

## ECOLOGY AND EVOLUTION OF MATING SYSTEMS OF FIDDLER CRABS (GENUS *UCA*)

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### I. INTRODUCTION

In an earlier paper (1957), and again in her recent monograph (1975), Crane identified what appear to be major evolutionary trends in the form of male courtship displays and other behaviour associated with reproduction in 62 species of fiddler crabs. Crane approached behavioural diversity in the genus primarily from the viewpoint of a taxonomist. Over an approximately 30-year period, she accumulated extensive descriptive information, frequently based on film analysis, of the movements and postures exhibited during courtship and aggressive interactions. Interspecific comparisons revealed differences in displays that followed apparent grades from simple or primitive to complex or socially advanced. Grades in the complexity of social behaviour generally paralleled patterns of morphological change. The behavioural data figured prominently in her taxonomic revision of the genus, while her views on relationships and phylogeny (Crane, 1975, chapter 7) have fared well in the light of recent biochemical evidence (Albrecht & von Hagen, 1981).

In contrast to the wealth of descriptive information on courtship displays, little is known about patterns of social organization and mating systems. In her monograph, Crane provides useful notes, based primarily on incidental observations made during collecting trips, on habitats, movement patterns, territoriality, precopulatory behaviour, and the locations of matings. These observations suggest a pattern of differences in mating systems among species that broadly correlates with grades in the complexity of courtship displays, differences in habitat, and phylogeny. Even less is known about the selection pressures that give rise to the differences in mating systems because, until recently, no attempt had been made to measure the reproductive success of individuals or to study the effects of ecological factors and social interactions on female breeding success and male mating frequency.

Our purpose in this paper is to (1) critically evaluate what is known about the evolution of reproductive behaviour in the group, (2) summarize and contrast our recent field studies on the mating systems of *Uca pugilator* (Bosc) and *U. vocans* (L.), and (3) based upon these studies, indicate how differences in key ecological features of these two species may account for basic differences in patterns of sexual selection, and hence, male and female reproductive behaviour in the genus. We recognize that extrapolation from two species to a group consisting of over 60 taxa is risky. On the other hand, our subjects occupy very different habitats, are distantly related and lie near opposite ends of Crane's ordination of species from primitive to complex. Furthermore, what little is known about other species suggests that while the details of their behaviour vary, their similarities to one of the two major patterns we describe outweigh the differences. Thus, our general framework may provide the first useful step toward testing how evolutionary processes may have given rise to the broad contrasts Crane discerned in the reproductive behaviour of all fiddler species.

## II. EVOLUTIONARY TRENDS

Fiddler crabs occur in the intertidal and supratidal zones of protected shores in estuaries, bays and sounds in tropical, subtropical and warm temperate regions throughout the world. Crane (1975) recognized 62 species which she assigned to nine subgenera. *Deltuca* (8 spp.), *Australuca* (3 spp.), *Thalassuca* (3 spp.), and *Amphiuca* (2 spp.) are confined to the Indo-Pacific where, Crane has argued (Crane, 1975, chapter 1), the genus most likely arose. Two subgenera contain a single species: *Boboruca*, which occurs in the west Atlantic and on the eastern Pacific coast of Central America, and *Afruca*, which occurs along the Atlantic coast of Africa. *Uca* (6 spp.), *Minuca* (12 spp.) and *Celuca* (26 spp.) occur in the Americas. Two additional *Celuca* species occur in the Indo-Pacific.

All *Uca* are sexually dimorphic. Females possess two small claws which they use to convey bits of substrate to their mouthparts when they feed. In contrast, only one claw of the male is used for feeding; the other is greatly enlarged, accounting for up to 48% of the body weight of a large adult (Altevogt, 1955 *a, b*; Christy, 1980). Males use their major chelae in the contexts of defence and threat, intermale combat and courtship. The most conspicuous display of the male ('waving' or 'beckoning') is a rhythmic elevation and lowering of the major chela which probably subserves both threat and epigamic functions in many species. Waving follows two basic spatial patterns; vertical, in which the flexed chela is raised and lowered in a single plane in front of the body, and lateral,

in which the chela is both raised vertically and extended outward to the side, then returned. Addition of chela jerking and circular motions, 'special steps' during the wave, and differences in the planes of extension and flexion create additional spectra of variation in the wave.

Crane (1975) constructed a likely phylogeny of the genus based on differences in the form and complexity of male waving display and on detailed comparisons of morphology. *Deltuca* and *Australuca* are closest to the hypothetical ancestral form. Species in these subgenera tend to occur on muddy substrates along tidal streams near or under mangrove cover. They show a number of morphological features suited to mud-living. Both sexes tend to be sedentary and lethargic. When uncovered by the receding tide, crabs emerge from and feed near their burrows into which they retreat periodically for brief periods. Both sexes interact aggressively with their neighbours, though threat and combat are most prevalent in males. Most species exhibit simple vertical waves. Copulation occurs on the surface near a burrow occupied by a female. Males may or may not wave as they approach females for mating. *Thalassuca* and *Amphiuca*, which show morphological affinities to the more primitive Indo-Pacific subgenera, tend to occur higher in the intertidal zone or on more exposed substrates. They generally are more active socially. Their waves are mainly vertical but the *Amphiuca* show a tendency to include lateral movements. Copulation still occurs on the surface but is often preceded by waving.

The American subgenera may have been derived from stock ancestral to the *Thalassuca*, following one or more migrations across the Behring land bridge. With the exceptions of *U. (Borboruca) thayeri* Rathbun and the two *Celuca* that occur in the Indo-Pacific (*U. triangularis* (A. Milne-Edwards) and *U. lactea* (De Haan)), all American subgenera exhibit lateral waving displays, as does *U. (Afruca) tangeri* (Eydox). American *Uca* occupy the full range of habitats present on protected shores. The *Minuca* are ecologically most similar to the *Deltuca* though *U. pugnax* (Smith) and especially *U. rapax* (Smith) tend to occur in more exposed areas and on sandier substrates, and the ecologically unique *U. panamensis* (Stimpson) occurs on cobble beaches. Species in the subgenera *Uca* and *Celuca* occur on partially shaded or open sandy-mud to sand substrates, and several burrow in the upper intertidal and supratidal zones. Although many American species probably emerge during low tide and feed near their burrows, individuals of several species are known to leave their burrows after nearby substrates have begun to dry, and move to the water's edge or moist areas in the lower intertidal zone to feed. This behaviour is apparently common in *U. (Celuca) pugilator* and *U. (Afruca) tangeri*, where feeding crabs form dense shifting aggregations (droves) low in the intertidal zone, often several meters away from the nearest burrows. Aggregations of feeding crabs also occur in *U. rapax* (Greenspan, 1975), *U. pugnax* and *U. minax* (Le Conte) (personal observations), and have recently been reported for *U. (Thalassuca) vocans* at a site in Japan (Nakasone, 1982; Murai, Goshima & Nakasone 1983). Unfortunately, movements associated with feeding have not been recorded systematically, so the occurrence of this behaviour in the genus is poorly known.

Precopulatory behaviour and the site of mating in the American subgenera contrast sharply with that of their Indo-Pacific relatives. Reproductively active males court from burrows often located near the upper limits of the distribution of a species along the elevation gradient (von Hagen, 1970; Crane, 1975). Courting males threaten and fight

their neighbours and aggressive wandering males who are seeking burrows. Sexually receptive females wander through the array of courting males, approach several, and follow them into their burrows before they choose their mates by remaining underground. Males so chosen return to the surface briefly and close their burrows with a plug of substrate, sealing both themselves and their mates underground where mating is known or presumed to occur. Surface copulations have been reported for a few species and locations (Crane, 1975, p. 500), but are apparently the exception rather than the rule.

Major differences in morphology, complexity of the waving display, levels of activity, and broad patterns of mating behaviour codified in Crane's phylogeny of *Uca* appear to be associated with changes in terrestriality. This is especially evident when one compares the Indo-Pacific *Deltuca* with the American *Celuca*. Crane noted that species that burrow high in the intertidal zone are active for longer periods per tidal cycle than species that burrow at lower levels, and hence have more time for prolonged aggressive interactions and courtship sequences. While probably true, this observation provides little insight into the selective factors favouring the development of complex displays in the more terrestrial species. Time may be a necessary condition permitting high levels of male social activity, but does not in itself explain why or how long and complex social interactions might enhance male fitness in the selective contexts of male-male competition for females, or female choice of mates. Since, in all fiddler crabs, female parental investment exceeds male, no hypothesis based entirely upon male behaviour and ecology can satisfactorily account for the evolution of basic patterns of sexual behaviour. A reappraisal of the behavioural ecology of reproduction is necessary, especially with reference to factors that might influence patterns of female choice. These considerations were important in our analyses of the mating systems of *U. pugilator* and *U. vocans*. In the following sections, we summarize these studies.

