

BURROW STRUCTURE AND USE IN THE SAND FIDDLER CRAB, *UCA PUGILATOR* (BOSC)

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Abstract. *Uca pugilator*, the sand fiddler crab, constructs two kinds of burrows in protected, sandy upper-intertidal and supratidal substrates on the west coast of Florida. Temporary burrows are built and used as a refuge by non-breeding crabs during high tide periods and at night when crabs cease feeding in the intertidal zone. Breeding burrows are constructed and defended by courting males and are the site of mating, oviposition and the incubation of eggs by females. Up to three ovigerous females may be accommodated in a single breeding burrow, each female sequestered in a separate terminal chamber. The construction and defence of burrows specialized for breeding may be an adaptive response by males to the preferences females exhibit when selecting a breeding site.

Uca pugilator (Bosc), the sand fiddler crab, constructs burrows on sandy shores in tidal marshes, bays and sounds from Cape Cod, Massachusetts to Corpus Christi, Texas (see e.g. Teal 1958; Smith & Miller 1973; Allen & Curran 1974; Crane 1975). Differences in an external feature of burrow morphology and in the use of burrows by breeding and non-breeding crabs suggest this species may construct two structurally and functionally distinct kinds of burrows: one used for breeding, the other a refuge for non-breeding crabs.

During the breeding season, reproductively active males dig, court from, and defend burrows in the upper-intertidal and supratidal zones (Crane 1975; Hyatt 1977; Hyatt & Salmon 1978; and references therein) for 6 to 8 days twice each lunar month when females choose mates (Christy 1978). Such males ('residents', Hyatt & Salmon 1978) defend their burrows from aggressive, wandering males during all tidal stages and court wandering females by 'waving' their single enlarged chelae and by 'rapping' them against the ground at their burrow entrances (see Salmon & Hyatt, in press, for a review). Sexually receptive females approach and descend the burrows of from one to about 15 residents before they choose a mate by remaining underground, whereupon the chosen male seals himself and the female into the burrow by closing its entrance with a sand plug (Hyatt 1977; Christy 1980). Previous authors have presumed mating occurs underground (e.g. Hyatt 1977; Salmon et al. 1978; but see Burkenroad 1947). About 14.5 days after choosing a mate, ovigerous

females emerge from the burrows around dusk (Hyman 1922; Christy 1978) and release larvae during high tide at night (Bergin 1978; DeCoursey 1979). This paper presents the first direct evidence that all stages of breeding occur in the burrows from which residents court (hereafter, 'breeding burrows'). Residents often construct a mound of sand shaped like a half-dome (a 'hood', Crane 1975, after Matthews 1930) over the entrance to their burrow (Salmon & Atsadies 1968; Crane 1975; Salmon et al. 1978).

In contrast, non-breeding crabs occupy burrows only during high tide. As the tide ebbs, they usually leave their burrows and feed near the water's edge (see e.g. Knopf 1966; Herrnkind 1968; Robertson et al. 1980). During flood tide, crabs stop feeding, returning to higher ground, enter an empty burrow or dig a new one and, usually, plug the burrow with sand. During the next low tide period they again emerge and feed (Knopf 1966; Herrnkind 1968; Hockett & Kritzler 1972). The burrows used by non-breeding crabs lack hoods. Since they are occupied only for short periods, they will be called 'temporary burrows'.

Although the sexes are synchronized in their reproductive activity, only about half of the females in a local population mate during each semilunar courtship period, some males do not court during every breeding cycle, and some court for only 1 or 2 days (Christy 1978, 1980). During the breeding season there always are some breeding and non-breeding crabs, and the two kinds of burrows can be found at the same site at any time.

Previous studies of the burrows of *U. pugilator* did not relate variation in burrow structure to

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how burrows were used (Dembowski 1926; Frey & Howard 1969; Frey & Mayou 1971; Allen & Curran 1974; Basan & Frey 1977). Consequently, only generalized descriptions of 'typical' burrows are available. The purpose of this paper is (1) to describe the morphology of the burrows of *U. pugilator*, (2) to describe how burrows are used during the breeding season, and (3) to relate burrow structure and use.

