

HABITAT SELECTION AND ENERGETICS OF THE FIDDLER CRAB (*UCA TANGERI*)

MARCEL KLAASSEN^{1,2} and BRUNO J. ENS^{2,3}

¹Max-Planck-Institut für Verhaltensphysiologie, D-82346 Andechs, Germany

²Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

³Institute for Forestry and Nature Research, P.O. Box 167, 1790 AD Den Burg, The Netherlands

ABSTRACT

We tried to unravel the possible links between the skewed predation risk in *Uca tangeri* (where large individuals are more at risk from avian predators) and size-dependent changes in the physiology and habitat choice of this fiddler crab species. Over a transect running from low to high in the tidal zone of a beach in Mauritania, the temperature profile at various depths in the substrate, the water-table level of seep water, salt concentration of seep water, depth of the aerobic level, operative temperatures on the surface, and size distribution of crabs were assessed. In addition, resting metabolic rates, Q_{10} and thermal and starvation tolerances were estimated. Going from low to high in the tidal zone, crab size and burrow depth increased. At the preferred burrowing depth, microclimatological conditions appeared to be equally favourable at all sites. At the surface, conditions were more favourable low in the tidal zone, where also food availability is sufficient to enable small crabs to forage in the vicinity of their burrows. Large crabs have higher energy requirements and are thereby forced to forage in flocks low in the tidal zone where food is probably more abundant. Low in the tidal zone, digging deeply is impossible as the aerobic layer is rather thin. Large crabs prefer living high in the tidal zone as (1) deep burrows ensure better protection against predators, (2) more time is available for digging holes and (3) the substrate is better suited for reproduction. Energy reserves in late summer ensured an average of 34 days of survival. It is argued that the allotment of energy to growth must be considerable even in reproducing animals; the rewards of growth being the disproportional increase in reproductive output with size.

1. INTRODUCTION

During high tide, fiddler crabs *Uca tangeri* hide in their closed burrows. During low tide they emerge to feed on the uncovered substrate. However, unfortunately for the fiddler crabs, avian predators are awaiting them when they want to surface for foraging; fiddler crabs are shown to be among the most important prey species for many waders that spend their winter on tropical intertidal flats as well as for other local and migratory birds that occur in these habitats (ZWARTS, 1985, and citations therein; ZWARTS, 1990; ENS *et al.*, 1993). The natural history of *U. tangeri* has been extensively described by ALTEVOGT (1959), HAGEN (1962), GÜNTHER (1963), CRANE (1975) and WOLFRATH (1992a, 1992b, 1993). Two feeding strategies in *U. tangeri* can be distinguished: (1) crabs stay in the vicinity of their burrow into which they quickly retreat upon approaching danger, and (2) crabs leave the burrowing zone and move in large flocks to feed elsewhere. Typically, small individuals occur mainly low in the tidal zone, where ample opportunity to feed in the direct vicinity of the burrow exists. Larger individuals burrow high in the tidal zone where no possibilities for

foraging are available and foraging in flocks is the only alternative strategy. Although crabs foraging near their burrow can be seen nearly every tide, the feeding activity of *Uca* was most intense on days following a spring high tide. Large crabs and crabs foraging in flocks suffer the highest avian predation. This is also true when predation is corrected for the fact that flocks do not occur every tide (ENS *et al.*, 1993). Now the question arises why large crabs have their burrows so high in the tidal zone and, therewith, choose for the strategy of foraging in flocks.

During an expedition to the Banc d'Arguin on the Mauritanian coast, where large numbers of *U. tangeri* occur (ENS *et al.*, 1993), we investigated interactions of an *U. tangeri* population with its abiotic environment and focused on alterations in these relations with size of the fiddler crabs that may explain their size-dependent distribution in and over the substrate. Throughout the three-dimensional potential environment of the fiddler crab, data were collected on temperatures, salt concentrations, moisture and oxygen profile of the substrate. These data were combined with measurements on the heat tolerance and energy

¹To whom reprint requests should be send

expenditure in relation to temperature and size. In addition, starvation tolerance was measured to see how long fiddler crabs can potentially remain underground. The results suggest that the characteristic size-dependent distribution cannot be explained by size-dependent changes in the physiology of *U. tangeri*. We propose that the reason for this distribution pattern must be sought in predation risk and/or altered needs for reproduction and growth that relate to size.

2. MATERIAL AND METHODS

2.1. RESEARCH AREA

Our study area was located in the Baie d'Aouatif on the Banc d'Arguin, Mauritania (19°45'N, 16°16'W). The field study site was a 30-m wide sandy beach between the mud flats and the sebkha. Fiddler crabs use the beach both for foraging and for making their burrows. Over the beach, perpendicular to the low water line, a transect was laid out starting on the mudflat at 30 cm above the average low-water line and ending high up the beach close to the sebkha, a flat area with a hard salt crust that is only flooded during the highest spring tides. See ENS *et al.* (1993) for a more detailed description of the area (site A in ENS *et al.*, 1993) and some general biological aspects of the fiddler crabs living there. For laboratory work we used the biological station of the Parc National du Banc d'Arguin, which was situated close to our field study site.