### III ECOLOGY AND REPRODUCTIVE BEHAVIOUR OF *U. PUGILATOR*

#### (1) *Distribution*

*U. (C.) pugilator* is abundant on protected shores in estuaries, bays and sounds from Cape Cod, Massachusetts, to western Florida (Salmon *et al.*, 1978). The burrows of this species tend to be most abundant in exposed and lightly vegetated sand and muddy-sand substrates in the upper intertidal zone in both salt marsh (Montague, 1980, and references therein; Colby & Fonesca, 1984) and mangrove (Smith & Miller, 1973) habitats. In salt marshes on the east coast of the United States *U. pugilator* also burrows lower in the intertidal zone along exposed sandy banks of tidal creeks (Teal, 1958). The following synopsis of the reproductive ecology and behaviour of *U. pugilator* is based primarily on a study zone done during the summers of 1973-1976 on several small (3-20 m wide) sand beaches on a mangrove island (Cayo Pelau) located in Gasparilla Sound on the west coast of Florida (Christy, 1978; 1980; 1982*a*; 1983). At this site the burrows of *U. pugilator* occur primarily in the supratidal rather than the intertidal zone. Comparative data on the ecology and mating behaviour of intertidal populations of *U. pugilator* in North Carolina (Salmon & Hyatt, 1983) indicate that spatial aspects of the mating system of this species, but not its general form, vary with the location of *U. pugilator* on the elevation gradient.

## (2) Behaviour of nonbreeding crabs

During the breeding season (March–October in southern Florida (Christy, 1980); April–September in South Carolina (Christy, 1982b)) two broad classes of animals could be distinguished by differences in their behaviour. During high tide and during all tide stages at night in mid-summer, most nonbreeding crabs occupied shallow (mean = 9.8 cm, range = 6–20 cm), nearly verticle (mean angle of descent = 79°) burrows ('temporary burrows', Christy, 1982a) in the upper intertidal and supratidal zones (30–60 cm above MWL; MHWS: 32–35 cm above MWL) on the sand beaches on Cayo Pelau. From 3–4 h after slack high water, crabs emerged from temporary burrows, walked several meters down-beach to the water's edge, and began to feed on substrates at MWL to about 5 cm below MWL. Nonbreeding crabs fed in dense shifting aggregations low in the intertidal zone until approximately mid-flood tide (or dusk) when they returned to the burrow zone, usually in groups or waves, and occupied empty temporary burrows or dug new ones where they remained until the next diurnal low tide. Nonbreeding crabs defended their burrows briefly while digging, repairing and closing them with a sand plug. Occupants sometimes were evicted and forced to look for other burrows. Occasionally 2–5 crabs shared a temporary burrow, though most were occupied by one crab. Nonbreeding crabs usually found and plugged burrows within 1 h after they stopped feeding.

Crabs who were not associated with a burrow, either because they were feeding in the intertidal zone or wandering in the zone with burrows, appeared to be much more susceptible to predation than crabs who occupied or were near burrows. Twenty species were observed preying on *U. pugilator* on the beaches of Cayo Pelau, including 16 species of birds, racoons (*Procyon lotor* (L.)), the xanthid crabs *Panopeus* sp. and *Eurytium limnosum* (Say) and an unidentified portunid crab. Only racoons, willets (*Catoptrophorus semipalmatus* Gmelin), whimbrels (*Numenius phaeopus* L.), and laughing gulls (*Larus atricilla* L.) occasionally took crabs near or in their burrows. Crabs in exposed areas away from burrows attempted to escape predators by burrowing rapidly 2–3 cm into soft mud, burrowing underneath tidal wrack, or moving into areas where the pneumatophores of *Avicinia germinans* L. or the prop roots of *Rizophora mangle* L. provided cover. Observations of the sex of the crabs eaten by an individual immature white ibis (*Eudocimus albus* L.) indicated this bird preferred to eat females. Males tended to move away less often from hunting birds and to move shorter distances than females, suggesting other avian predators may have shared a preference for females. Temporary burrows probably function primarily as refuges from predators and, perhaps, stressful environmental conditions when nonbreeding crabs are not feeding.

Although most nonbreeding crabs alternately fed and occupied temporary burrows, some males (20–50% of the maximum number feeding at low tide) continued to feed at the water's edge during high tide. In the laboratory, male *U. pugnax* ingest food at about half the rate of females because they have only one claw which they can feed, but they feed for about twice as long (Valiela *et al.*, 1974). This may explain, in part, why males, but not females, tended to feed during all tide stages. Other contributing factors may include especially strong selection on non-breeding males to maximize their nutrient or calorie intake, and lower rates of predation by some of the common avian predators on feeding males than on females.

*(3) Behaviour of reproductively active males*

In contrast to the tide-related movements of feeding crabs, reproductively active males spent most of their time in the supratidal zone where they fought for, defended and courted from burrows that were the site of mating, oviposition and incubation of eggs by females (Christy, 1982*a*). Such breeding burrows differ structurally from the temporary burrows used as refuges by feeding crabs. Breeding burrows are deeper (mean = 27.1 cm, range: 17–54 cm), descend more gradually (mean angle of descent = 41°), and are characterized by expanded terminal chambers and half-dome-shaped hoods at their entrances. Reproductively active males did not accept empty temporary burrows as courtship sites, but they readily courted from and defended empty breeding burrows with or without intact hoods (Christy, 1982*a*), indicating the underground structure of breeding burrows broadly determines their suitability as breeding sites.

Two classes of reproductively active males can be distinguished (Crane, 1957; Hyatt & Salmon, 1978): wanderers, who seek breeding burrows, and residents, who court from and defend breeding burrows. Males become wanderers when they first enter a period of reproductive activity or when they abandon breeding burrows or lose them in combat. Wanderers attempted to obtain breeding burrows by digging new ones, winning them by fighting residents or by dashing rapidly into open burrows when residents were active on the surface several centimeters from their burrow entrances.

Analysis of combat outcome in relation to the size of competing wanderers and residents revealed that residents won 99% (Hyatt & Salmon, 1978) to 100% (Christy, 1980) of their fights when larger, and 30% (Christy, 1980) to 76% (Hyatt & Salmon, 1978) of their fights when smaller, than the challenging wanderers. When turnovers in burrow ownership occurred, however, wanderers were almost always larger (carapace width, CW) than the residents they defeated (93% (Christy, 1980) to 98% (Hyatt & Salmon, 1978) of the time). Consequently, the distribution of males by size should reflect spatial and temporal effects of competition among wanderers and residents for breeding sites.

In general, significant positive correlations occurred between resident size and burrow elevation or distance above the mean water mark on the beaches of Cayo Pelau. Such correlations were especially strong during periods with high tides and when many males were competing for breeding burrows. Sexually mature males in five size classes (13.0–23.0 mm CW) were allowed to establish burrows without competition from larger males. All preferred to court from burrows at the same up-beach elevations. In other experiments, reproductively active males of different sizes were placed in high breeding burrows. They accepted them as courtship sites, but small residents were rapidly displaced by large wanderers. These results suggest that the correlation between resident size and burrow elevation is established and maintained through contest competition for burrows located high on the beach.

Although most aggressive interactions occurred between wanderers and residents, residents also threatened and fought their neighbours. Hoods impart direction to the entrances and upper shafts of breeding burrows. Most residents spent over 90% of their surface time within  $\pm 90^\circ$  of the axes formed by their burrow shafts and within 5 cm of their burrow entrances, though courtship occurred at all locations and at greater

distances. There was a significant negative exponential relationship between inter-burrow distances and rates of aggressive interaction between neighbouring residents. Residents separated by distances of 16 cm or more interacted little or not at all. Orientations of neighbouring breeding burrows probably also affected interaction rates, though this was difficult to demonstrate because burrows of close neighbours (< 10 cm) tended to face away from each other.