Study Site and Methods

Study Site

Burrow structure and use were studied during the summers of 1973–1976 on the southwest shore of Cayo Pelau, an island in Gasparilla Sound, located 2.4 km northeast of Boca Grande, Lee County, Florida. Crabs and burrows were common on several beaches and on sandy substrates beneath and behind the mangroves (*Rizophora mangle* and *Avicinia germinans*) that border the island.

Burrow Structure

The following aspects of burrows were studied: (1) the presence of hoods, (2) the presence, location and dimensions of chambers, (3) burrow shaft width in relation to crab carapace length and sex, (4) the angle of descent of the upper shaft, and (5) burrow depth and its relation to burrow elevation. Measurements were made on plaster or cement casts of burrows and on burrows I dug up. The angle of descent of a burrow is the acute angle formed between the surface of the sand and the axis of the upper shaft above any bends. Burrow width and crab carapace length (the distance from the posterior edge of the carapace to the apex of the rostrum) were measured with a vernier caliper rule to the nearest 0.1 and 0.02 mm, respectively. Burrow elevations were measured with a theodolite and are expressed relative to mean water level (MWL), calculated from tide heights recorded by a gauge mounted on a piling in the water adjacent to the study beaches.

Behavioural Observations

Marked and unmarked individuals were observed to determine how crabs used burrows. Crabs were marked by 'gluing' a numbered plastic tag to the carapace. Most observations of crabs were made on 300 females and 209 males in an enclosed portion of a natural population on a small beach ('White Beach'). The crabs were confined by a rectangular fence, 3 m wide by

6.5 m long, built from wire mesh and aluminium flashing. The long axis of the enclosure was perpendicular to the water's edge and the lower end extended to MWL. From 15 July to 21 August, 1976, I watched these marked crabs for an average of 5 h each day. Details of the construction of the enclosure and the methods for marking and observing crabs are reported elsewhere (Christy 1978, 1980).

An experiment was done to determine if males would court from and defend empty burrows that had been occupied by (1) a resident and had the hood intact, (2) a resident but had the hood removed, and (3) a non-breeding crab. On each of three days during ebb tide, five empty temporary burrows were located when non-breeding crabs left them to feed. Ten nearby breeding burrows were selected, the residents removed, and the hoods on five of the burrows destroyed. Each empty burrow was covered with a plastic cup. The cups were removed during flood tide when most crabs were seeking burrows, and the burrows that were occupied by males who defended them and used them as a site for courtship were noted. The results obtained on each of the 3 days have been pooled.

Burrow Excavations

The approximate sequence, duration and location of events during breeding were determined by digging up 48 natural and 10 artificial breeding burrows at intervals ranging from 5 min to 7 days after they were entered by females and then plugged by residents. Artificial burrows were made at the upper limit of the distribution of breeding burrows in the enclosure containing marked crabs by digging a pit about 20 cm in diameter to the depth of nearby breeding burrows (approximately 35 cm). A nylon cord was tied to a brass wire ring (4 cm in diameter) and passed through a length of pipe (2 cm in diameter). The end of the pipe with the ring was centred in the bottom of the pit, the pit was half filled with sand, and the pipe was wiggled to create a space at the bottom of the pit. The pit was then filled to the surface with sand. When the pipe was removed, the brass ring remained in the cavity at the bottom and the cord marked the shaft that was created. From 30 July to 12 August (the end of a period of courtship), marked residents courted from and defended these burrows and several females chose them as a breeding site (see below). I have assumed crabs used artificial burrows the same way they used natural burrows.

Morphological Correlates of Female Receptivity

Uca mate in the intermoult stage when females' gonopores are occluded by immobile, calcified opercula (Hartnoll 1968a). A female's opercula must be temporarily decalcified for intromission and oviposition to occur (Hartnoll 1968a; von Hagen 1970). If only females who remain with residents in breeding burrows possess mobile opercula, then this would indicate mating, oviposition, or both occur in breeding burrows. This possibility was studied by testing the mobility of the opercula of 136 feeding females captured on White Beach from 5 to 12 August, 1975, and 28 non-ovigerous females who were dug from breeding burrows in the enclosure built on White Beach in 1976. Opercular mobility was determined by probing the vulvae (Hartnoll 1968b) of each female with a blunt No. 0 insect pin. An operculum was judged to be mobile if the tip of the pin penetrated the vagina.

