, the length of the beach was divided into twenty 50-metre sections, marked by posts in the sand. At the time of peak beach use (approximately 15:00h) the number of people situated in each of the twenty sections of beach was counted. The following morning, the number of crab burrows located in each of the twenty sections was recorded. The surveying process was carried out five times in 1994, during the months of July and August: thus, 100 data pairs were obtained.

On several occasions in the summer of 1994, crabs were hand-caught at night when they had emerged from their burrows. No particular selection criteria were applied. Carapace length and width were measured using Vernier callipers and these data, together with some obtained in 1996, were used to investigate morphometric relationships. In addition, measurements of the cheliped dimensions were made to enable an assessment of handedness to be carried out. In the summer of 1996, the diameters of a number of varying sized burrows were measured using Vernier callipers. The burrows were then excavated and, if a crab was found, its carapace length and width were measured thus enabling crab size to be related to burrow diameter.

In 1994 a 50 m wide zone on the eastern side of the beach was observed for staggered four hour periods on successive days to complete a 24-hour survey of crab emergence activity. Nocturnal observations made use of background light, aided by use of a night sight or supplemented as necessary by brief use of torchlight. This study was extended in 1996, when crab counts were carried out at hourly intervals throughout a 72-hour period.

Environmental temperatures (air, sand surface, sediment column) were recorded at six hourly intervals during 24-hour periods in July 1994 using a portable digital temperature probe (R.S. Components). This procedure was carried out at the same site on four separate dates.

Behavioural observations, with the greatest emphasis on aspects of feeding, were carried out in all three years. The data were obtained from a series of casual observations made throughout the summer in each of the three years of the study.

RESULTS

Distribution, number and size of burrows

Of a total of 77 beaches surveyed along the coast of northern Cyprus in 1994, 68 were found to have *O. cursor* present. The burrows occurred in a distinct horizontal band. At the Alagadi study area this band started approximately 3 m horizontally from the water's edge and extended a further 13 m up the beach. Each burrow excavated (n=25) contained only one occupant.

The total number of burrows in the Alagadi study area changed significantly (ANOVA F = 40.07, P <0.01) during the months of July, August and September in 1994. Throughout July, the burrow numbers remained relatively constant (mean = 129.9 ± 6.8, n = 4). An increase was then observed during August, with the peak count being recorded in the middle of the month. The burrow count for August (mean = 211.5 ± 28.4, n = 4) was significantly greater than that for July (t-test, p <0.01). This sudden increase in the number of burrows appeared to be attributable to the appearance of burrow openings which measured less than 10 mm in diameter. A decrease in the total number of burrows then followed and the decline continued throughout September. The number of burrows recorded during September was significantly lower than during August (t-test, p<0.01). Similar relationships were found in 1996 (see below).

Of those crabs caught in July 1994 (n = 75), 86.6 % were adults, of which 20% were female and 80 % were male. The remaining 13.4 % were juveniles. In contrast, the September sample (n = 63) contained 33.3 % males, 26.7 % females and 40 % juveniles. In both the July and September samples there were roughly equal numbers of left and right handed adult crabs. The juveniles were distinguished from the adults not only by their size, but by their pleopod structure and their colouration. Many of the adults were a buff colour with a wide bluish streak running down the back of the carapace. Other adults, which had perhaps recently moulted, were uniformly buff in colour. The juveniles had a distinct brown dappled pattern over the dorsal surface of their light-coloured carapaces.

TABLE 1. - The number of *Ocypode cursor* burrows recorded during July in the four different zones of a 50 m wide stretch of Alagadi beach.