Aggressive interactions between neighbours did not appear to affect time budgets or patterns of space use of smaller or less aggressive residents in ways that reduced their chance of attracting females. Residents were sometimes successful, however, in forcefully evicting close neighbours who faced them, or in causing them to abandon their burrows. Winning residents usually destroyed their previous neighbours' burrows by filling them with sand and tamping the surface smooth around their entrances (see also Zucker, 1977). Such behaviour contributed to an even dispersion of burrows over a broad range of densities (4.4–35.0 residents/m<sup>2</sup>) and a tendency for the burrows of nearest neighbours to face away. Residents frequently attempted to disrupt courtship sequences of neighbours by fighting them or displacing the females they attracted. Residents whose neighbours were distant and faced away were disrupted during courtship significantly less often than those whose neighbours were near and faced toward them. Hence, aggression between residents may function primarily to increase the frequency with which males court females successfully.

Individual males exhibit alternating 6–8 d cycles of reproductive activity (competing for and courting from a breeding burrow), followed by feeding and occupation of temporary burrows. Wandering males sometimes fought for burrows on the same days they fed in the intertidal zone. Residents, however, never fed near their breeding burrows. But, when provided experimentally with either moist or air-dried substrate collected from intertidal areas where nonbreeding crabs fed, residents fed readily. Preliminary experiments demonstrated the amount of time residents spent at breeding burrows could be lengthened by periodically provisioning them with material scraped from intertidal substrates. These observations suggest the rate at which males accumulate energy and nutrients when feeding determines the amount of energy and time they can expend on reproductive activities. More generally, the cyclic reproductive behaviour of males may be, in part, a consequence of the disjunct distributions of areas in which crabs feed and those in which burrows that are preferred by females as breeding sites can be constructed (see below).

Males were synchronized in their reproductive activity. Peaks of courtship occurred twice each lunar month, about 5 days before each spring tide. Semilunar timing of male reproductive activity probably is an adaptive response to semilunar variation in the abundance of receptive females.

#### (4) *Reproductive behaviour and cycles of females*

Female *U. pugilator* also exhibited cycles of reproductive activity. However, in contrast to males, individual females bred approximately once per lunar month (Christy, 1978). Non-breeding females fed and occupied temporary burrows for about 2 weeks. During this time, their gonopores were shielded by (immobile) opercula which prevented insemination. Presumably after accumulating reserves sufficient to produce a clutch of eggs, females began to respond to courting males by approaching them and

following them into their burrows ('sampling'). Such females usually had decalcified opercula.

On the days females chose their mates, most sampled males and breeding burrows immediately after emerging from temporary burrows, though some sampled as they ascended the beach after feeding. Females spent about 9.5 min sampling 1-18 males and burrows before choosing their mates by remaining underground. Females moved rapidly between burrows as they sampled and they often paused by and partially entered temporary burrows where they retreated when disturbed. A few minutes after females chose their mates, the males closed the entrances and upper shafts of their burrows with sand plugs, sealing both themselves and their mates underground. Excavations made a few minutes to 7.5 days after females chose their mates revealed that all stages of breeding (copulation, oviposition and incubation) occur in the expanded terminal chambers of breeding burrows. Residents who mated opened their burrows after their mates had completed oviposition, 1-3 days after plugging them. Males who remained at their burrows after mating dug new terminal chambers and built new hoods on their burrows, isolating their mates with loose sand plugs in the original terminal chambers. Some males mated sequentially with 2-3 females while defending the same burrows, each female occupying a separate terminal chamber. Most females remained underground for 14.5 days before finally emerging at dusk or soon thereafter and walking to the water's edge. Though larval release was not observed at the Florida site, it probably occurred near the time of the nocturnal high tide (DeCoursey, 1979; Bergin, 1981; Christy & Stancyk, 1982). Ovipigerous females were rarely seen moving about or feeding on the surface; it seems unlikely that females fed much while incubating underground.

Within a local population, there were two groups of females who bred during alternate semilunar periods. On Cayo Pelau peaks of mating occurred about 5 days before each spring tide, with peaks of larval release during neap tide periods. On the mid-Atlantic coast of the United States larval release by *U. pugilator* and several other estuarine brachyurans occurs predominantly during spring tide periods (Wheeler, 1978; Dollard, 1980; DeCoursey, 1981; Christy, 1982*b*; Christy & Stancyk, 1982; Salmon & Hyatt, 1983). Although the phase relationship between the time of larval release and the semilunar cycle differs between the Gulf and the Atlantic coasts, females at all sites release larvae predominantly during periods when high tides occur shortly after sunset and when the amplitudes of nocturnal ebb tides reach semilunar maxima. This results in rapid transport of larvae by nocturnal ebb-directed currents away from the upper estuary and, at some sites, into the coastal ocean (Christy & Stancyk, 1982). The timing of larval production may be an adaptive response to selective factors such as lethal combinations of temperature and salinity or predation by diurnal plantivores that cause high larval mortality during the day in the upper estuary (Christy, 1982*b*).

##### (5) *The mating system*

Patterns of female choice in *U. pugilator* were studied with respect to two variables: the elevation or distance of breeding burrows above MWL, and the size of courting residents. The elevation of breeding burrows was chosen as a potentially important variable because males compete for burrows located high on the beach, and because patterns of competition among males ought to reflect female mating preferences. Female choice based on male size was studied because size is correlated with the ability of males

to compete for breeding burrows, their ability to defend their mates during the early stages of breeding, male mating success, age, and by inference, genetic quality.

Analysis of reproductive activity and mating patterns among marked crabs in an enclosed portion of a natural population revealed great temporal variation in the locations of matings and large males during two consecutive mating periods. When tides were relatively low, females mated in breeding burrows located over a broad range of elevations, males of all sizes had space to court from burrows at the elevations females preferred, and the males who mated were not significantly larger than those who failed to attract mates. In contrast, when tides were relatively high, females preferred to breed higher on the beach where larger males tended to court and from which smaller males had been excluded. Under these circumstances, the males that mated were larger than those that did not. Under no circumstances, however, did females show a preference for mating with larger males among those defending burrows at the elevations where they preferred to breed.

Measurements of surface and groundwater levels revealed that by mating high in the supratidal zone, most females chose burrows that were neither inundated by the tide nor flooded by groundwater, during mating and oviposition if not their entire breeding periods (Christy, 1983). *U. pugilator* from North Carolina produce relatively large clutches (mean = 10250 zoeae, female carapace width 1.00–1.95 cm) (Salmon & Hyatt, 1983). These protrude beyond the margins of the space between the abdomen and sternum, even when newly laid (Fig. 1). Females are especially susceptible to egg loss if they are physically disturbed during oviposition when their eggs have been extruded from their bodies but have not yet attached to their abdominal appendages. Choice of high burrows probably is a result of selection against females who loose eggs because they oviposit in burrows that flood or collapse. A few ovigerous females chose low burrows. They left them when they were flooded by groundwater and collapsed, and moved to higher burrows. These observations suggest females probably also require stable burrows in which to incubate their eggs successfully but may be unable to choose such burrows with certainty because few reliable cues of long-term burrow stability are available when they choose mates and breeding sites (Christy, 1983).

There are several possible reasons why females do not prefer larger males among those defending burrows of equal quality, as measured by their structural stability during breeding. First, variation in the size of males defending high quality burrows may often be so small (mean coefficient of variation of the length of the propodus (the fixed finger on the major chela) for two 6-day mating periods = 6.11 %) that females gain little by choosing relatively large males. Second, temporal variation in the magnitude of male size variation (range, daily coefficient of variation of the propodus length: 1.89–24.55 %) at high quality burrows may make it difficult for females to predict when they would gain most by choosing larger males. Third, costs to females that sample long enough to choose a male above average in size among those available at high quality burrows may exceed the gains. Costs associated with long sampling bouts may include an increase in the risk of predation and, since females exhibit semilunar, diel and tidal synchrony in mate choice, a decrease in the chance of finding a suitable breeding burrow due to choice by other females. Finally, male size may be only weakly correlated with genetic quality.