Results

Burrow Structure

Only courting males built hoods on their burrows. They used their walking legs, large chela and the dorsal surface of their carapace to tamp moist sand gathered from the surface or inside their burrow into the arching shape of a hood. When dry, hoods were more firm than when wet, presumably because sand grains were bound by salt crystals and the dried finer sediments. Dry hoods had the texture of fragile cement.

Although hoods were a characteristic feature of breeding burrows, the presence or absence of a hood had no effect on whether or not a male accepted an empty burrow for courtship. Males occupied and courted from 11 of the 15 (73%) burrows with hoods and 13 of the 15 (87%) burrows without hoods (log likelihood ratio test, Sokal & Rohlf 1969: $G = 0.847$, 1 *df*, $P > 0.10$). Males did discriminate between breeding and temporary burrows. Courting males occupied only two of the 15 (13%) empty temporary burrows while they accepted 24 of the 30 (80%) empty breeding burrows as courtship sites ($G = 19.486$, 1 *df*, $P \leq 0.005$). Males showed a strong preference for courting from burrows that had been occupied previously by residents. This suggests differences other than hoods may influence whether or not burrows are suitable for courtship.

Breeding and temporary burrows differed structurally (Fig. 1). The terminal 8 to 10 cm of

breeding burrows was expanded and formed a distinct chamber, averaging (\pm SD) 33.1 ± 2.81 mm high and 39.5 ± 3.69 mm wide, compared to an upper shaft diameter of 20 mm or less (measurements from 10 casts). Temporary burrows lacked chambers. The angle of descent of the two kinds of burrows differed significantly (Watson's U^2 test, Zar 1974; $U^2 = 0.645$, $P \leq 0.001$). Temporary burrows descended at an average angle of 79° (range = 47 to 90° , $N = 32$), whereas breeding burrows descended gradually at an average angle of 41° (range = 28 to 52° , $N = 10$). There was a significant positive correlation between the angle of descent and the depth of breeding burrows (Kendall's coefficient of rank correlation, Sokal & Rohlf 1969; $\tau = 0.527$, $N = 10$, $P < 0.05$), but no such correlation for temporary burrows ($\tau = 0.089$, $N = 34$, $P > 0.20$). Breeding burrow length and depth were not correlated ($\tau = 0.387$, $N = 10$, $P > 0.10$), suggesting the angle of descent of deep breeding burrows may be increased such that the lengths of all breeding burrows are nearly equal.

Breeding and temporary burrows differed in depth and the relationship between depth and elevation. Breeding burrows averaged (\pm SD) 27.1 ± 6.69 cm in depth (range = 17.5 to 34 cm, $N = 54$), whereas temporary burrows were significantly shallower, averaging (\pm SD) 9.8 ± 3.44 cm deep (range = 6 to 20 cm, $N = 34$) (Student's *t*-test: $t = 51.98$, 86 *df*, $P \leq 0.001$). Temporary burrow depth and elevation were not significantly correlated ($r = 0.31$, 32 *df*, $P > 0.05$). The depth and elevation of breeding burrows

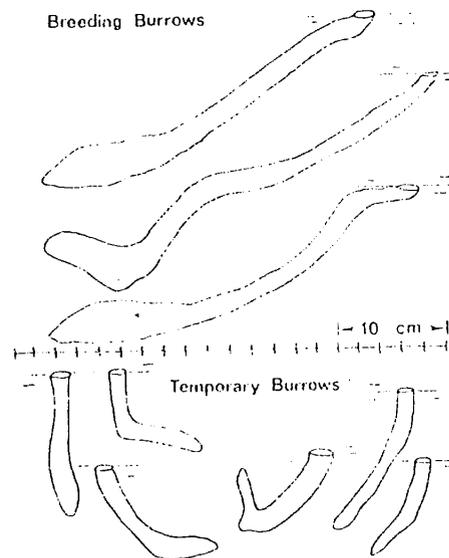


Fig. 1. Profiles of breeding and temporary burrows sketched from plaster casts.