Zone 1	Zone 2	Zone 3	Zone 4
37	62	28	0
34	67	36	0
30	57	34	0
38	58	36	0

A significant difference (ANOVA F = 60.39, P<0.01) was found between the numbers of burrows that occurred in zones 1-3 of the study area in July 1994 (Table 1): no burrows were found within zone 4 of the survey area. Significantly more burrows were found in zone 2 than in either zones 1 and 3. Within zone 1, burrows were never present in the first 2 metres from RD and only a few were observed in the next metre up the shore. The majority of the burrows in zone 1 were at relatively high density in the remaining three metres of the zone (starting at 0.29 m above RD). Crab burrows were found over the entire area of the horizontal zone 2. In zone 3, burrows rarely occurred in the top metre of the zone and most occurred in the first 4 metres (0.65-1.0 m above RD) of the zone. Crab tracks extended 8 m into zone 4, i.e. 26 m from the sea. However, the only burrows seen at a level equivalent to zone 4 of the survey area occurred beside carcasses of dead animals or were associated with turtle nests (see below). Burrow densities in the general crab zone varied from 0.04 m^{-2} to 0.67 m^{-2} along the length of the beach.

TABLE 2. – The percentage of *Ocypode cursor* burrows belonging to each of the five size categories recorded in the three zones of the 50 m wide band where burrows were present on Alagadi beach. The numbers of burrows in zones 1-3, respectively, are 138, 246 and 135.

Burrow size class (mm)	Zone 1	Zone 2	Zone 3
<10	22.5	11.4	2.2
10-19	55.1	37.4	23.7
20-29	16.7	30.1	29.6
30-39	5.8	14.6	21.5
40-50	0	6.5	22.9

Both the numbers and the sizes of the burrows varied along the transect. Within zone 1, there was a predominance of small burrows; there were no burrows with a diameter >40 mm in zone 1 (Table 2). Significantly more burrows were observed in the size category 10-19 mm than in the other categories (ANOVA, F = 25.7, P<0.05). In zone 2 the proportions of burrows in size categories 10-19 mm and 20-29 mm were similar, with fewer crabs in the smaller and larger size categories. In zone 3, all but the smallest size category of burrows were represented in roughly equal proportions.

The frequency of burrows in different size classes was investigated further in 1996 when the situation in July was compared with that in September. In both July and September, the greatest numbers of burrows recorded were in the size categories 10-19 mm and 20-29 mm (Fig. 1). In July, very few small burrows (<10 mm) were recorded but, in September, the number of these small burrows was much higher (an 11-fold increase) as a result of the recruitment of juveniles to the population during the summer.

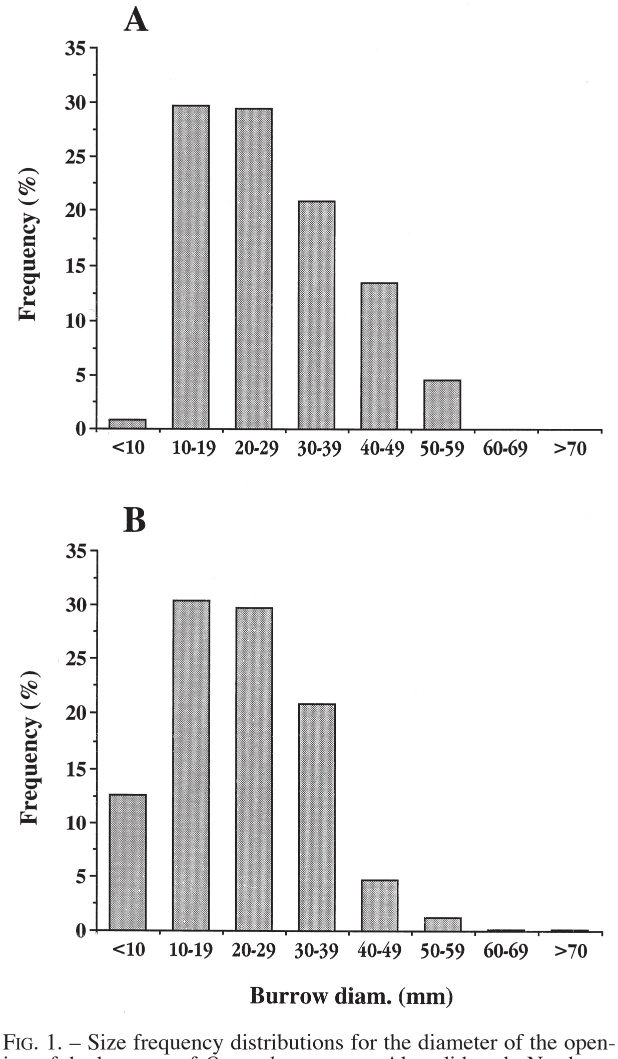

FIG. 1. – Size frequency distributions for the diameter of the opening of the burrows of *Ocypode cursor* on Alagadi beach, Northern Cyprus measured in (A) July and (B) September.