In the area a desert climate prevails. During the period of our observations, which lasted from 3 August until 25 September 1988, mean ambient temperature was 27°C with a typical diurnal variation of 6°C. Only during offshore winds temperatures occasionally reached above 40°C.

2.2. ABIOTIC MEASUREMENTS ALONG THE BEACH TRANSECT

Along the transect, temperatures in the sediment were measured at 1, 5, 10, 20, 35, 55 and 80 cm depth, using a calibrated thermistor probe. Measurements were conducted over the whole transect at two-meter intervals. These temperature profiles were taken every three hours during three days in August on which successively neap, spring, and neap tides occurred.

Operative temperatures were measured using a dead and dried crab with a carapace width of 35 mm in which a thermistor was centrally placed. This model was positioned randomly along the transect. Temperature readings were taken after allowing the temperature in the model to stabilize, at varying times of the day and at various occasions throughout the research period.

Holes were dug in the beach along the transect at

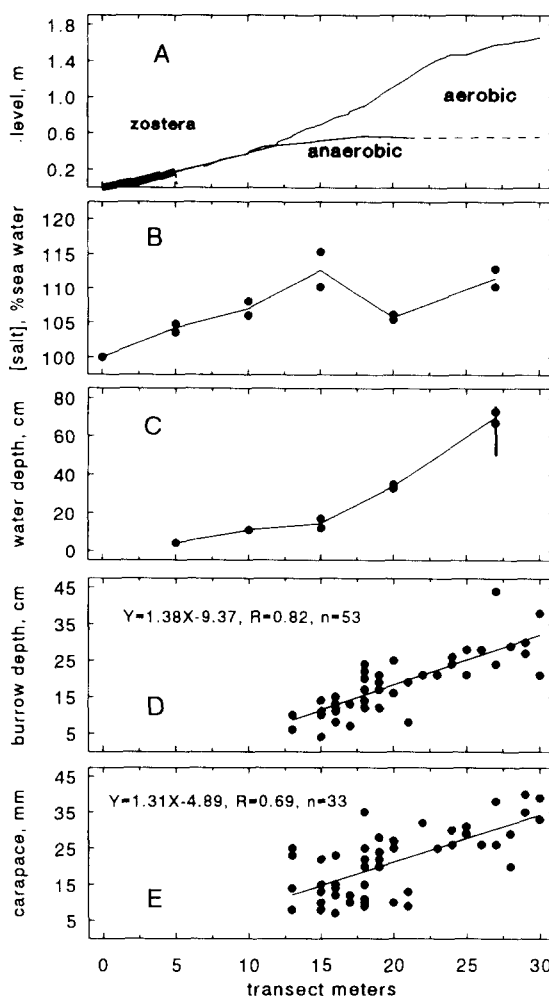


Fig. 1. Description of some abiotic variables and *Uca tangeri* distribution in a beach along a transect set out perpendicular to the water line on the Banc d'Arguin, Mauritania.

-(A) A cross-section of the beach, with seagrass (*Zostera*) vegetation zone and the border between aerobic and anaerobic substrate indicated (the various levels were measured relative to an arbitrarily chosen reference point which was 30 cm above the average low-water line).

-(B) Concentrations of salt in the seep water relative to the concentration of local sea water.

-(C) Water-table profile in the beach (in cm from the surface) as measured on 20 and 21 August 1988, and the fluctuation in minimal daily water-table level measured at meter-27 between 6 and 20 September 1988.

-(D) Burrow depth (in cm from the beach surface).

-(E) Crab size (carapace width, mm) of 53 crabs dug out from the beach.

5, 10, 15, 20, and 27 m, on 20 and 21 August (neap tide). The water-table level and the depth of the aerobic layer were measured, in addition to the electro conductivity of a sample of seep water. Comparing

these results with the electro conductivity of a sample of sea water, the salt concentration of the seep water was estimated relative to that of sea water. At meter-27 on the transect a 1.5-m long pipe was dug into the beach to allow water-table measurements of the seep water at regular intervals during a period of 15 days at low and high water.

2.3. SIZE DISTRIBUTION OF CRABS ALONG THE BEACH TRANSECT

Burrows of crabs were randomly selected along the transect. Burrows less than 7 mm in diameter, which occurred on the lower part of the beach transect exclusively, were neglected. Before handling the shovel, burrow width was measured to the closest mm, after which the burrow was carefully excavated and burrow depth was measured. Carapace width of the crabs in the excavated burrows was measured to the closest mm. In the cases that the crabs were able to escape the excavator, burrow size was taken as an estimate of carapace width, as these are strongly correlated (ZWARTS, 1985).

2.4. UPPER THERMAL TOLERANCE

Thermal resistance was measured at six different temperatures, ranging from 36 to 44°C. At each trial eight crabs, recently caught from flocks on the beach, were individually placed in a sealed plastic container with a floor surface of 100 cm². In half of the containers, crabs were provided with 50 cm³ of water to create a water-saturated atmosphere. The containers were submerged in a water bath for one hour after which mortality was scored.