were measured on two days when tides were relatively low (12.6 and 20.5 cm above MWL on 19 and 21 June, 1976, respectively) and on two days when tides were relatively high (25.3 and 25.9 cm above MWL on 25 June and 7 July, 1976, respectively; Fig. 2). Breeding burrow depth and elevation were not significantly correlated when tides were low ($r = 0.49$, 13 *df*; $r = 0.54$, 10 *df*; $P > 0.05$ for both days), but they were when tides were high ($r = 0.85$, 12 *df*; $r = 0.86$, 11 *df*; $P < 0.01$ for both days). Regressions of burrow depth on burrow elevation were calculated for both days when tides were high (Fig. 2). The elevations but not the slopes of the regression lines differed significantly (slopes compared: $t = 1.397$, 23 *df*, $P > 0.20$; elevations compared: $t = 4.453$, 24 *df*, $P < 0.001$). On these 2 days, low breeding burrows (35 to 45 cm above MWL) were shallow (mean \pm SD, depth = 20.7 ± 2.73 cm, $N = 7$) compared to the 2 days when tides were relatively low (mean \pm SD, depth = 26.3 ± 4.39 cm, $N = 7$). This difference is marginally significant (Mann-Whitney *U*-test, $U = 38$, $P = 0.05$).

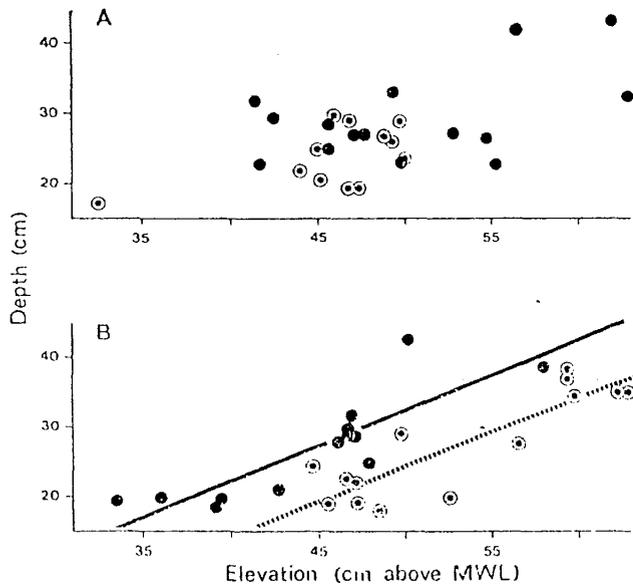


Fig. 2. Relationship between breeding burrow depth and elevation. A: samples from 19 (dots) and 21 (circled dots) June, 1976, when the tides were relatively low (12.6 and 20.5 cm above MWL, respectively) and burrow depth and elevation were not correlated (see text). B: samples from 25 June (circled dots) and 7 July (dots), 1976, when tides were high (25.3 and 25.9 cm above MWL, respectively) and there were significant positive correlations between burrow depth and elevation. Broken line: regression of burrow depth on elevation for 25 June, $Y = 0.93X - 22.31$ cm. Solid line: regression for 7 July, $Y = 1.03X - 19.04$ cm.

Burrow shaft diameter and crab length were significantly correlated for both males ($r = 0.74$, 40 *df*, $P < 0.001$) and females ($r = 0.90$, 17 *df*, $P < 0.001$), but the relationship between these variables differed between the sexes (Fig. 3). The elevations but not the slopes of the regression lines of breeding burrow diameter on male length and temporary burrow diameter on female length differed significantly (slopes compared: $t = 0.987$, 57 *df*, $P > 0.20$; elevations compared: $t = 2.285$, 58 *df*, $P < 0.05$). Comparison of the adjusted means (Snedecor & Cochran 1967) of burrow diameter shows a breeding burrow dug by a male of a given length was 1.85 mm wider than a temporary burrow dug by a female of the same length. This is because the effective length of a male is determined by carapace length plus the width of the flexed major chela adjacent to the buccal region.