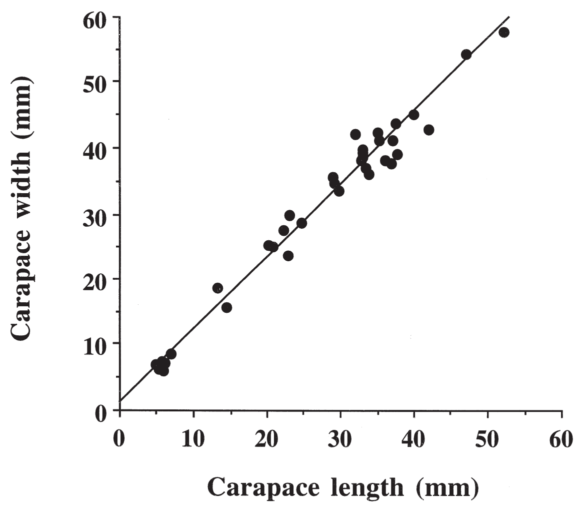

FIG. 2. – The relationship between carapace width and carapace length of *Ocypode cursor* from Northern Cyprus. The equation of the regression line fitted to the data is $Y = 1.15 + 1.11X$; $r^2 = 0.982$.

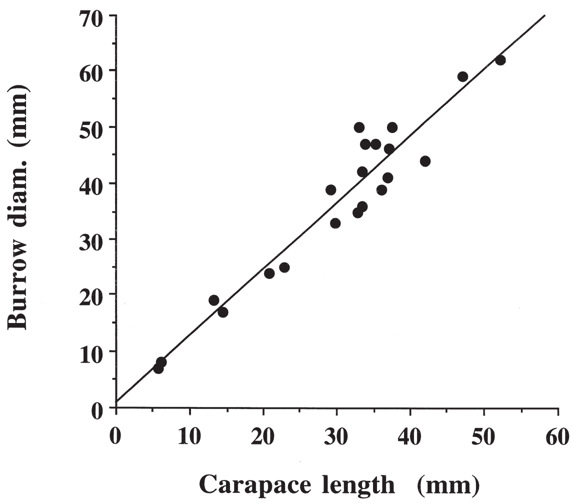

FIG. 3. – The relationship between the diameter of the burrow opening and the carapace length of *Ocypode cursor* from Northern Cyprus. The equation of the regression line fitted to the data is $Y = 0.87 + 1.18X$; $r^2 = 0.924$.

Crab size: burrow size relationships

In order to test whether burrow width reflected crab size, the relationship between carapace length (reflecting the orientation of the crab within the burrow) and burrow width was investigated using data collected in 1995 and 1996. Since carapace width was the normal dimension recorded for the crabs, it was necessary to establish the relationship between carapace width and carapace length. These two parameters were strongly correlated ($r^2 = 0.982$, $P<0.01$, $n=34$) (Fig. 2). Burrow diameter and carapace length were also strongly correlated ($r^2 = 0.924$, $P< 0.01$, $n=21$) (Fig. 3).

Effect of human activity on crab density

Human use of Alagadi west beach was seen to be considerably higher than that of Alagadi east beach. The beaches were used for bathing and picnicking, but driving on the beaches was forbidden due to the presence of vulnerable turtle nests. Beach use varied temporally and spatially. On weekends, people were observed over the entire beach at Alagadi west, whereas on many week days several parts of the beach would remain free of human activity. Crab density was higher on Alagadi west beach in which it was divided into 20 sections indicated a positive correlation between the presence of crabs (burrow counts) and the number of people using these sections of beach ($r = 0.314$, $P >0.01$).