2.5. STARVATION EXPERIMENTS

On 5 August, 98 fiddler crabs were taken from a flock on the beach and divided over three crates with a floor surface of 2500 cm² filled with ca 0.5 cm of sea water. An additional 30 individuals were placed solitarily in white plastic beakers with a floor surface of 100 cm² and some water. On 10 August, an additional 52 crabs were caught from a flock and individually housed. Average size of all crabs was 27.5 mm (SD = 6.6, median = 29, range = 15-40 mm). The crates and beakers were placed in a room of the biological station where a normal day-night cycle and an ambient temperature of about 27°C prevailed. Every day, water was refreshed and the number and size of the casualties noted.

To estimate the energy content of the body tissue lost during the period of starvation, ash-free dry mass values of starved and non-starved individuals were compared. 85 Crabs were collected from flocks and instantly killed in a deep-freezer. These crabs, together with 34 crabs starved to death, were subsequently dried to constant weight at 70°C, after which

they were stored in sealed plastic bags until analysis. In the Netherlands, ash-free dry mass (AFDM) was measured as described by ZWARTS & BLOMERT (1990).

2.6. OXYGEN CONSUMPTION

Oxygen consumption was measured in crabs of varying size and of both sexes taken from flocks or dug out from burrows. In addition some of the crabs from the starvation experiments were used in the metabolic experiments after 2 to 14 days of starvation. Oxygen consumption was measured using a closed manometric respirometer, which was connected to a compensatory chamber by a water filled V-shape tube. An NaOH solution acted as CO₂ absorber in the respirometer chamber. Pressure changes due to oxygen consumption were noted by shifts in the water level in the V-shape tube. These pressure changes were compensated by adjusting the volume of the respirometer chamber with a micrometer; the decrease in volume being equal to oxygen consumption. Two types of devices were used, one for small crabs and one for large subjects, with floor surfaces of 28 and 95 cm², respectively. The devices were submerged in a thermostated water bath and the system was allowed to come to equilibrium for at least three hours before the oxygen-consumption measurements started. Experiments were always conducted around high water, at temperatures varying between 24 and 34°C, and lasted at least one hour. Over this period the average oxygen consumption rates were calculated and corrected to standard temperature and pressure conditions. For calculation of energy expenditure from oxygen consumption, a conversion factor of 20 kJ·dm⁻³ O₂ was used.

3. RESULTS

3.1. THE NATURAL ENVIRONMENT AND SIZE DISTRIBUTION OF *UCA*

Along the first (lower) 12 m of the transect, where the substrate is completely anaerobic just below the surface, no *Uca* burrows were found (Fig. 1). From 12 meter up, *Uca* sizes progressively increased and so did burrow depth, a general pattern also reported by ZWARTS (1990) and ENS *et al.* (1993). The relation between burrow depth and crab size (not presented) is in close agreement with that described by ZWARTS (1985) for Guinea Bissau and the Banc d'Arguin (ZWARTS, 1990). Burrows were exclusively dug in aerobic substrate and generally above the minimum daily water-table level. All except the burrows highest on the beach were flooded twice daily. High on the beach, the water-table was never found to be deeper than 71 cm below surface. Although burrows here were about 35 cm deep and thus always above the maximum water-table level, the substrate at this level always remained damp. The salt concentration of the

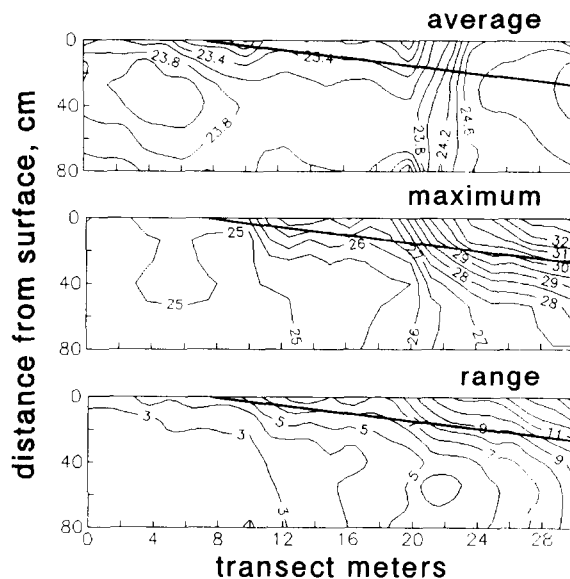


Fig. 2. Three profiles of substrate-temperature parameters of the beach. Isolines of average temperature, maximum temperature and temperature range (all in °C) are plotted in relation to depth measured from the surface (vertical axis) and transect position (horizontal axis). In each panel the predicted burrow depth in relation to transect position (from Fig. 1D) is drawn.

seep water increased moderately with distance from the mudflats (Fig. 1).