Burrow Use by Non-breeding Crabs

Observation of activity cycles and burrow use by non-breeding crabs corroborate the reports of others (cited in introductory material). Non-breeding crabs occupied temporary burrows during high tide and, in the summer, during all tidal stages at night. During low tide they left

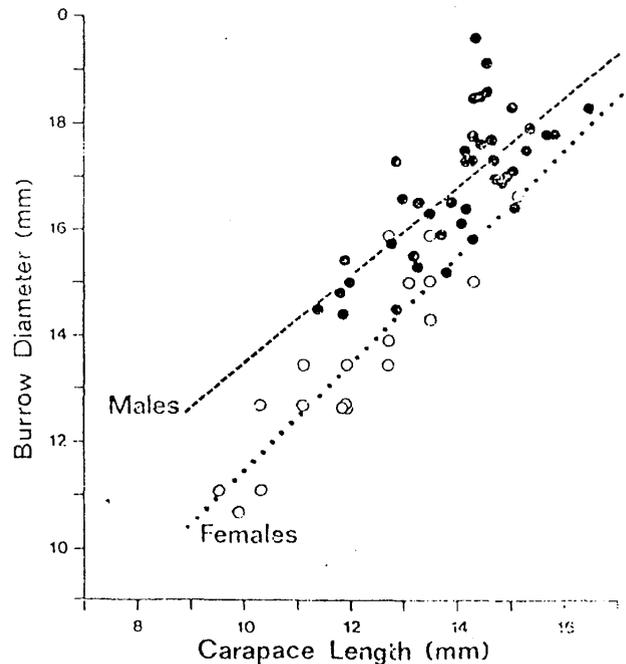


Fig. 3. Relationship between male carapace length and breeding burrow diameter (dots) and female carapace length and temporary burrow diameter (circles). Males, $Y = 0.84X + 5.12$ mm; females, $Y = 1.01X + 1.30$ mm; where Y = burrow diameter (mm) and X = carapace length (mm).

their burrows and fed in large aggregations low in the intertidal zone, where they were frequently exposed to predators, including raccoons (*Procyon lotor*), white ibis (*Eudocimus albus*) and portunid and xanthid crabs (Christy 1980). When they ceased feeding, crabs moved up-beach and occupied and plugged a burrow where they remained until they again emerged to feed.

Burrow Use by Breeding Crabs

Several lines of evidence indicate females mate, oviposit and incubate their eggs in breeding burrows. The incidence of females with mobile genital opercula depended strongly on whether they were dug from breeding burrows or captured from the feeding aggregation ($G = 42.264$, 1 *df*, $P \leq 0.005$). Twenty-five of the 28 (89%) females dug from breeding burrows had mobile opercula, while the opercula of 31 of the 136 (23%) feeding females were mobile. Fifty-four feeding females were captured on 12 August 1975, 1 day before the first quarter moon; 16 of these females had mobile opercula. Peaks of mating on White Beach in July and August, 1976, occurred during the quarter moons (Christy 1978). Some feeding females, especially those sampled on 12 August, may have mated the day they were tested, perhaps explaining the unexpectedly high proportion with mobile opercula. Twenty-seven ovigerous females were found in the terminal chambers of 48 breeding burrows that were plugged by residents after they attracted females. Eleven of these excavations were made from 2 to 7.5 days after females chose their mates. One marked female, who was dug from a breeding burrow 72.5 h after she chose a marked male as a mate, was observed while ovipositing. She was in the terminal chamber and had laid about one-half to one-third of her clutch, most of which had not yet adhered to the setae on the exopodites of her pleopods. Finally, analysis shows there was a marked bimodal distribution in the number of days females disappeared from the surface in the enclosure on White Beach (Fig. 4). Although most marked females were absent for 3 days or less (518 out of 767, 67.5%), 21.5% (165) disappeared for 10 to 23 days. The mean (\pm SD) length of absence for 30 females who were known to have mated was 14.5 ± 0.64 days (range = 11 to 17 days; Christy 1978). The remaining 135 females probably also disappeared for relatively long periods because they were breeding underground in burrows.

Excavations of artificial burrows revealed that a resident can mate sequentially with up to three females while defending the same burrow, and that each female oviposits and incubates in a separate terminal chamber (Fig. 5). The females who first mated with the residents at these burrows were found in the original terminal chambers which were marked with brass rings. One to 3 days after attracting a female, residents emerged, removed sand from the burrow, built a hood and continued to court, suggesting they dug a separate terminal chamber for each of their mates. Non-ovigerous females were never found in burrows from which a resident had emerged after attracting a female. This indicates a male remains underground with his most recent mate until she completes oviposition.