Although females show no preference for mating with large males, male size and

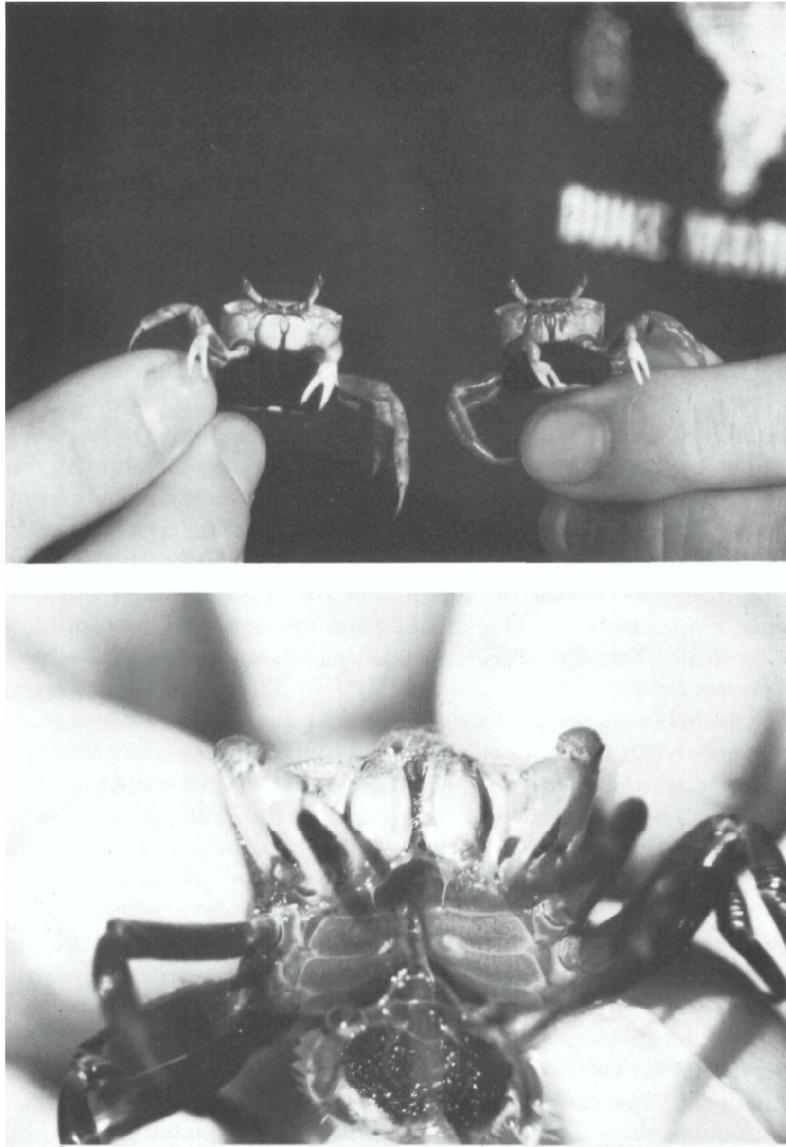


Fig. 1. Typical clutch sizes for *U. pugilator* (above) and *U. vocans* (below).

mating frequency were significantly positively correlated. Large males mated more often than small males because they spent more time each mating period courting from and defending burrows located at the elevations where females preferred to mate. Large males also tended to court from preferred breeding sites on days receptive females were most abundant during the semilunar cycle. Sexual dimorphism in chela size and morphology in *U. pugilator* appear to be maintained through the selective advantages that males with large claws enjoy in the context of competition for a resource females

require in order to breed successfully. *U. pugilator's* mating system may be classified as resource-defence polygyny, with males acting as contest competitors for breeding sites that females prefer.

#### IV. ECOLOGY AND REPRODUCTIVE BEHAVIOUR OF *U. VOCANS*

##### (1) *Distribution*

*U. (Thalassuca) vocans* occurs throughout the tropical western and Indo-Pacific (Crane, 1975). It is most abundant on exposed muddy flats seaward of the mangrove fringe, extending in elevation from approximately MHWN to somewhat below MLWN (Macnae, 1966; Crane, 1975; Hartnoll, 1975; Icely & Jones, 1978; Frith & Brunenmeister, 1980). Alcock (1892, 1902), Pearse (1912), and Altevogt (1955*a*, 1955*b*) provided general accounts of the behaviour of this species. More recently, Zann (1978) has described spatial distributions and agonistic behaviour of *U. vocans* on the eastern Australian coast, and Nakasone (1982) and Mauri, Goshima & Nakasone (1983) have described daily activity patterns and feeding movements on Okinawa Island. The only detailed description of the reproductive ecology and mating system of *U. vocans* comes from a single study carried out from October 1981 through February 1982 on a population at a site approximately 1.0 km from Cape Ferguson, Chunda Bay, Queensland (Salmon, in press). The following summary is based on this study.

The Chunda Bay study site was an exposed mud-sand beach bordered above by a mixed stand of *Avicennia* and *Sonneratia* mangroves. *U. vocans* occupied burrows in the lower 6 m of the intertidal zone. Larger adults occurred in two spatially defined colonies, about 50 m apart, and each small enough to be contained within 4 × 4 m grids. The substrate in the East Colony consisted of a muddy sand layer 10–15 cm deep with a few large rocks over a layer of coarse shell, rocks and sand. Large females and males ( $CW > 1.80$  mm) were most abundant where *Sonneratia* roots and pneumatophores were dense (about  $\frac{1}{3}$  of the colony area). The West Colony was located in a slightly elevated (2–3 cm) area with a deeper (20–25 cm) upper layer of muddy sand that lacked roots or rocks near or on the surface. Smaller adults were most abundant in the 'flat' between the two colonies, as well as above them in higher, more sandy, areas.

##### (2) *Movements, feeding and burrow defence*

Some male and most female *U. vocans* defended burrows to which they returned every few minutes when active on the surface during low tide. The sexes exhibited several agonistic behaviours in common, including waving, often thought to be restricted to males. These involved various movements and postures of the walking legs and chelae. The latter in both sexes were identically and brightly coloured in combinations of orange, pink, violet and white. Some acts were restricted to each sex. Carapace pushing and kicking were employed in combats between females, while several forceful movements of the major chelae were used in male-male fights. Aggressive interactions between the sexes were relatively infrequent. Males fought both their neighbours and, more commonly, wandering males. In contrast, most female fights occurred when neighbours met in foraging areas between burrows. Most combats between males (89%) and between neighbouring females (72%) were short (< 15 sec). Though uncommon (17%), half of the fights between resident and wandering females were relatively long (16 sec to > 1 min).

Both sexes changed burrows frequently. However, females remained at their burrows for significantly longer periods than did males. For example, 81 % of moves by males to new burrows occurred within 1–4 days of residency, while only 47 % of the burrow changes by females occurred before they had spent 4 days at the same burrow. The distances individuals moved to new burrows varied greatly. However, males moved long distances (6–30 m) more often than did females. Females in high density areas tended to move more often than females with fewer neighbours. The frequency with which males changed burrows appeared unaffected by density, but increased during spring tide periods.

Soon after the tide uncovered their plugged burrows both sexes emerged. Females then immediately fed near their burrows while males walked and fed some distance from their burrows while courting females. As the ground near their burrows dried, females sallied further from their burrows, returning to enter them, usually for brief (< 30 sec) periods, every 60–80 sec. Females moved up to 1 m from their burrows to feed in moist depressions or along the edge of a tidal stream. When feeding in moist areas, females frequently scraped up small amounts of substrate with their walking legs and carried this material into their burrows. Males who courted exhibited little if any carrying behaviour, feeding instead in low moist areas during low tide, and as they sallied from their burrows and courted females at the beginning and the end of their activity periods.

We believe such 'carrying' behaviour functions to provision burrows with relatively food-rich material on which females need during high tide (see also Nakasone, 1982). Several observations support this contention indirectly. First, it is possible for *U. vocans* to feed underground during high tide because air remains trapped in their plugged burrows and most burrows probably remain intact even when inundated. Second, although females sometimes gathered substrate to repair and plug their burrows, such material was always obtained from areas near their burrows. Third, resident male *U. pugilator*, who never fed near their burrows (or elsewhere), exhibited identical carrying behaviour when presented experimentally with food-rich substrate from the lower intertidal zone.

### (3) Mating behaviour

Male *U. vocans* used several techniques to obtain mates. Most (80 %) courtships leading to copulations were initiated when wandering or resident males approached females active on the surface near their burrows. Males often did not wave as they approached potential mates. Females responded to rapid approaches by moving immediately back and just into their burrow entrances. When approached slowly or by small males, females usually remained on the surface near their burrows. Females sometimes threatened approaching males but they rarely deterred them. Courting males touched and stroked the lateral and dorsal surfaces of their potential mates with their walking legs and minor chelae. Stroking bouts lasted 20 sec to several min. More than one stroking bout usually occurred before the female faced the male directly, lowered her abdomen and permitted copulation. Copulation lasted from 3–7 min. Copulating males slowly rocked from side to side which presumably aided in intromission and sperm transfer.