Average temperatures in the beach sediment were very constant and ranged from 23°C low to 25°C higher up the beach (Fig. 2). With increasing depth, conditions became more constant. High on the beach the variations were larger than close to the low-water line. Going from low on the beach higher up and considering conditions at typical burrow depth, we found ranges in maximum temperature from 25.5 to 30°C and minimum temperatures from 19.5 to 20.5°C. The environmental temperature range of crabs in their burrow thus never spanned more than 10.5°C. Low on the beach, it was even 5°C only. Also POWERS & COLE (1976) in Texas and MACINTOSH (1978) in Malaysia note for several species of *Uca* that, despite great fluctuations in surface temperature, temperatures are remarkably constant at burrow depth.

In contrast, operational temperature on the surface showed much higher variation (Fig. 3A). Around noon, operational temperatures could reach values as high as 45°C. This was not exclusively due to a higher surface temperature of the beach: also after correction for surface temperatures, operative temperatures remained on average elevated around noon (Fig. 3B). Selecting cases around noon, between 10 a.m. and 15 p.m. local time, a positive correlation between operative temperature and position on the transect was apparent (inset Fig. 3A:

$0.18^{\circ}\text{C}\cdot\text{m}^{-1}$, $R = 0.407$, $P < 0.001$, $n = 67$). Thus, crabs higher on the beach experienced higher operative temperatures than crabs lower in the tidal zone.

3.2. THERMAL AND STARVATION TOLERANCES

The upper thermal tolerance was lower in crabs in saturated air than in dry air, which was very likely due to the possibility of evaporative heat loss in the latter (Fig. 4). For crabs in saturated air, LD_{50} was around 39°C. For crabs in dry air LD_{50} was not estimated very accurately and was in the range 40–42°C. Similar differences between thermal tolerance in saturated and dry air were reported by WILKENS & FINGERMAN (1965) in *U. pugilator*, with LD_{50} values of 40.7 and 45.1°C, respectively, after one hour of exposure. Comparable experiments in other fiddler crab species in saturated air invariably report LD_{50} values below 42°C. Over short intervals, however, *Uca*'s can show a much higher thermal tolerance (MACINTOSH, 1978, and citations therein).

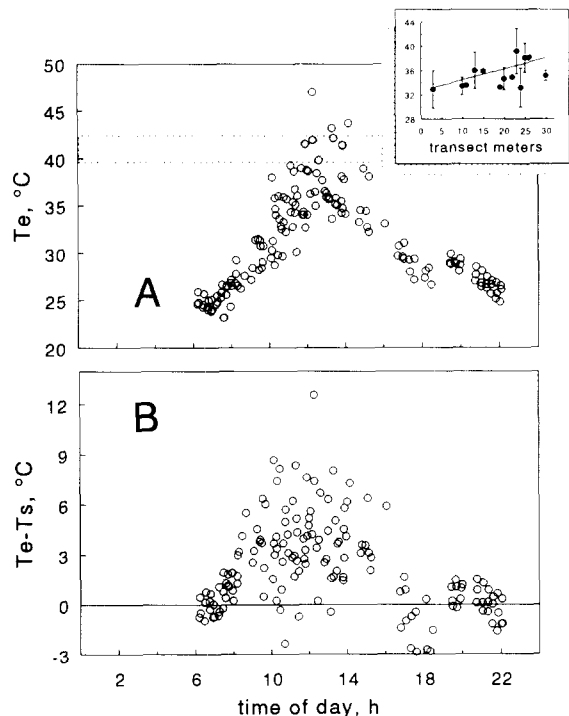


Fig. 3. (A) Operative temperature (T_e , °C) as measured in a dead and dried fiddler crab and (B) operative temperature corrected for surface temperature (T_s , °C) in relation to time of the day. In panel A the horizontal shaded bar indicates the upper thermal tolerance for *U. tangeri* in dry air. The inset in panel A describes the relation between T_e and position along the transect for the measurements taken around noon (between 10 a.m. and 3 p.m.).

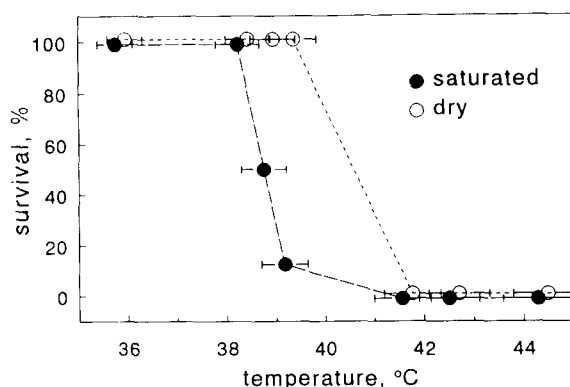


Fig. 4. Survival of *U. tangeri* in relation to a one-hour exposure to different ambient temperatures in water-saturated and dry atmospheres. Each dot represents a survival percentage among 8 crabs. Ranges in temperature are indicated by horizontal bars.