Discussion

The structural differences between breeding and temporary burrows may be attributed to their functional differences. A temporary burrow is a simple hole in the ground, a refuge that may provide escape from predators and potentially stressful environmental conditions when non-

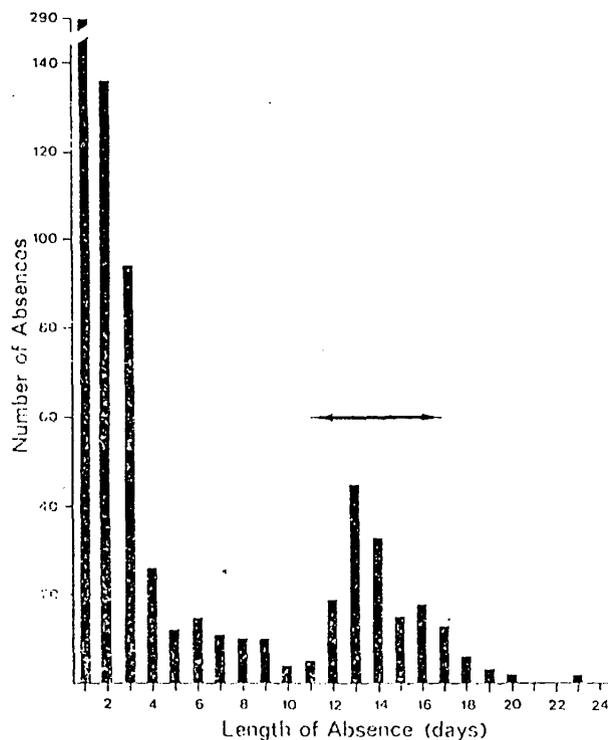


Fig. 4. Distribution of the number of days marked females were not seen in the enclosure on White Beach. The arrow indicates the range in the lengths of absences of 30 females who were known to have mated and produced a clutch of eggs.

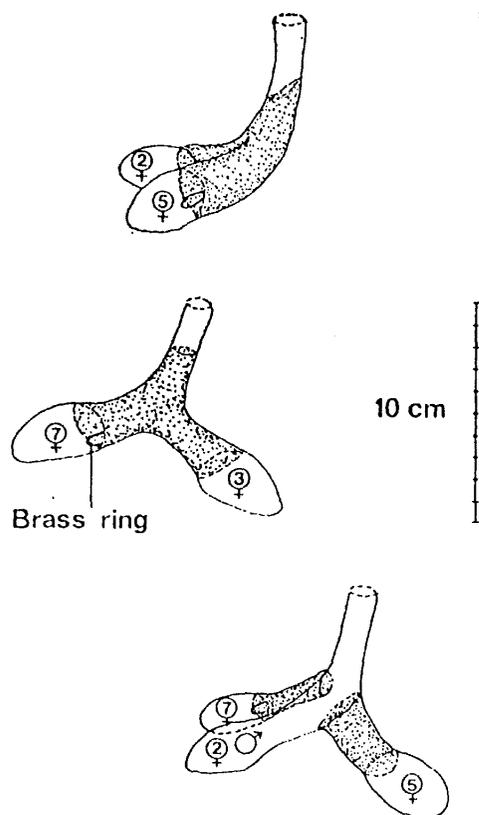


Fig. 5. Terminal chambers of artificial breeding burrows in which males mated with more than one female. The numbers on the female symbols are the number of days between when each female chose a mate and the day each burrow was dug up. A male was present only in the lower burrow, which was plugged at the surface, and only his most recent mate had not oviposited. Each male's first mate was located in the burrow's original terminal chamber (marked with a brass ring), which was created when the burrow was made. Oviporous females were isolated in separate chambers by loose sand plugs (stippling). (After a drawing by Wendy Beard-Allen.)

breeding crabs are not feeding. Some of the characteristic and more complex features of breeding burrows appear to be modifications that function during breeding and fights for burrows.

Hoods may aid males in burrow defence. Residents commonly brace themselves during combat by pressing their carapace against the inner surface of the hood. To evict a resident, the challenging male often must lift the defending male through the hood and out of his burrow (Hyatt & Salmon 1978). The mass of the hood and its cohesive texture when dry may increase the effective inertia of a resident and reduce the likelihood he will lose his burrow in combat. The gradual angle of descent of a breeding burrow may also aid residents in defence, though more

needs to be known about the mechanics of combat to decide if this is reasonable.