Females who were wandering through the colony, either because they were changing burrows or because they were gathering substrate to provision their burrows, evoked

'herding' behaviour (Crane 1975, p. 496) by some courting males. Herding males attempted to direct the paths of passing females to their own or nearby empty burrows. Often several males simultaneously herded a single female. Both sexes usually waved during herding. Wandering females also sometimes elicited 'out and back' courtship, which began when a resident walked several centimeters away from his burrow and paused motionless. If the female entered his burrow the male would dash back to the burrow entrance and female, and initiate stroking. A similar courtship tactic is sometimes used by male *U. pugilator*, especially after females have initially sampled them and their burrows (Christy, 1980). Finally, toward the end of a tidal cycle, male *U. vocans* occasionally dug females out of plugged burrows and initiated stroking, which frequently lead to copulations.

Copulations in *U. vocans* always occurred on the surface near the entrance of a female's burrow. The sexes remained together only for courtship and mating. Both sexes were promiscuous. Some males obtained up to five matings during a single semilunar cycle and some mated twice with different females during a single low-tide period. The mean number ( $\pm$  s.d.) of matings by females observed to mate at least once per semilunar cycle, averaged over three cycles, was  $1.65 \pm 0.126$ . Some females paired with two males on the same day.

#### (4) Reproductive cycles and female reproductive behaviour

Females displayed semilunar cycles of reproductive activity. Copulations were observed on all but 4 days of a 6 week period of observation (1 December–15 January) of marked crabs in an enclosure built in the East Colony. Mating frequencies increased slightly for 5–7 day periods during the full moon and just before the new moon spring tides. The opercula shielding their gonopores were almost always partially or wholly decalcified, indicating that females were capable of insemination at most times and at all stages of reproduction. Females produced two relatively small (mean = 8119 zoeae, female carapace width 1.5–2.3 cm) clutches each lunar month, new clutches being laid within a few days after larval release. Most females copulated when carrying eggs. Females probably oviposited in their burrows or while active on the surface near the burrow entrances. Clutches of newly laid eggs were too small to be visible externally; they could be contained entirely in the space between the sternum and abdomen (Fig. 1). As in other species of *Uca* (Feest, 1969; von Hagen, 1970; Greenspan, 1975; Christy, 1978) incubation took approximately 12–15 days. Females were active on the surface during their entire breeding cycle.

Females were broadly synchronous in their reproductive activity. Larval release occurred predominantly on the days of the lunar month when high tides peaked between 1800 and 2200 h, 4–6 days before the new and full moons. Maximum nocturnal tidal amplitudes occurred 1–2 days before the full moons and 4–5 days before the single new moon during the 6-week observation period. Hence females released larvae 2–4 days before the maximum ebb tides associated with the full moon, but during the maximum ebb tides around the time of the new moon. Females who release larvae on large but not maximum amplitude nocturnal ebb tides that occur several days before the full moon may best escape visual predators that hunt spawning females, or may decrease the chance of their larvae being taken by planktivores whose feeding rates increase on bright moonlight nights.

Males did not exhibit strong cycles of reproductive activity, probably because females were receptive at most times. The frequency with which males wandered and changed burrows, however, did increase during the spring tides when matings were most frequent and females released larvae. By wandering and changing locations, males may have been seeking areas with high densities of breeding females.

When courted females failed to mate, it was not possible to determine if this was so because they were receptive but found the males who courted them unacceptable as mates, or because they were unreceptive to any male. However, it was possible to determine if females chose males larger or smaller than themselves by examining the sizes of males and females in 157 mating pairs. No female mated with a male whose size differed from hers by more than 25%, though females showed no preference for mating with larger or smaller males. Females who mated more than once per cycle accepted as their final mates males larger and smaller than themselves with equal frequency. The size distribution of the males chosen by females who mated once did not differ from the size distribution of the last mates of females who mated more than once. Thus, females who mated more than once did not do so because their initial mates were particularly small. Females also showed no apparent preference for males who were residents at nearby burrows compared to males who were wandering through their area. It is also clear that females could not choose mates on the basis of the quality of a defended resource, since males transfer only sperm to their mates.

Females did show preferences for particular males. These were revealed when, on occasion, other males interrupted copulating pairs. Males larger than the copulating male initiated interruptions about as often as males smaller than the interrupted male. Although males were better able to deter smaller than larger interruptors, most interrupted males (12 of 16 field observations; 10 of 13 enclosure observations) eventually completed copulation regardless of their size. In addition, while females readily accepted their original mate after an interruption, only one (of 30) accepted an interrupting male, thus showing an apparent preference for mating with their initial suitors.

About 50% of the marked females mated once each fortnight and of these, about one-half mated more than once over periods of several days. Most females required more than one bout of courtship before they mated. Taken together, these features of the reproductive biology and behaviour of females suggest they discriminated among potential mates. At present, we suggest that females chose males on the basis of the duration, vigour, or movements employed during courtship. The adaptive value of choice based on such characters remains to be elucidated, but it is clear that females do not prefer larger (older) males over younger males. Perhaps mortality among sexually mature males is relatively low and unpredictable (Type III survivorship, Wilson & Bossert, 1971), while differences in male 'attractiveness' result in large disparities in male reproductive success, regardless of size. Such a situation might favour female choice based upon courtship technique alone, especially since only the largest females at Chunda Bay could compete for, and hold, breeding burrows in clusters where large males were reliably present (see below).

##### (5) *The mating system*

Larger males *U. vocans* consistently defeated smaller males in combat. Males who lost fights were displaced from their burrows or otherwise forced to move away from

the vicinity of their victors. Males who won fights appeared to gain, at least temporarily, the opportunity to court females in a local area without further aggressive approach from the males they defeated. These observations suggested that aggressive interactions among males may temporally or spatially segregate males according to size, in ways that may affect male reproductive success.

To detect possible temporal effects of male-male competition, the times in the tidal cycle at which small ( $CW < 1.79$  cm,  $N = 17$ ) and large ( $CW > 1.80$  cm,  $N = 18$ ) marked males copulated in the enclosure in the East Colony were compared for the 6-week observation period. No significant difference occurred between the temporal distributions of copulation times of males in the two size classes (109 total copulations). Possible spatial effects of aggression between males were examined by plotting the distributions in the East Colony enclosure of large males, small males, and females. The upper portion of the enclosed area contained *Sonneratia* pegroots and a well developed subsurface root system. Lower muddy areas lacked roots but contained rocks that provided shelter for mud crabs (*Thalamita* spp.), occasional predators on *U. vocans*. Most large females occupied burrows in the area with *Sonneratia* roots, perhaps thereby avoiding contact with *Thalamita*. The burrows from which large males sallied were concentrated where females were most abundant. In contrast, the burrows of small males were more evenly distributed in the enclosure extending into peripheral zones surrounding the areas where larger males and females were dense. Similarly, large males obtained most of their copulations where females were abundant, while smaller males copulated throughout the area. Although these observations suggest large males may have excluded small males from the area where females were most abundant, small males may also have been displaced from such areas by aggression from larger females, or they may have preferred to burrow in peripheral zones.

Size-based dominance effects in *U. vocans* were not reflected by significant differences in the means or variances of the mating frequencies of large and small males. Small marked males mated at the mean rate ( $\pm$  s.d.) of  $1.6 \pm 1.43$  per semilunar breeding period, while large males mated at the rate of  $1.7 \pm 1.03$  per cycle.

The effects of size on male reproductive success appear twofold. First, large males tended to mate more often than small males in areas where larger females were abundant. They may, therefore, have consistently fathered larger clutches, since bigger females produced more young. Second, if one assumes larger females aggregated in areas where they were most likely to breed successfully, then by mating where large females were dense, large males may have produced more offspring even though small males mated as often.

The mating system of *U. vocans* can be characterized as resource free (*sensu* Alexander, 1975) and promiscuous. Food sufficient for growth and reproduction is available immediately outside or near the burrows females occupy. Hence females tend to be sedentary and aggressive, defending their burrows for several days and fighting and displacing other females from common feeding areas. At approximately semimonthly intervals, females produce relatively small clutches that do not extend beyond the margins of their abdomens until late in their incubation periods. Although the selective factors that govern spawning frequency and clutch size are unknown, the consequences for the mating system seem clear. Since newly laid eggs are not exposed directly to the environment, females need not search for breeding sites safe from physical disturbances and extremes of temperature and dessication. They oviposit instead while either on the

surface or in their own burrows. Ovigerous females are active on the surface daily even toward the end of the incubation period when their egg masses swell, presumably through water up-take (Davis, 1968; Wear, 1974), and protrude beyond their abdominal margins. Because they defend and remain near their burrows, females always have access to a refuge from conditions that could cause egg mortality. Hence the primary requisites for successful reproduction by female *U. vocans* (food, safe sites and locations suitable for breeding) appear to be abundant and available throughout their habitat. From the male's viewpoint, there are no resources that can be defended and provided to females as a way of obtaining mates. Females themselves do not appear to be directly defensible. Conditions operating against female defence include the relatively low probability that a given female will mate per fortnight (0.78), high densities of competitors, and the inability of males to control the movements of neighbours and wandering males to the degree necessary to ensure exclusive or even primary sexual access to several resident females.