Behavioural observations of crab activity

Three separate surveys carried out in July and again in September 1996 all demonstrated that crabs showed significantly more activity during the night than during the day ($\chi^2 = 22.67$, $P >0.019$, d.f.) During July, very little crab activity was observed during the day but in September the amount of diurnal activity increased (Fig. 4). The main activities observed were feeding and burrow excavation.

Burrow excavation was observed regularly during the first hours of daylight. Sand was repeatedly (at ca 2 min intervals) carried from a burrow and

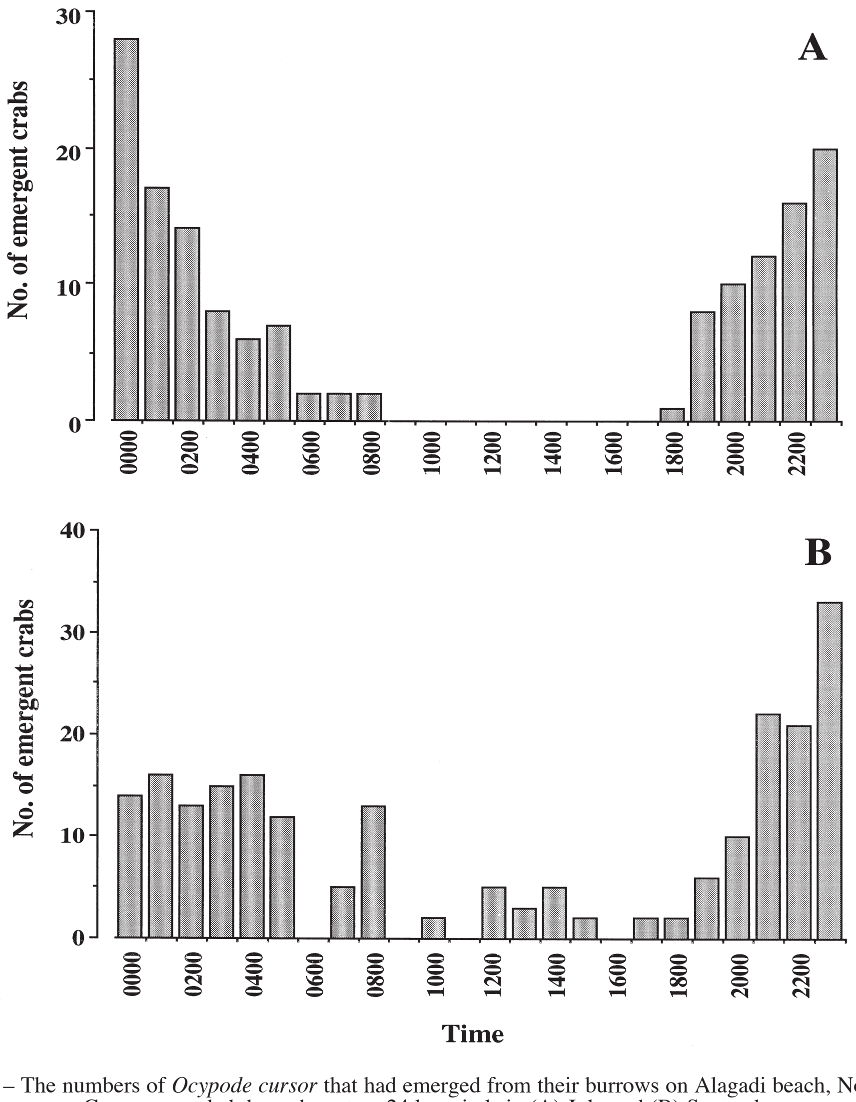

FIG. 4. – The numbers of *Ocypode cursor* that had emerged from their burrows on Alagadi beach, Northern Cyprus recorded throughout two 24 h periods in (A) July and (B) September.

TABLE 3. – Descriptions of the burrow casts obtained from Alagadi beach. ? = sex not known. All have the general L/J shape with the exception of burrow 7.