Breeding burrow depth and elevation were correlated only on the two days when tides were high and the depths of low burrows were reduced. Nearly all breeding burrows at the study site were in the supratidal zone. Measurements made on White Beach in 1976 of water levels in standpipes spaced along an elevation transect showed that maximum groundwater levels in the supratidal zone depended on maximum tide heights. Females lose eggs when made to oviposit in water or saturated sand, and when they chose breeding sites and mates they discriminated against burrows that would be flooded by groundwater and collapse during breeding (Christy 1979, 1980). Residents at low burrows may have reduced burrow depth when tides were high in response to the mating preferences of females. It is unclear why there was a significant difference between the elevations of the regression lines describing the relationship between burrow depth and elevation on 25 June and 7 July (Fig. 2). Comparison of the adjusted means showed that breeding burrows were 5.8 cm deeper on 7 July even though the tide was 0.6 cm higher. A total of 5mm of rain fell on the study site from 2 to 7 July, while 59 mm were recorded from 22 to 25 June. However, measurements on 25 June and 7 July showed groundwater levels were not affected by this difference in rainfall (Christy 1980). There was no significant relationship between temporary burrow depth and elevation, suggesting variation in groundwater levels is not important to non-breeding crabs.

The difference between the regression lines describing the relationship between resident size and breeding burrow diameter and female size and temporary burrow diameter has implications for the range in the size of females with which a male of a given size can mate. Data on the sizes of 85 pairs of mating males and females show that no females mated in breeding burrows with shafts narrower than those of temporary burrows used by females of their size (Christy 1980). In addition, there was no tendency for females to choose males of their own size as mates, as reported for *Uca rapax* (Greenspan 1980). It is clear from the horizontal distance between the two regression lines in Fig. 3 that a resident of a given size can mate only with females less than about 1.5 mm larger in carapace length.

The limits imposed by burrow diameter on the range of the sizes of females which a male can mate may be reflected in the courtship behaviour

of small males. Hyatt (1977) found that small male *U. pugilator* in North Carolina wave less than large males. Assuming mature males of all sizes encountered wandering females at equal rates, this suggests small males were, on the average, less likely to wave when they perceived a female than were large males. Perhaps small males court only females that are small enough to descend their burrows.

The expanded terminal chamber of a breeding burrow appears to be a modification to accommodate a breeding female. Males of most neotropical *Uca* court from and defend burrows to which wandering females come to mate (Crane 1975). Although little is known about the structure of these burrows, males of many species may construct burrows with chambers that are used for breeding (e.g. *Uca rapax*, Greenspan 1975). The exceptions within the genus are likely to be those species, primarily found in the Indo-Pacific, that mate near or in burrows occupied for long periods by comparatively sedentary females (Crane 1975). The construction and defence by reproductively active males of burrows specialized for breeding may be an adaptive response to the preferences mobile females exhibit when selecting a breeding site and a mate (Christy 1979, 1980).