As an alternative to resource or female defence we suggest males act as scramble competitors, i.e. they have adopted behaviour that permits them to search most efficiently for receptive females, thereby maximizing their copulation rates. Males change burrows frequently, especially around spring tide periods when many females are receptive, and they often move several metres before establishing new burrows. By so doing males may encounter more receptive females each breeding period than if they repeatedly courted the relatively few females available within their range at a single burrow. In addition, large dominant males tend to establish burrows in areas where females are most abundant, suggesting further that males behave in ways that increase the rate at which they encounter receptive females. Finally males spend very little time in a given courtship bout (< 2 min), they copulate quickly (< 7 min), and can do so in rapid succession (some males mated twice within 15 min). Aggressive interactions among male *U. vocans* seem to subserve two functions, depending on the context of the encounter and status of the combatants. Residents who win fights with their neighbours may obtain the freedom to court local females without interference from the males they defeat. 'Neighbourhoods of dominance' are, however, ephemeral and shift as males move about. Combats between wanderers and residents probably reflect, simply, the former's attempt to establish a residence in a new area without incurring the costs in time and energy of digging a new burrow, and the latter's attempt to remain in the area. Wanderers sometimes won burrows, but abandoned them almost immediately and moved on and fought other residents. It is unclear what might be gained by such behaviour. Perhaps wanderers who fight residents receive information about both their ability to win fights with the residents in a local area, and the intensity with which these residents defend their burrows. Wanderers might use the former information to judge their probable dominance status should they establish a burrow in the area. If the intensity with which residents defend their burrows reflects the frequency with which they have encountered receptive females, then wanderers might use this information to assess their probable mating success in the area.

V. ECOLOGICAL DETERMINANTS OF MATING SYSTEMS IN *UCA*

Differences between the mating systems of *U. pugilator* and *U. vocans* are associated with major contrasts in their ecology (Table 1). We have suggested for each species the manner in which ecological factors may act as selective agents moulding the reproductive biology and behaviour of females and, hence, the competitive behaviour males use to obtain mates. Here we summarize these selective relationships, discuss their different modes of action in *U. pugilator* and *U. vocans*, and speculate on how they may operate and vary among other species in the genus.

The mating systems of *U. pugilator* and *U. vocans* differ at the most fundamental level, in that female *U. pugilator* require access to a specific microhabitat controlled by males in order to breed successfully, while female *U. vocans* do not. This difference has apparently led to the evolution of a resource-defence mating system in *U. pugilator* and a resource-free mating system in *U. vocans*. As reviewed in the introductory material, males of most species of the American subgenera and *U. (Afruca) tangeri* probably court from and defend burrows to which females come for breeding, suggesting most may possess resource-defence mating systems, broadly similar to that exhibited by *U. pugilator*. In contrast, courtship and mating in the Indo-Pacific subgenera occur most often on the surface or in burrows females defend, suggesting broad similarities with the resource-free mating system of *U. vocans*. Understanding why females of some species require and must seek out a specific microhabitat in which to breed, and why others do not, may provide a first step toward understanding the conditions leading to the evolution of different types of mating systems in the genus.

(1) *Clutch size and breeding site requirements*

The different breeding-site requirements of *U. pugilator* and *U. vocans* appear to be related to differences in clutch size. Female *U. pugilator* produce clutches that are too large to be contained under their abdominal flaps or even to be bounded at their protruding margins by the plumose setae on the exopodites of their pleopods (Fig. 1). Although the processes of egg extrusion and attachment and the behaviour of ovipositing females have yet to be described fully, it is clear that females that produce large clutches are vulnerable to massive egg loss if physically disturbed during oviposition. Hence production of large clutches probably narrowly limits the range of microhabitats in which females can oviposit successfully. The suitability of sites for incubation also may be affected by clutch size. Incubation environments may affect female reproductive success in two ways. First unprotected eggs may be especially susceptible to mortality when exposed to environmental extremes such as hot dry conditions. Second, there is an increasing body of evidence that female *Uca* experience strong selection to release their larvae at a precise time in the semilunar cycle (see Christy, 1982*b*, for a review). The lengths of embryonic life of 21 decapod species, including 14 brachyuran crabs, were found to decrease exponentially with an increase in temperature (Wear, 1974); we expect a similar effect of temperature on development and incubation periods in *Uca*. Eggs that protrude from under a female's abdomen are more likely to equilibrate rapidly with local environmental temperatures than are those that lie under the abdominal flap. Hence females that produce large clutches may experience relatively strong selection to avoid extremes of temperature that might affect the precise timing of larval release through

Table 1. *Major contrasts in ecology and behaviour of U. pugilator and U. vocans*

<i>U. pugilator</i>	<i>U. vocans</i>
Resource-defence mating system	Resource-free mating system
	<i>Distribution</i>
Upper-intertidal and supratidal zones; exposed sandy substrates with little or no vegetation.	Mid-intertidal and lower intertidal zones; exposed muddy flats below vegetation line.
	<i>Predation</i>
Predators abundant. Crabs away from burrows are especially vulnerable.	Predators abundant. Crabs readily escape into nearby burrows.
	<i>Feeding</i>
1. Substrates near burrows lack food sufficient to support feeding.	1. Substrates near burrows are relatively food-rich.
2. Non-breeding crabs migrate daily from burrows to feed in the lower-intertidal zone.	2. Non-breeding crabs feed near their burrows.
3. Breeding males and females rarely feed.	3. Both sexes feed when breeding
	<i>Reproductive Behaviour and Ecology</i>
1. Lunar breeding cycles in females; females receptive for short periods.	1. Semilunar breeding cycles in females; females receptive at most times.
2. Semilunar cycles of reproductive activity in males.	2. Males reproductively active at most times.
3. Relatively large clutch, eggs exposed as soon as laid.	3. Smaller clutch; eggs protected by abdominal flap until late in the incubation period.
4. Females require access to a specific microhabitat in order to breed successfully.	4. Females able to breed successfully in most parts of habitat.
5. Abundance and location of good breeding sites limited and variable.	5. Good breeding sites available widely.
6. Breeding and feeding areas do not overlap; females not able to defend breeding sites	6. Females able to remain near, feed by and defend breeding sites.
7. Females cryptically coloured and relatively unaggressive.	7. Females brightly coloured and aggressive.
8. Males obtain mates by fighting for and defending breeding sites (burrows).	8. Males obtain mates by searching in areas where females are abundant.
9. Female choice is based on the quality of the breeding sites (burrows) males defend.	9. Female choice may be based on male epigamic characters.

an advance or delay of egg development rates. In contrast, females of species such as *U. vocans*, which produce clutches small enough to be contained largely under, and therefore be protected by, their abdominal flaps (Fig. 1), ought to be able to oviposit and incubate successfully in a relatively broad range of microenvironments. We suggest that resource-free mating systems will be found to be common among species that

produce relatively small clutches, while resource-defence mating systems ought to prevail among species that produce relatively large clutches. Unfortunately, little is known about how clutch sizes vary with interspecific contrasts in ecology, biogeographical patterns or evolutionary relationships within the genus.

(2) *Adaptive radiation and trends in ecology and mating systems*

Any hypothesis purporting to explain the divergence of mating systems in fiddler crabs must, at the minimum, be consistent with the more obvious patterns in modern species. Based upon what little is known, we assume that the American ancestral stock, following their migration across the Behring land bridge, underwent an explosive radiation. Forty-five of the 62 species recognized by Crane occur in the tropics of Central America; 32 of these are now found on the coasts of Panama. Most exist as highly specialized forms compared to those species found in the Indo-Pacific (Crane, 1975). This is especially true of the *Celuca*, 17 species of which are regionally sympatric in areas on the Pacific coast of Central America.

Adaptive radiation by the American subgenera has been manifest by an extension of the genus into the upper intertidal and supratidal zones, and apparently by finer division of the intertidal zone among relatively many species. In addition, extensive, though probably never total, microgeographic sympatry occurs among a few species. High species diversity in tropical and subtropical America is not associated with lower densities per species. On the contrary, American *Uca*, especially the small *Celuca*, but also medium and large species of *Mimuca*, exist at much higher densities than their Indo-Pacific relatives (evidence cited below). We assume that, as a consequence, heightened competition for food and other resources must have affected the American species to an extent not usually evident among the ancestral stock.

