

Comparative Studies of Reproductive Behavior in Mantis Shrimps and Fiddler Crabs¹

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SYNOPSIS. Comparative ethological studies of closely related species can place into clear perspective the functions of behavioral traits as species diverge and adapt to different environments. In this paper we contrast the reproductive behavior of species within two crustacean groups: the mantis shrimps (stomatopods) and the fiddler crabs (genus *Uca*). For the stomatopods, we identify probable selective relationships between features of species' ecology and their mating systems. Population density, the kind and availability of shelters in which these shrimps live, the intensity of predation and spawning cycles all play important roles in molding reproductive behavior in this group. Associations between the ecology and mating systems of fiddler crabs have been discussed recently elsewhere. Here we focus on a comparative analysis of sexual communication in these crabs. A study of competitive courtship signaling and mate choice in the fiddler crab *Uca beebei* has shown that certain male courtship signals are highly attractive probably because they exploit female sensory-response systems that have been molded by selection for escape from predators. Interspecific comparison of male courtship displays and the responses of females to these displays suggest that sensory exploitation may play an important role in the evolution of sexual signals in the genus. Comparative studies have advanced our understanding of how natural and sexual selection affect the reproductive behavior of both stomatopods and fiddler crabs.

INTRODUCTION

Ethological studies emphasize the importance of observing and comparing the behavior of organisms in their natural ecological and social settings (Tinbergen, 1951). Comparisons of behavioral traits among populations of a single species or among closely related species can reveal evolutionary trends in behavioral adaptations to different environments and identify how phylogenetic constraints imposed by body plan and physiology limit possible routes of adaptation. Armed with such knowledge for a wide variety of organisms, it becomes possible to recognize how suites of behavioral characters arise under the influence of contrasting selective forces (Clutton-Brock and Harvey, 1984).

Terrestrial organisms have been relatively well studied from a comparative perspective, especially with reference to relationships between ecological divergence and contrasts in adaptive patterns of reproductive behavior (Tinbergen, 1959; Crook, 1964; Jarman, 1974). Yet, about 70% of the earth's surface is populated by organisms that live in the sea. The ecological contrasts between life on land and in the ocean have led to marked differences in many features of the reproductive biology and behavior of terrestrial and marine organisms including how mates are found, which life history stages disperse and the amount and kind of parental care.

Here we summarize and review studies of the mating systems of mantis shrimps and the courtship displays of fiddler crabs. We show how the comparative approach can increase understanding of the adaptive significance of both general patterns of social organization and specific behavior. We chose these two groups, both members of the crustacean class Malacostraca,

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because their reproductive behavior is diverse and relatively well known.

GENERAL REPRODUCTIVE FEATURES

The larger and better known malacostracans are benthic inhabitants of shallow coastal tropical and subtropical seas. Adults usually defend burrows, crevices or cavities in small home ranges. The sexes typically are separate and dispersed, requiring searches for mates that can involve considerable risk, especially for smaller and poorly defended species. The sexes usually associate only briefly to court and mate, though longer more complex associations occur (Seibt and Wickler, 1979; Atema, 1986; Christy, 1987; Wilbur, 1989). Females commonly bear all the costs of the production of young. In stomatopods, extruded eggs, which are fertilized by sperm stored in the female's seminal receptacles, adhere and form a ball that the female carries in her maxillipeds. Fertilization in fiddler crabs is internal and the extruded eggs attach to setae on the female's abdominal appendages. Females of both groups guard, fan and clean their eggs until they hatch. Egg hatching usually occurs during a specific and brief period in the lunar or semilunar cycles when the strongest currents are available to transport the planktonic larvae away from shallow reef and intertidal habitats where larval predators are most abundant (Reaka, 1976; Christy and Stancyk, 1982; Morgan, 1990). Precise timing of gonadal cycles and choice of sites for ovulation, incubation and larval release are prominent features of the reproductive behavior of both groups.

MANTIS SHRIMP

Ecology and behavior

Mantis shrimps (stomatopods) capture prey with powerful, rapid, outwardly directed strikes of their large, paired raptorial appendages. "Spearmen" impale soft bodied prey (shrimp, fish) on barbed appendages, while "smashers" break apart armored victims (crabs, snails) with more powerful, heavily calcified appendages (Caldwell and Dingle, 1975). Both groups may inflict mortal blows during fights over

ownership of shelters essential for defense against predators.