Burrow No.	Opening diam. (mm)	Distance from sea (m)	Burrow depth (mm)	Length of near-vertical component (mm)	Length of near-horizontal component (mm)	Sex of occupant
1	35	3.6	410	430	270	M
2	30	3.5	400	470	320	M
3	38	7.0	600	780	400	?
4	40	4.0	430	450	350	?
5	45	5.7	440	520	420	M
6	40	4.1	420	470	300	?
7	43	6.0	590	650	630	M

deposited beside the opening so that it formed a mound. The crab then dispersed much of this sand to a location approximately 0.5 m from the burrow and trampled the remaining sand until the former pile was flattened. Some crabs did not transport the excavated sand to a further location. The burrows of such crabs were significantly larger than those which lacked mounds (χ^2 = 61.1, P<0.001, 6 d.f.) and appeared to be associated mainly with the burrows of male crabs (χ^2=4.950, P< 0.05, 1 d.f.).

Feeding behaviour consisted of scavenging and predation. No deposit feeding was observed and no sand pellets (indicative of this feeding mode) were seen at any of the study sites. During one night, a group of five crabs was seen feeding on a beached fish. A similar number of crabs was also observed feeding on a gull carcass.

On one occasion, at approximately 1500 h (when temperatures were near their daily maximum), a group of around ten crabs was observed feeding upon a cow carcass. The position of the carcass was relatively high up the beach, above the normal burrow zone. Yet, surrounding the carcass were crab burrows, all with openings >35 mm in diameter. Another example of communal feeding was when a number of crabs converged on a dead rat. Normally crabs were solitary feeders. Crabs were sometimes observed to predate eggs within turtle nests which were landward of the normal crab zone. On these occasions, they burrowed into turtle nests and egg shells were often scattered around burrow openings. Chelar marks were visible on the eggshells.

The crabs were also seen to prey upon the hatchling turtles as they traversed the beach en route to the sea, usually by night but occasionally at dawn. Crabs waiting within their burrow openings darted out to snatch passing hatchlings which were taken into the burrow. Often crab tracks would be seen around newly hatched nests. Hatchlings would be seized and dragged down into the crab's burrow. Occasionally, hatchlings fell into crab burrows and were taken by the occupants.

Occasionally, crabs were seen to target butterflies traversing the beach and flies that were associated with food discarded by tourists. Such discarded food was consumed mainly during the night. This was indicated indirectly, by morning observations of crab tracks converging on food such as watermelon skins (on which chelar impressions could be seen) and bread. Captive crabs accepted a wide range of foodstuffs - watermelon, banana, bread, grapes and fish.

Burrow morphology

Only burrows with an opening diameter of >30 mm were cast successfully. Details of seven burrows, derived from casts, are given in Table 3. These came either from zone 1 or zone 2. All these burrows had a single surface opening, orientated seawards. The burrow descended obliquely before levelling out. Thus, six of the burrows were approximately L-shaped or J-shaped (i.e. 'horizontal' section slightly recurved upwards distally), whereas the other had the same basic shape but the horizontal portion extended further and was somewhat sinusoidal. Burrow depth was greatest furthest from the sea, because the depth to the water table was greater. The deepest part of the burrow was always located at least 1 cm above the water table.

Physical variables

Within the band of the beach occupied by the crabs, the depth of the water table was 10 cm below the sand surface at the extreme seaward side of the zone and 1 m below the sand surface at the shoreward side. The beach consisted of medium grade sand. The slightly finer granulometry at the top of the shore probably represents accumulation of wind-

TABLE 4. – Granulometry data relating to the sand samples collected from the four zones on Alagadi beach. Md = median grain (ø); σ_I = inclusive graphic standard deviation (ø) ; Sk_I = inclusive graphic skewness (see Folk, 1974).

	Md (ø)	σ_I (ø)	Sk_I
Zone 1	1.40	0.41	-0.08
Zone 2	1.56	0.59	-0.31
Zone 3	1.87	0.42	-0.08
Zone 4	2.18	0.39	-0.16

blown sand. Granulometric characteristics of the sand are given in Table 4. These results indicate that the mainly medium grade sand is well sorted, with either symmetrical (zones 1 and 3) or somewhat coarse skewed (zones 2 and 4) particle distribution (see Folk, 1974). As expected, when measured at constant depth (40 cm), the water content of the sand decreased with distance from the sea, from approximately 14 % by weight in zone 1 to 8 % in zone 3. At 40 cm depth in zone 4, where crabs rarely occurred, the water content was 4 %. The water content of the damp sand near the bottom of crab burrows (burrows do not penetrate to standing water) was approximately 14 %.