Early in the radiation of American *Uca*, species may have retained the resource-free mating system that now appears to be so prevalent among their modern Indo-Pacific relatives. But as specialization coupled with higher densities within species became the norm, females may have been forced to adopt alternative reproductive strategies, because of intense competition for burrows where they could oviposit free from disturbance from other crabs, and because the costs of defence of areas around such burrows, where a suitable food supply for growth and reproduction might exist, became prohibitive. If this scenario bears any resemblance to reality, it would set into motion selection favouring male competition for and defence of burrows suitable for mating, oviposition and incubation, and female patterns of foraging, independent of burrows, in the lower intertidal zone or other food-rich areas.

It is not clear whether the production of exceptionally large clutches is best viewed as a cause contributing to or a consequence of the evolution of resource-defence mating systems. On the one hand, increased specialization and the evolution of smaller adult body size may have resulted in relatively high rates of accumulation of reserves that could be used for egg production. Hence, competitive interactions may have stimulated the evolution of characters that lead to the production of relatively large clutches and strong selection on females to choose mates on the basis of burrow quality. On the other hand, once females relinquished defence of burrows and associated foraging areas, female choice of males/breeding sites may have lead to the construction and defence by males

of especially good breeding sites. Females who were capable of producing clutches that protruded beyond their abdominal margins could do so at such sites and experience little egg loss or mortality. Clearly, neither evolutionary route could proceed independently of the other.

(a) *Crab densities and competition for food*

Certain elements of the natural history of present-day forms support portions of this hypothesis. First, there is evidence in some populations that crabs are so numerous that their food supply is locally compromised. The bulk of the diet of most fiddler crabs probably is edaphic algae (Montague, 1980; Robertson *et al.*, 1980; Robertson, Fudge & Vermeer, 1981), though vascular plant detritus and its associated microbial community may be an important food source for some species in some habitats (Montague, 1980). *U. pugilator* in a Georgia saltmarsh rapidly deplete algal biomass in the upper 1–2 mm of substrate near their burrows. Consequently they move each low tide period away from burrows and over long distances in search of food (Robertson *et al.*, 1980). Although *U. pugilator* probably burrows in relatively food-poor areas, it seems reasonable that depletion of food at a given site may be a general problem encountered by any species that exists at high densities. In such situations, females who adopt burrow defence might produce relatively small clutches compared to those that follow other, more optimal, feeding trajectories.

Second, contrasts between typical densities of Indo-Pacific species of *Deltuca* and *Thalassuca* and Indo-Pacific and American species of *Celuca* and *Minuca* support the idea that female defence of breeding sites may be more common at low densities, while males may more often defend breeding sites when densities are high. Frith & Brunenmeister (1980) have provided a detailed description of the distributions and abundances of *U. (Deltuca) forcipata* (Adams and White), *U. (D.) urvillei* (Milne-Edwards), *U. (Thalassuca) vocans* and *U. (Celuca) lactea* along a transect through mangrove habitat on Phuket Island, Thailand. *U. forcipata* occurred at an average density of 1.2 adults ( $> 3.5$  mm carapace length)/m<sup>2</sup>, *U. urvillei* at 2.7/m<sup>2</sup>, *U. vocans* at 1.6/m<sup>2</sup> and *U. lactea* at 7.2/m<sup>2</sup>. At most, two species occurred at the same sampling site along the transect. Within sites, species showed either negative or random association among sampling units (quadrats), suggesting moderate to little microgeographic sympatry. *U. vocans* occurs at higher densities at other sites (approximately 19–60/m<sup>2</sup> maximum densities depending on location (Icely & Jones, 1978; Nakasone, 1982; Salmon, in press)), though it seldom is as dense as *U. lactea* (80–90/m<sup>2</sup> maximum densities (Icely & Jones, 1978; Nakasone & Kawa, 1983)). By contrast, American species often are much more dense than the *Deltuca* and *Thalassuca*. *U. (Minuca) pugnax* regularly occurs at densities above 100/m<sup>2</sup> (Montague, 1980, and references therein) up to a maximum of about 250/m<sup>2</sup> (Aspey, 1978). *U. pugilator* exists at densities around 50/m<sup>2</sup> in temperate salt marshes (Montague, 1980; Colby & Fonesca, 1984) and commonly at densities of 120–200/m<sup>2</sup> in mangrove habitats in Florida (Christy, unpublished). Recent observations (Christy, unpublished) on several *Celuca* on the Pacific coast of Panama indicate that densities of these small species regularly exceed 150/m<sup>2</sup>. Crab size, and density and number of sympatric congeners, appear to be broadly correlated with mating-system type within the genus.

Third, we expect that intraspecific variation in mating systems might occur when

there is significant variation in local population density. *U. (C.) lactea*, a moderately small species, commonly exists at densities between 50 and 100 adult crabs/m<sup>2</sup>. As in other *Celuca*, male *U. lactea* usually court from and defend burrows (located in muddy-sand substrates in the upper-intertidal zone) to which females come for mating (Altevogt, 1957; Crane, 1975). In contrast, Yamaguchi (1971) reported that 83 of 86 matings observed in this species over a 3-year period at a site in Japan occurred on the surface near burrows ('nests') that females defended and used for breeding, and around which they fed. Males courted from and defended hooded burrows, but they waved little or not at all when they approached and mated with females on the surface; three females copulated normally with males that lacked major chelae. Underground copulations occurred infrequently in the burrows males defended, and involved females who had left their burrows and wandered through the colony. Densities at this site were apparently low for the species. Approximately 2000 adults occupied a 300 m<sup>2</sup> area, giving a density estimate of about 6.7 crabs/m<sup>2</sup>. Feest (1969) also reported that surface copulations were common in *U. lactea* in India, but density estimates were not given. Although female burrow defence and foraging behaviour in higher density colonies have not been reported, these observations suggest that the low densities in Yamaguchi's colony permitted females to obtain sufficient food near their burrows, leading to burrow defence and use as a breeding site.

The site of mating in *U. vocans* also appears to vary with density. In the Okukubi River estuary on Okinawa Island, Japan, *U. vocans* exist at relatively high densities (54.3/m<sup>2</sup>) in burrows in the mid- to lower intertidal zone (Nakasone, 1982). During summer low tides, both sexes leave their burrows and feed on relatively food-rich substrates near the water-line. Although surface copulations between feeding or wandering crabs are common (Nakasone, 1982), some males, especially large males, court and attract females into their burrows where mating occurs (Y. Nakasone, personal communication). In the spring (March–May), at the beginning of the breeding season, few crabs leave their burrows to feed, and most matings occur on the surface near females' burrows in the manner summarized above from Salmon's study at Chunda Bay. Hence at low densities (Chunda Bay), or at high densities but when females are relatively sedentary (early breeding season, Okinawa), surface copulations near females' burrows are the rule. At high densities, and when crabs wander and feed, mating may take place either on the surface between wandering crabs or in burrows males defend.

#### (b) Habitats and mating systems

The defensibility of breeding sites by females may be related to their location in the intertidal or supratidal zones, as well as to crab densities. As implied above, females may be expected to defend breeding sites only if they do not suffer fitness losses due to reduced rates of energy and nutrient accumulation, compared to females that forage freely. Although the factors that affect the distribution and abundance of edaphic algae in soft bottom intertidal habitats are not well known (Round, 1971), in general, biomass decreases with increasing particle size, height in the intertidal zone, shade and exposure to scouring from tidal currents and waves. Concentrations of chlorophyll a (Robertson *et al.*, 1980) and organic nitrogen (Nakasone & Kawa, 1983; Murai, Goshima & Nakasone, 1982) in fiddler crab habitats are known to vary similarly along one or more of these environmental gradients. To a fiddler crab, shaded, sandy, upper intertidal or

supratidal substrates and those in areas exposed to wave action or strong tidal currents ought to be least food-rich. Muddy mid- to lower intertidal substrates, in protected areas within a mangrove forest or salt marsh that receive sufficient light to ensure high algal productivity, ought to contain the most food. We, therefore, expect there may be a trend in the genus favouring female defence of breeding sites in species that occupy relatively food-rich muddy substrates that are regularly exposed to sunlight in the mid- to lower intertidal zone (e.g. *U. vocans*). Conversely, species that occupy exposed sand substrates high on the shore ought to be predisposed toward the evolution of male resource defence (e.g. *U. pugilator*). This trend should be especially evident when comparing species that are similar in size and that exist at similar densities.