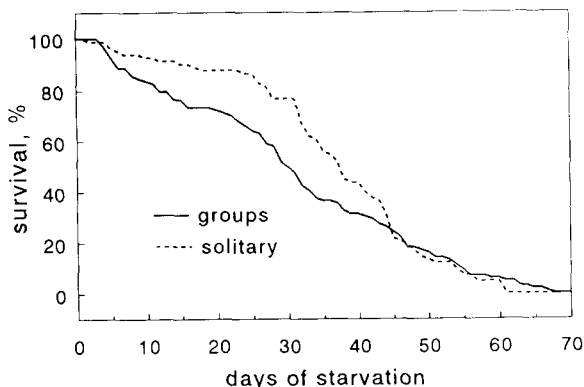


Fig. 5. Survival of *U. tangeri* ($n = 180$) in relation to number of days of starvation. No significant differences between sexes and size groups. Solitarily kept crabs lived 5 days longer on average than crabs held in groups.

In the starvation experiments, death occurred after an average of 33.9 days ($SE = 1.2$, $n = 180$, median = 34), with no significant effect of crab size or sex (analysis of variance). However, whether crabs were kept solitary or in groups had a significant effect, single crabs living 5 days longer on average (mean = 36.9, $SE = 1.5$ versus mean = 31.4, $SE = 1.8$; median test $\chi^2_1 = 8.73$, $P = 0.003$, $n = 180$; Fig. 5). Probably the crabs kept in groups were expending more energy for activity due to interactions. Starvation to death led to a decrease in AFDM ranging from 30% in the largest individuals in the experiments (40 mm) up to 60% in the smallest (15 mm; Table 1). As also the energy density of the AFDM decreased (ZWARTS & BLOMERT, 1990; Table 1), the total energy-content loss of the crabs in starvation ranged from 35 to 60% in males and 45 to 70% in females, for largest and smallest crabs, respectively.

TABLE 1

Allometric relations for predicting ash-free dry mass (AFDM, mg) from carapace width (C , mm) in *Uca tangeri* for the two sexes and for starved and non-starved (i.e. immediately killed after collecting from flocks) individuals ($AFDM = \exp(a + b \cdot \ln(C))$). In addition, energy density of the AFDM as estimated by ZWARTS & BLOMERT (1990) is given.

	a	b	n	r	$\text{kJ} \cdot \text{g}^{-1}$ AFDM
non-starved	-2.217	2.805	41	0.96	20.2
starved to death	-4.351	3.288	19	0.94	18.6
non-starved	-2.245	2.803	44	0.98	22.1
starved to death	-4.749	3.375	15	0.98	18.6

3.3. OXYGEN CONSUMPTION

Oxygen consumption increased with crab size (Fig. 6A) and ambient temperature (Fig. 6B). There were no significant differences between the sexes and between newly caught animals from the beach and animals in the starvation experiment. VERNBERG (1959) reports a dramatic decrease during the first day after capture in *U. pugnax* and proposes to measure oxygen consumption in animals starved for 1 to 3 days only. However, our procedure using animals 3 to 20 hours after capture, giving them at least 3 hours time to settle, and measuring them around high tide (rest phase) only, was apparently sufficient to deal with this problem. The effect of ambient temperature was minor only and over the range of 24 to 34°C the Q_{10} was 1.31. VERNBERG (1959) found comparable Q_{10} values, ranging from 1.22 to 1.90 in *U. minax*, *U. rapax* and *U. pugnax*, in approximately the same temperature range. These small Q_{10} values are thought to be an adaptation to life in intertidal environments (BURGGREN & MCMAHON, 1981), where environmental temperatures may fluctuate considerably as depicted in Figs 2 and 3. However, outside the range of normally occurring temperatures, Q_{10} values may be much higher (VERNBERG, 1959).

4. DISCUSSION

4.1. BURROW MICROCLIMATOLOGICAL CONDITIONS

The range of temperatures at which oxygen consumption measurements were conducted (24 through 34°C) does not completely encompass the whole range of temperatures experienced by the crabs in their burrows (19.5 through 30°C). Nevertheless, from the low Q_{10} estimated, it is conceivable that energy