Air and sediment temperatures

Measurements made during July showed that the mean air temperature (n = 4) above the sand surface ranged from 22.8 °C at 06:00 h to 35.5 °C at 12:00 h. The surface sand also exhibited daily temperature fluctuations, ranging from a mean of 22.8 °C at 06:00 h to 51.3 °C at 12:00 h (n = 4). In contrast, the temperatures taken from various depths within the sand column were seen to remain relatively constant, varying by less than 3 °C over a 24-hour period (Table 5). During the night, sediment column temperatures were slightly higher than the outside air and sand surface temperatures.

TABLE 5. – The mean temperatures taken at 6-hour intervals through a 24-hour period in July 1994. Temperature readings were taken from depths of 10 cm, 20 cm, 30 cm and 40 cm within the sand column. Recordings of the sand surface temperature (S.S.) and the air temperature at 20 cm above the sand (A.T.) were also taken.

	Mean temperatures (°C)					
Time	A.T.	S.S.	10 cm	20 cm	30 cm	40 cm
06:00	22.8	22.8	30.2	30.6	30.4	30.2
12:00	35.5	51.3	31.7	29.9	29.3	29.2
18:00	28.6	32.7	30.9	30.8	30.5	29.8
00:00	26.7	26.6	31.3	31.6	32.1	30.5

DISCUSSION

Crab distribution and population characteristics

O. cursor was found to be widely dispersed around the coast of Northern Cyprus. They were absent from some sandy beaches, but the reasons for this were not investigated.

In west Africa, where both *O. cursor* and *O. africana* occurred on the same beaches, *O. cursor* (as *O. hippeus*) occurred nearer to the sea in the supralittoral and upper eulittoral zones (Rathbun, 1921; Gauld and Buchanan, 1956; Vannini, 1976). In N Cyprus, *O. cursor* is the only ghost crab species present. Here, tidal influences are minimal: *O. cursor* occurs above the watermark, but its zone is close to the sea.

A study of a population of *O. cursor* in northern Israel by Shuchman and Warburg (1978) recorded annual fluctuations in the crab densities and dispersal patterns. During autumn, the crabs were found in greater numbers in the crab belt furthest from the sea. At the end of autumn the crabs were evenly dispersed throughout the whole crab region. During winter and spring fewer crabs were observed, as indicated by their burrow numbers (however, reduced crab activity during the winter could have led to fewer burrows being noticed). The burrow numbers then increased during the spring. By late spring the greatest burrow density was within the crab belt which occurred between five and ten metres from the sea (Shuchman and Warburg, 1978). This is similar to the study area on Alagadi beach, where the most densely populated area was between three and twelve metres from the water's edge.

The size of the crab population within the study area on Alagadi beach was found to vary throughout the three-month study period. The high numbers in August seemed to be due to recruitment of large numbers of juveniles. Crab numbers then slowly decreased, perhaps due to predation. Crab remains, which were found within the territory of a rat, appeared to be those of juvenile crabs.

Within the study area at Alagadi beach, the distribution of the crabs up the shore was seen to vary with the size of the crab. Juvenile crabs were generally found closer to the sea with the larger adults being located at a greater distance from the sea. No burrows with openings greater than four centimetres in diameter were found within the first zone. At the landward margin of the crab zone, very few burrows were found with diameters of less than one centimetre. A similar relationship between the size of the crab and its position on the beach was found for the *O. cursor* population of north Atlit, northern Israel (Shuchman and Warburg, 1978).

Differences in zonation between the sexes have been recorded for a number of *Ocypode* spp. (Fellows, 1966, 1975; Horch, 1975; Vannini, 1980a; Eshky, 1985), but were not investigated for *O. cursor* either at Alagadi beach, or at Atlit (Israel) (Shuchman and Warburg, 1978).