We have assumed in the above arguments that fiddler crab habitats are heterogeneous with respect to sites where females may oviposit without losing eggs. Though this seems a reasonable assumption, it is worth considering what factors may affect the quality of burrows as breeding sites and, therefore, determine their distribution and abundance as a resource for which males may compete. At present only one source of physical disturbance that may adversely affect ovipositing females has been identified – burrow collapse due to tidal inundation or flooding by groundwater. Total collapse of a burrow around an ovipositing female is likely to be an important source of egg loss only for species that burrow in relatively homogeneous sandy substrates; few species in the genus other than *U. pugilator* and its close relative *U. panacea* Novak and Salmon burrow in sandy beaches with any regularity (Crane, 1975). Most species occupy silty or clayey sediments in which burrows may persist for many years (Basan & Frey, 1977). In such stable substrates, factors that may cause loss of newly laid eggs include burrow flooding (but not collapse), disturbance by other crabs that enter a burrow from the surface or while digging or modifying one nearby, and encounters with predators such as xanthid, grapsid and portunid crabs, birds that probe burrows, and racoons. Unfortunately little is known about how these factors may vary and interact to determine the locations and availability of optimal oviposition sites. For most species, burrows that are isolated from the labyrinth of interconnected cavities and channels that riddle muddy intertidal substrates, and perhaps those that terminate under shells, stones or among roots, may provide the best protection from most sources of disturbance. Aggressive interactions between neighbouring male and female fiddler crabs usually have been interpreted in terms of the effects of threat and combat on male courtship (Zucker, 1974; Christy, 1980) or female foraging behaviour (Salmon, in press). It is possible, however, that spatial intolerance of near neighbours, which has been shown to promote spacing of burrows (Zucker, 1977; Christy, 1980), may also function to increase or ensure isolation of breeding sites.

The factors that may affect egg mortality during incubation are even less well understood. The following may apply to most species. First optimal oviposition sites probably always are good incubation sites. Second, females probably can tolerate exposure to a broader range of microenvironments when incubating than when ovipositing, suggesting that third, male defence of sites used only for mating and oviposition probably is more common than defence of burrows used for all stages of breeding. Females ought to remain underground during their 12–14 day incubation period only if, when moving about on the surface, they themselves are especially susceptible to predation or they regularly expose their eggs to lethal conditions or

thermal environments that might affect the timing of larval release. Further, since females that incubate underground probably feed little if at all, the negative effects of such risks and factors on female fitness must exceed the potential gains due to increased rates of reproduction, or larger clutch sizes that may result if females feed during incubation. In general, we expect underground incubation in species that produce relatively large clutches and that feed in exposed areas away from the protection of vegetation and their burrows.

#### VI. CONCLUSIONS

We have outlined the general features of some of the ecological factors and selective processes we believe may have shaped the evolution of the reproductive behaviour and mating systems of fiddler crabs. The vulnerability of ovipositing females to egg loss and the effects of incubation environments on the rates and success of development interact with clutch size to determine, in part, the criteria females may use when choosing mates and breeding sites. Access to a good breeding site, and, hence, choice based on site quality, probably is most important in species that exist at high densities or that burrow in relatively food-poor areas. Both conditions might require females to move frequently in search of food, preventing them from establishing and defending burrows and feeding sites that could be used for breeding. The mating system of *U. pugilator* illustrates how female choice of a breeding site leads to competition among males for the opportunity to court from sites that females will prefer. By contrast, the reproductive behaviour of male *U. vocans* in Australia illustrates how males compete for females that do not require, and thus do not seek, specific breeding sites.

Broad differences between the American and Indo-Pacific *Uca*, exemplified by these two species, probably arose rapidly, and perhaps irreversibly, during a period of speciation and radiation in the Neo-tropics. Factors favouring the evolution of resource-based mating systems in the western Atlantic and eastern Pacific probably include (1) feeding specializations leading to relatively rapid accumulation of reserves that can be allocated to eggs, (2) decreased crab size, perhaps making production of relatively large clutches more likely, (3) a decrease in the abundance and defendability by females of stable safe breeding sites due to higher population densities, more frequent microgeographic sympatry and the greater vagility of feeding females in species that invaded the upper intertidal and supratidal zones, and, finally, (4) positive feedback between female choice of breeding sites and the production of especially large clutches.

#### VII. SUMMARY

1. General accounts of the natural history and behaviour of fiddler crabs suggest there exist two broad mating patterns in the genus. Most western and Indo-Pacific species mate on the surface of intertidal substrates near burrows females defend. The sexes associate only briefly during courtship and mating. In contrast, males of many American species court from and defend burrows to which females come for mating. Copulation occurs underground in burrows plugged at the surface; the sexes usually remain together for at least several hours.

Here we summarize and contrast recent detailed field studies of the mating systems of *U. pugilator*, an American species, and *U. vocans*, a species widely distributed in the western and Indo-Pacific. We indicate how differences in the breeding ecology of these

two species may account for basic differences in modes of sexual selection leading to the two broad mating patterns in the genus.

2. *U. pugilator* burrows in protected sandy substrates in the upper intertidal and supratidal zone. During ebb tide, nonbreeding crabs leave burrows they occupy during high tide to forage on food-rich substrates in the lower intertidal zone. Reproductively active males remain in the burrow zone where they fight for and defend burrows from which they court. Large males win most fights for burrows and tend to defend burrows high on the elevation gradient, especially during periods with relatively high tides. Females usually approach and descend the burrows of several males before choosing their mates by remaining in males' burrows. Males remain underground with their mates for 1–3 days until after they oviposit their eggs. Some males then emerge and leave their burrows while others sequester their mates in the chambers where mating and oviposition has occurred, dig new chambers and resume courtship, perhaps attracting additional females. In either case, females remain underground for approximately 2 weeks, finally emerging to release their planktonic larvae. Burrows that do not collapse due to tidal inundation or flooding by groundwater are best for breeding and usually are located relatively high on the elevation gradient. Females choose mates indirectly by preferring to breed in burrows that will remain intact while they oviposit and incubate their eggs. Large males mate more often than small males because they are better able to defend burrows at locations females prefer to breed. The mating system of *U. pugilator* may be classified as resource-defence polygyny.

3. *U. vocans* burrows in open muddy substrates in the mid- to lower intertidal zone. At a site near Chunda Bay, Australia, where the reproductive behaviour of this species has been studied in depth, both sexes feed near burrows they defend. Females tend to occupy their burrows for longer periods and move shorter distances than do males. Mating occurs on the surface near the burrows that females defend. Females accept both resident and wandering males as mates. They show no preference for mating with larger males. Female choice may be based on other male morphological or behavioural characteristics. Females oviposit their eggs either while on the surface or in their burrows. They produce relatively small clutches and are active on the surface throughout their breeding periods. Males fight both their neighbours and wandering males. Large males tend to win fights and defend burrows in areas where large females, which produce relatively many eggs, are most dense. Such areas may offer greater protection from predators than areas occupied by smaller females. Small males mate about as often as large males but may father fewer larvae. The mating system of *U. vocans* is resource-free and promiscuous.

4. The mating systems of *U. pugilator* and *U. vocans* differ fundamentally in that female *U. pugilator* require access to a specific microenvironment to breed successfully, while female *U. vocans* do not. We suggest this difference occurs because of contrasts in clutch sizes and the mobility and movement patterns of feeding females. Female *U. pugilator* produce relatively large clutches and probably experience more intense selection from factors that can cause egg loss and mortality than do *U. vocans*, which produce clutches of sufficiently small volume to be protected by their abdominal flaps. Hence, the range of suitable breeding environments for *U. pugilator* is small compared to that for *U. vocans*. In addition, *U. pugilator* burrows in areas that are relatively food-poor, leading to daily migrations to and from food-rich substrates in the lower

intertidal zone, preventing female defence of an area suitable for both breeding and feeding. *U. vocans*, however, burrows in areas sufficiently rich to support feeding, leading to relatively low female mobility and defence of burrows that are also suitable breeding sites.

5. Adaptive radiation of the genus *Uca* in the Americas is manifest by trends toward smaller adult size, higher population densities, more frequent microgeographic sympatry and increased terrestriality, compared to species in the western and Indo-Pacific regions. We outline the general features of the selection mechanisms tying each of these trends to the evolution of resource-defence mating systems. Intraspecific variation in the courtship behaviour and site of mating in *U. lactea* and *U. vocans* supports our contention that resource-defence behaviour tends to occur at high population densities. Additional data are needed to evaluate the other hypotheses critically.

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