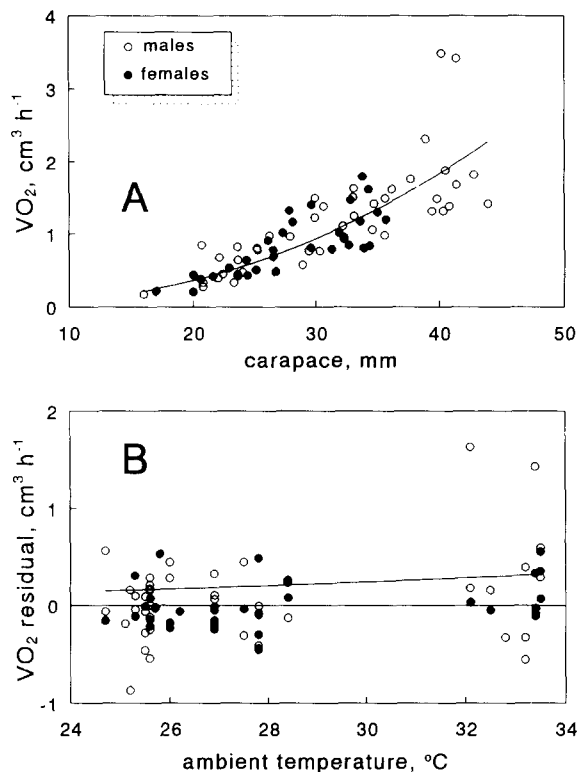


Fig. 6. (A) Oxygen consumption (VO_2 , $\text{cm}^3 \text{h}^{-1}$) in relation to carapace size for *U. tangeri*; a power curve is fitted. (B) The residuals from the fitted curve in Fig. 6A are plotted in relation to ambient temperature, portraying the significant, yet small, effect of temperature on metabolism within the range of temperatures measured. The overall relation between oxygen consumption and temperature (T , $^{\circ}\text{C}$) and carapace width (C , mm) is $VO_2 = 2.97 \cdot 10^{-5} \cdot C^{2.293} \cdot T^{0.769}$ ($R = 0.891$, $P < 0.001$, $n = 77$).

expenditure for all crabs was rather constant irrespective of the site where they chose to dig. This is particularly so because average burrow temperatures were almost constant around 24°C . Given the upper thermal tolerance of *Uca* in damp air (39°C), the maximum temperatures experienced in the burrows (30°C) never reached life threatening levels.

Salt concentration of the seep water increased with distance from the low-water line. However, this increase was moderate. Salinity of sea water on the Banc d'Arguin is about 38 (KLAASSEN & ENS, 1990) and thus the maximum relative salt concentration of 116% sea water corresponds with an absolute salinity of 44. Conceivably, this high salt concentration will not have posed any problems for *U. tangeri*. In other species of *Uca* from comparable environments even salt concentrations twice this value were tolerated (RABALAIS & CAMERON, 1985). Moreover, as the burrows were generally above the water-table level during low tide and

water was thus penetrating from above and below during high tide, micro-environmental salt concentrations for *Uca* will have been lower in their burrows than the values measured in the seep water. This water-penetration scheme probably also ensures the influx of oxygen rich water, although, oxygen provisioning is probably also ensured by air trapped in the closed burrow (WOLFRATH, 1992a). In conclusion, microclimatological conditions appear to be equally favourable at all sites in the beach at the preferred depth.

4.2 SURFACE MICROCLIMATOLOGICAL CONDITIONS

In contrast to burrow temperature, operational temperature was occasionally very high and even reached the upper thermal tolerance of the crabs. However, all crabs had ample opportunity to escape for the problem of overheating in our study area. Crabs foraging close to their burrow always had the possibility to retreat and cool off. Indeed, MACINTOSH (1978) showed for several species of *Uca* in Malaysian mangroves that the frequency of burrow retreat increased with environmental temperature. However, it is questionable whether the prime stimulus for this burrow-retreat response has a thermoregulatory function, as first suggested by WILKENS & FINGERMAN (1965). According to SMITH & MILLER (1973) regular retreat is necessary to replace water losses, water being indispensable for feeding, besides evaporative heat loss. Indeed, evaporative water loss is generally very high in land crabs (WOLCOTT, 1992). Nevertheless, whatever the principle impetus, the burrow retreat response solves both problems simultaneously.

Flocking crabs did not have a cool burrow to their disposal while foraging, but were always foraging low in the tidal zone, where operative temperatures were much lower and many tidal pools to cool off were available. Only upon return to their burrows, flocking crabs might potentially run in trouble when unable to find a burrow in time.

4.3. SIZE-SPECIFIC SPATIAL DISTRIBUTION

Below the surface, microclimatological conditions were almost equally favourable in any burrow. In contrast, surface conditions were more favourable low in the tidal zone. This was so not only from a microclimatological viewpoint but also considering food availability: the sandy upper intertidal zones are poor in food, whereas muddy mid- to lower intertidal substrate contains most food (MURAI *et al.*, 1982; CHRISTY & SALMON, 1984). ENS *et al.* (1993) make conceivable that large crabs necessarily need to forage further away from their burrows than small crabs, to cover their energy requirements. Thus, with the increase in size and energy requirement the value of the burrow as a safe haven becomes progressively less. Under

these circumstances it might as well pay to leave the area around the burrow and temporarily move to places where food is very abundant; i.e. at our study site, to the seagrass beds where burrowing is not possible as the anaerobic substrate starts almost directly below the surface. Thus, large crabs nearly always have to flock. Yet, the question remains open why then large crabs prefer to burrow high up the beach.