Burrow depth increased with distance from the sea, reflecting the increasing depth of the water table. An upper limit to their distribution was where the depth of the water table exceeded seventy centimetres. Burrows terminated at least one centimetre above the water table. *Ocypode* spp. are able to take up water from damp sand via tufts of setae between the third and fourth pereiopods (Wolcott, 1976, 1984; Eshky, 1985). Thus, the moisture content of the sand may limit the distribution of *O. cursor* up the shore.

Warburg and Shuchman (1978) suggested that the distribution of *O. cursor* on the beach could be explained to a certain extent by the gradient of the moisture content of the sand. Crabs were most abundant where the sand water content was 15 %, close to the 14 % suggested in the present work. Laboratory experiments have shown that *O. cursor* could discriminate between sand samples in which the water content differed by only 1 % (Shuchman and Warburg, 1978). Small crabs have higher rates of water loss than larger individuals (Eshky, 1985) and this might partly explain why the juveniles occurred in the zone closest to the sea.

On Alagadi beach the presence of people on the beach did not appear to have any harmful effects on the crab population. The crabs appeared to benefit from the activities of the visitors to the beach since they were attracted to discarded food. Thus, beach areas frequented by people were amongst the regions most densely populated by crabs. Human activity can have both beneficial and harmful effects on ghost crabs. Studies of *O. quadrata* populations in North America have shown that human activities can be beneficial for similar reasons to those described for *O. cursor*, but that off-road vehicles may have detrimental effects by causing injury, mortality and disturbance (Steiner and Leatherman, 1981; Wolcott and Wolcott, 1984).

Collections of *O. cursor* from Alagadi beach during July and September indicated that there was a difference in the sex ratios of the adult crabs during these two months. In July, there appeared to be fewer adult female crabs on the beach than adult male crabs. The apparent reduction in the numbers of female crabs observed during July may have been because they were residing in the burrows of male crabs as has been reported for *O. saratan* (see below). It is also possible that ovigerous female crabs might plug their burrow openings as in the case of *O. ceratophthalma* (Fellows, 1973). In the Red Sea, an equal ratio of *O. saratan* was found during the winter but this ratio also appeared to change during the warmer months, when fewer females were observed (Eshky, 1985). The deviation from a 1:1 sex ratio at this time coincided with the start of the breeding season when many mature females remained underground in the male burrows (Linsenmair, 1967).

Burrow morphology

The variation in burrow shape seen in a number of ghost crab species has been reviewed by Vannini (1980a) who showed that the burrows of juveniles were either I, J or U-shaped, whereas those of the adults showed greater variability and included Y and spiral configurations in addition to the burrow shapes shown by juveniles. Each species shows a particular range of burrow morphologies. Burrows of males may differ from those of females as in the case of *O. ceratophthalma* (Fellows, 1966) and *O. saratan* (Linsenmair, 1967; Eshky, 1985). Geographic variation in burrow form has been shown for *O. ceratophthalma* (Fellows, 1966) and may occur in other species.

In northern Israel, Shuchman and Warburg (1978) found the structure of *O. cursor* burrows to be generally Y-shaped, with one of the upper branches terminating 3 to 15 cm below the sand surface. In some cases both the ascending arms opened to the surface. Closer to the sea, U-shaped burrows inhabited by juvenile crabs were found. Yet, on Alagadi beach, all of the *O. cursor* burrows examined appeared to have only one opening. Seven burrows were successfully cast at Alagadi (other attempts failed to produce complete casts). Six of these were L-or J-shaped. The other burrow had a longer, sinusoidal horizontal component than the others, but was similar in other respects. Further research is necessary to investigate the variation in burrow form seen in this species, and to determine if there are differences which can be related to site, season and sex.

Burrows had their openings directed towards the sea. This has also been reported for other species, e.g. *O. ryderi, O. ceratophthalma* and *O. saratan* (Vannini, 1980b; Fellows, 1966; Eshky, 1985).