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REFERENCES

- Allen, E. A. & Curran, H. A. 1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. *J. Sediment. Petrol.*, 44, 538-548.
- Basan, P. B. & Frey, R. W. 1977. Actual palaeontology and neoichonology of salt marshes near Sapelo Island, Georgia. In: *Trace Fossils 2, Geological Journal Special Issue 9* (Ed. by T. P. Crimes & J. C. Harper), pp. 41-70. Liverpool: Seel House Press.
- Bergin, M. E. 1978. Hatching rhythms in *Uca pugilator* (Bosc) (Decapoda, Brachyura) from North Inlet estuary, South Carolina. M.S. thesis, University of South Carolina.
- Burkenroad, M. D. 1947. Production of sound by the fiddler crab *Uca pugilator* Bosc, with remarks on its nocturnal and mating behavior. *Ecology*, 28, 458-462.
- Christy, J. H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: a hypothesis. *Science, N.Y.*, 199, 453-455.
- Christy, J. H. 1979. Resource-defense polygyny in the sand fiddler crab, *Uca pugilator*. *Am. Zool.*, 19, 933 (abstr. 432).
- Christy, J. H. 1980. The mating system of the sand fiddler crab, *Uca pugilator*. Ph.D. thesis, Cornell University.
- Crane, J. 1975. *Fiddler Crabs of the World, Ocypodidae: Genus Uca*. Princeton, N. J.: Princeton University Press.
- DeCoursey, P. J. 1979. Egg-hatching rhythms in three species of fiddler crabs. In: *Cyclic Phenomena in Marine Plants and Animals* (Ed. by E. Naylor & R. G. Hartnoll), pp. 399-406. Oxford: Pergamon Press.
- Dembowski, J. 1926. Notes on the behavior of the fiddler crab. *Biol. Bull.*, 50, 179-200.
- Frey, R. W. & Howard, J. D. 1969. A profile of biogenic sedimentary structures in a Holocene barrier island-salt marsh complex, Georgia. *Gulf Coast Geol. Soc. Trans.*, 19, 427-444.
- Frey, R. W. & Mayou, T. V. 1971. Decapod burrows in Holocene barrier beaches and washer fans, Georgia. *Senckenberg. Marit.*, 3, 53-77.
- Greenspan, B. N. 1975. Male reproductive strategy in the communal courtship system of the fiddler crab, *Uca pugnax*. Ph.D. thesis, The Rockefeller University.
- 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.
- Hagen, H. O. von. 1970. Anpassungen an das spezielle Gezeitenzonen-Niveau bei Ocypodiden (Decapoda, Brachyura). *Forma Functio*, 2, 361-413.
- Hartnoll, R. G. 1968a. Mating in the Brachyura. *Crustaceana*, 16, 161-181.
- Hartnoll, R. G. 1968b. Morphology of the genital ducts in female crabs. *J. Linn. Soc. Lond., Zool.*, 47, 279-300.
- Herrnkind, W. F. 1968. Adaptive visually-directed orientation in *Uca pugilator*. *Am. Zool.*, 8, 585-598.
- Hockett, J. C. & Kritzler, H. 1972. Capture-recapture methods with *Uca*. *Biol. Bull.*, 142, 49-56.
- Hyatt, G. W. 1977. Field studies of size-dependent changes in waving display and other behavior in the fiddler crab *Uca pugilator* (Brachyura, Ocypodidae). *Mar. Behav. Physiol.*, 4, 283-292.
- Hyatt, G. W. & Salmon, M. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. *Behaviour*, 65, 182-211.
- Hyman, O. W. 1922. Adventures in the life of a fiddler crab. *Rep. Smithsonian Inst.*, 1920, 443-460.
- Knopf, G. N. 1966. Observations on behavioral ecology of the fiddler crab, *Uca pugilator* (Bosc). *Crustaceana*, 11, 302-306.
- Matthews, L. H. 1930. Notes on the fiddler crab *Uca leptodactyla* Rathbun. *Ann. Mag. Nat. Hist., Series 10*, 5, 659-663.

- Robertson, J. R., Bancroft, K., Vermeer, G. & Plaisier, K. 1980. Experimental studies on the foraging behavior of the sand fiddler crab *Uca pugilator* (Bosc, 1802). *J. exp. mar. Biol. Ecol.*, **44**, 67-83.
- Salmon, M. & Atsadies, S. P. 1968. Visual and acoustic signaling during courtship by fiddler crab (genus *Uca*). *Am. Zool.*, **8**, 623-639.
- Salmon, M. & Hyatt, G. In press. Communication. In: *Biology of the Crustacea*, Vol. 4 (Ed. by D. E. Bliss), New York: Academic Press.
- Salmon, M., Hyatt, G., McCarthy, K. & Costlow, J. D. Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs *Uca panacea* and *U. pugilator*. *Z. Tierpsychol.*, **48**, 251-276.
- Smith, W. K. & Miller, P. C. 1973. The thermal ecology of two south Florida fiddler crabs: *Uca rapax* Smith and *U. pugilator* Bosc. *Physiol. Zool.*, **46**, 186-207.
- Snedecor, G. W. & Cochran, W. G. 1967. *Statistical Methods*. Ames, Iowa: The Iowa State University Press.
- Sokal, R. R. & Rohlf, F. J. 1969. *Biometry*. San Francisco, California: W. H. Freeman.
- Teal, J. M. 1958. Distribution of fiddler crabs in Georgia salt marshes. *Ecology*, **39**, 185-193.
- Zar, J. H. 1974. *Biostatistical Analysis*. Englewood Cliffs, N. J.: Prentice-Hall.

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