Among the avian predators of fiddler crabs on the Banc d'Arguin were Curlew, *Numenius arquata*, and Bar-tailed Godwit, *Limosa lapponica*, species that use their long bill to extract crabs from their burrow. Whimbrel, *Numenius phaeopus*, may use this strategy as well, but mainly relies on chasing crabs on the surface (ENS *et al.*, 1993). Maximum bill lengths for these three species are 18, 11 and 8 cm, respectively (CRAMP & SIMMONS, 1982). The combined data of Figs 1D and 1E suggest that crabs with a carapace width lower than 20 mm are thus not safe from these probing waders at their typical burrow depth (see also ZWARTS, 1985 and ENS *et al.*, 1993). Given the fact that birds prefer large crabs over small crabs (ZWARTS, 1985, 1990; ENS *et al.*, 1993) it would be especially beneficial for large crabs to burrow at least 16 cm into the substrate to guarantee escape from probing avian predators. But not only birds may be a good reason for living deep in the substrate. Digging deeper burrows might ensure a lower risk of predation by high-tide predators such as fishes and the blue crab *Calinectes marginatus* too. After a high tide, we often found pits in the sand suggesting fishes or blue crabs had been digging there for food. Thus, the capacity of digging deeper lowers predation risk. Yet, given the abiotic structure of the beach, especially with regard to oxygen availability, digging deeply can only be done high on the beach. If possible at all, given the energetic and physical limitations imposed by their

size, small crabs would only dig high in the tidal zone when food availability low in the tidal zone does not counterbalance the higher predation risk there.

High in the tidal zone there is also more time available for excavating a burrow. Especially for flocking crabs that are unable to find a vacant burrow upon return, this extra time available might be essential. However, the observation of CHRISTY (1983), that females of *U. pugilator* prefer burrows high on the beach, might be more important. He proposes that the negative effect of flooding and collapse on female breeding success may select for stable burrows. In addition, high in the intertidal zone, reproducing males might benefit by having more time to attract mates and excavate extra chambers for them. Another possible reason for reproducing crabs to live high in the tidal zone comes from HAGEN (1962). He proposes that the dry and more firm substrate high on the beach gives a better transmission of the vibrations produced during drumming of the male with its major cheliped, which has a function in territorial and courtship behaviour.

4.4. ENERGY RESERVES

The energy reserves in *Uca* ensured an average of 34 days of survival without food, independent of sex and size of the crabs. A prediction of day of death, by combination of energy reserve available (Table 1) and size-specific energy expenditure at 27°C (Fig. 6), results in a remarkably similar value (Fig. 7). From these calculations we do not predict much influence of size on day of death. However, thus calculated, survival time in males appears to be about 20% shorter than in females.

Energy reserves are not equally large throughout the year (ZWARTS & BLOMERT, 1990; WOLFRATH, 1993). Using the energy content values for crabs in spring at the Banc d'Arguin (ZWARTS & BLOMERT, 1990) and assuming size-specific energy expenditure and energy content of starved individuals to be the same, we calculated that crabs in spring would die on average on the 20th day of starvation (Fig. 7). These seasonal differences in energy reserves probably relate to differences in foraging activity, fiddler crabs in Mauritania showing an increase in foraging activity from winter to spring (ZWARTS, 1990), maintaining a high foraging activity in summer (pers. obs.). Foraging activity on its turn is geared to ambient temperature (POWERS & COLE, 1976). Reproduction takes place in summer (ALTEVOGT, 1959; HAGEN, 1962; WOLFRATH, 1993) and it is for this event that mature crabs probably need extra energy reserves. Males need it for sperm production and courtship. During the reproductive period they do not forage, because males that leave the vicinity of the breeding burrow risk losing their burrow to another male (CRANE, 1975; CHRISTY & SALMON, 1984). Females need extra energy reserves for egg production and the fast associated with the

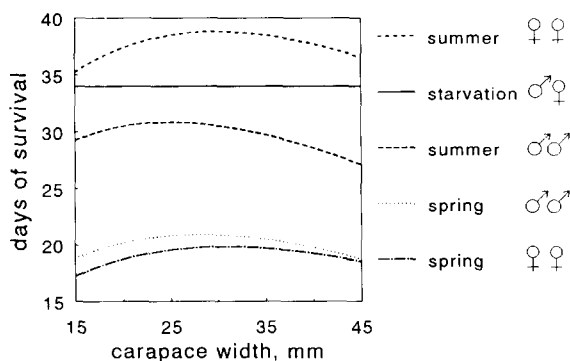


Fig. 7. Calculated numbers of days of survival from endogenous energy reserves in summer (Table 1) and spring (ZWARTS & BLOMERT, 1990) and energy expenditure at 27°C for males and females *U. tangeri* in relation to their size. The full horizontal line indicates the average number of days of survival as measured in the starvation experiments.

incubation of the eggs in the sealed breeding burrow (CHRISTY, 1983). Remaining energy reserves are probably invested in growth, non-reproducing animals probably allocating all the available nutrients in growth. From the very high starvation endurance found, it is conceivable that even in reproducing animals the allotment of energy to growth is considerable. This investment in growth can probably be understood from the fact that reproductive output increases disproportionally with size in fiddler crabs (GREENSPAN, 1980; CHRISTY, 1983). However, for a full understanding of size distribution within a population and the marked differences in size of *U. tangeri* between sites (HAGEN, 1962; pers. obs.) more quantitative information is needed on costs of growth and reproduction and size-dependent reproductive output in addition to predation risks by birds and other animals.