An equal number of left and right handed crabs were seen to exist in the O. cursor population. Similar results were found for *O. ceratophthalma* in Mozambique (Barrass, 1963) and for *O saratan* in the Red Sea (Linsenmair, 1967; Eshky, 1985), but most *O. ryderi*. examined by Vannini (1980b) in Somalia had the major claw on the right.

Activity patterns

On Alagadi beach *O. cursor* was observed to be nocturnal. Vannini (1976) has reviewed diel activity in *Ocypode* spp. and found most to be nocturnal or crepuscular. Intraspecific variation in peak activity times occurs and may relate to differences in factors such as weather, site, season and crab size (Vannini, 1976, Shuchman and Warburg, 1978).

On Alagadi beach, *O. cursor* was frequently observed close to the water's edge at night. They also appeared to wander landwards throughout the night since, in the mornings, crab tracks were observed within the top zone of the beach where no crab burrows were found. When the crabs were observed around dawn, they were either found to be positioned in their burrow openings or involved in burrowing activities. Only on one occasion were adult crabs observed out of their burrows during the day. They had been attracted to an animal carcass on the beach and were feeding from it. However, the juvenile crabs were frequently observed darting in and out of their burrows during the day. Similar behaviour has been reported for the juveniles of other *Ocypode* species (Hughes, 1966) and two of the authors have observed it for *O. saratan*.

Feeding

O. cursor on Alagadi beach was seen to be both a scavenger, feeding on animal carcasses, picnic remains and vegetable matter and a predator, preying upon hatchling sea turtles. As no sand pellets were found it was assumed that they did not deposit feed. It is not known whether they fed upon marine invertebrates. They were, on several occasions during the night, observed close to the water's edge. It is possible that at these times they were feeding upon the littoral infauna as reported for some other *Ocypode* species (Vannini, 1976; Wolcott, 1978; Eshky, 1985). These incidental observations on feeding require further work in order to establish the full range of natural diet.

Ocypode species feed in various ways. Many deposit feed, leaving characteristic pellets on the sand surface. They are also opportunistic scavengers. Some species take plant material and some are active predators (Vannini, 1976, 1980b; Wolcott, 1978; Eshky 1985). Gibson-Hill (1947) has also reported that ghost crabs (species uncertain: either *O. ceratophthalma* or *O. cordimanus*, see Tweedie, 1950) feed on turtle hatchlings as seen in the present study.

Burrowing

On Alagadi beach, *O. cursor* was seen to be involved in burrowing activities in the hours around sunrise. The activities observed involved the excavation of sand from within the burrow, the formation of a sand pile outside the burrow opening and then the scattering and transportation of the sand pile. In some cases the sand pile was not removed but was left to accumulate, with successive excavations adding to the size of the mound. On the New Jersey shore, observations of *O. quadrata* have shown that this species also burrows at dawn (Milne and Milne, 1946). The burrowing activity described is similar to that observed for *O. cursor* at Alagadi. Sand piles were formed at the burrow opening and were then levelled out later in the morning. Sand piles beside burrow openings are reported for a number of species; in the case of *O. rotundata* (Pretzmann, 1975) and *O. saratan* (Linsenmair, 1967) they are produced by males to attract females. No such behaviour has been observed in *O. cursor*; Shuchman and Warburg (1978) stated that sand piles were not present beside burrow openings of *O. cursor* at Atlit. It is therefore unlikely that they have any signal function in this species.

Temperature study

The air temperatures and surface sand temperatures of Alagadi beach exhibited large daily fluctuations. The air temperatures were seen to vary between 22.8 °C and 35.5 °C, a range of 12.7 °C. The surface sand temperatures fluctuated between 22.8 °C and 51.3 °C, a range of 28.5 °C. The greatest temperature fluctuation observed within the sand column was found at a depth of 20 cm, where the temperatures ranged from 29.9 °C to 31.6 °C, a range of only 1.7 °C. Burrow temperature closely follows sand column temperature (Atkinson and Taylor, 1988) and thus the burrows of *O. cursor* afford the crabs protection from the high external temperatures. The importance of the burrow in providing ghost crabs with protection from environmental extremes has been discussed by Vannini (1980a); Atkinson and Taylor (1988) and Eshky *et al*. (1988).

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