Acknowledgements.—We thank the Mauritanian authorities, in particular the Director of the Parc National du Banc d'Arguin, Mr Hadya Amadou Kane, for the permission to carry out this study and for permission to use the field station. Indispensable help was received from personnel of the Parc of whom Mr. Abou Gueye, Mr El Hassane ould Mohammed el Abd and Mr Samba should especially be mentioned. Tom van Spanje organized the logistics. Peter de Wilde put the manometric oxygen analyzers at our disposal. Leo Zwarts and Anne-Marie Blomert completed the starvation experiments when we had to leave prematurely and analyzed the crabs on their ash-free dry mass. Leo Zwarts also provided the equations relating ash-free dry mass to carapace width. We are indebted many thanks to all of them. The project was made possible thanks to financial support by the Netherlands Marine Science Foundation.

5. REFERENCES

- ALTEVOGT, R., 1959. Ökologische und Ethologische Studien an Europas einziger Winkerkrabbe *Uca tangeri* Eydoux.—Z. Morph. Ökol. Tiere **48**: 123-146.
- BURGGREN, W.W. & B.R. MCMAHON, 1981. Oxygen uptake during environmental temperature change in hermit crabs: adaptation to subtidal, intertidal, and supratidal habitats.—Physiol. Zool. **54**: 325-333.
- CHRISTY, J.H., 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*.—Behav. Ecol. Sociobiol. **12**: 169-180.
- CHRISTY, J.H. & M. SALMON, 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*).—Biol. Rev. **59**: 483-509.
- CRANE, J., 1975. Fiddler Crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton: 1-736.
- CRAMP, S. & K.E.L. SIMMONS, 1982. The birds of the Western Palearctic. Vol III. Oxford University Press, Oxford.
- ENS, B.J., M. KLAASSEN & L. ZWARTS, 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour.—Neth. J. Sea Res. **31**: 477-494.
- GREENSPAN, B.N., 1980. Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*.—Anim. Behav. **28**: 387-392.
- GÜNTHER, H.-J., 1963. Untersuchungen zur Verbreitung und Ökologie von *Uca tangeri* an der SW-Iberischen Küste.—Z. Morph. Ökol. Tiere **53**: 242-310.
- KLAASSEN, M. & B.J. ENS, 1990. Is salt stress a problem for waders wintering on the Banc d'Arguin, Mauritania?—Ardea **78**: 67-74.
- MACINTOSH, D.J., 1978. Some responses of tropical mangrove fiddler crabs (*Uca* spp.) to high environmental temperatures. In: D.S. MCLUSKY & A.J. BERRY. Physiology and behaviour of marine organisms. 12th Eur. Mar. Biol. Symp: 49-56.
- MURAI, M., S. GOSHIMA & Y. NAKASONE, 1982. Some behavioral characteristics related to food supply and soil texture of burrowing habitats observed on *Uca vocans vocans* and *U. lactea perplexa*.—Mar. Biol. **66**: 191-197.
- POWERS, L.W. & J.F. COLE, 1976. Temperature variation in fiddler crab microhabitats.—J. exp. mar. Biol. Ecol. **21**: 141-157.
- RABALAIS, N.N. & J.N. CAMERON, 1985. Physiological and morphological adaptations of adult *Uca subcylindrica* to semi-arid environments.—Biol. Bull. mar. biol. Lab. Woods Hole **168**: 135-146.
- SMITH, W.K. & P.C. MILLER, 1973. The thermal ecology of two south Florida fiddler crabs: *Uca rapax* Smith and *U. pugilator* Bosc.—Physiol. Zool. **46**: 186-207.
- VERNBORG, F.J., 1959. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. II. Oxygen consumption of whole organisms.—Biol. Bull. mar. biol. Lab. Woods Hole **117**: 163-184.
- VON HAGEN, H.-O., 1962. Freilandstudien zur Sexual- und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien.—Z. Morph. Ökol. Tiere **51**: 611-725.
- WILKENS, J.I. & F. FINGERMAN, 1965. Heat tolerance and temperature relationships of the fiddler crab, *Uca pugilator*, with reference to body coloration.—Biol. Bull. mar. biol. Lab. Woods Hole **128**: 133-141.
- WOLCOTT, T.G., 1992. Water and solute balance in the transition to land.—Amer. Zool. **32**: 428-437.
- WOLFRATH, B., 1992a. Burrowing of the fiddler crab *Uca tangeri* in the Ria Formosa in Portugal and its influence on sediment structure.—Mar. Ecol. Prog. Ser. **85**: 237-243.
- , 1992b. Field experiments on feeding of European fiddler crab *Uca tangeri*.—Mar. Ecol. Prog. Ser. **90**: 39-43.
- , 1993. Observations on the behaviour of the European fiddler crab *Uca tangeri*.—Mar. Ecol. Prog. Ser. **100**: 111-118.
- ZWARTS, L., 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau.—Ardea **73**: 3-12.
- , 1990. Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time.—Ardea **78**: 279-300.
- ZWARTS, L. & A.-M. BLOMERT, 1990. Selectivity of Whimbrel feeding on fiddler crabs explained by component specific digestibilities.—Ardea **78**: 193-208.