Sensory specializations and ecology also distinguish these two stomatopod groups (Reaka and Manning, 1981). Smashers typically are active during the day, live in cavities in coral reefs in clear water and often are surrounded by neighboring stomatopods. They are brightly colored and have excellent form and color vision with up to 10 visual pigments (Cronin *et al.*, 1988; Cronin and Marshal, 1989). The olfactory sense also is well developed. Neighbors and the winners and losers of fights recognize each other by odor (Caldwell, 1982, 1985). By contrast, most spearmen live in burrows in soft sediments, often in turbid water. They generally are drab in color and their visual sensory system is not as well developed as in smashers. Most spearmen occur at lower densities than do smashers, rarely encounter neighbors and probably can not identify each other by odor (Caldwell, personal communication).

Differences in frequency and intensity of combats in the two groups of stomatopods are associated with the kinds of shelters they occupy (Dingle, 1983). The preformed cavities of smashers vary in value and defensibility according to the relationship between cavity volume and mantis shrimp body size. In most coral frameworks there are few cavities large enough for larger individuals and large smashers defend their shelters vigorously. The simple burrows spearmen dig are not usually limiting and fights for burrows are less vigorous (fewer strikes/combat) and potentially less harmful. This pattern is reversed in smashers that occupy abundant crevasses and in spearmen that invest heavily in elaborate burrow systems (Caldwell and Dingle, 1975).

Mating systems

Stomatopod species vary in which sex searches for mates, the location of mating, the number of mates acquired per brood, the occurrence and behavior associated with sperm storage, the length of the pair bond and the male's role in breeding (Caldwell, 1991).

The effects of selection for tight breed-

ing synchrony are evident in the reproductive behavior of *Gonodactylus bredini*. This smasher is a serially monogamous species in which both sexes search for mates in shallow reef habitats. Most commonly, males search for a receptive female and then fight for entrance into the female's cavity. Laboratory observations and the distribution of size relationships between paired shrimps in the field indicate that females usually allow only larger males to enter. Less often, females leave their cavity and enter the cavity of a male. Males admit prospecting females without a fight and females are less choosy when they search. Predation on searching shrimp is very high and males suffer greater mortality with size, age and repeated breeding episodes than do females. Paired shrimps copulate repeatedly and the male defends his mate and the cavity until the female extrudes her eggs. The male then leaves, probably because the cavity is too small to accommodate both adults and the egg mass. Female breeding cycles are so highly synchronized and tightly linked to the lunar cycle that males seldom find another unmated female after they leave their first mate. By copulating frequently and guarding their mates males are assured of their paternity for at least one clutch. Tight breeding synchrony coupled with male mate guarding may explain why some females search. Most females search during new moon tides when most females are receptive. Since females can not delay ovulation, the longer an unpaired receptive female waits in her own cavity the lower the probability that she will be found by a prospecting male and the greater the probability that she will ovulate without mating. Females do store sperm but they can produce only one fully fertile clutch without remating (Caldwell, personal communication). Hence, as each new moon breeding period progresses, an unpaired receptive female with depleted sperm stores must leave her own cavity and find a mate or stay and pay the cost of producing unfertilized eggs. The effects of selection for tight breeding synchrony are manifest in many features of the reproductive behavior of *Gonodactylus bredini*.

The mating system of *Haptosquilla* illustrates how cavity availability may affect mantis shrimp reproductive behavior. These shallow reef smashers are cavity limited in the extreme (Caldwell, 1991). In the laboratory, only males search for mates. Courtship may last up to 30 min, mating occurs at the female's cavity entrance, and the male then leaves. Females mate only with smaller males, store sperm and may mate repeatedly for each clutch. Large males are a threat to females as they often attempt to evict females rather than court them. Prolonged courtship may allow females to assess male size and intent. Females remain partially in their cavities during mating, a positional advantage for cavity defense, and they possess a heavily armored telson (tail segment) used to block the cavity opening during disputes. Sperm storage and the independence of receptivity and egg maturation cycles allows females to mate whenever they encounter suitable males and to remain in their cavities throughout reproduction.

Similar promiscuous mating systems may occur under different conditions. *Oratosquilla*, a Japanese spearer, burrows in temperate muddy bays. Under laboratory conditions, males search for females, courtship is brief and copulation occurs on the surface near females' burrows (Hamano, 1988). Males leave after mating and females mate repeatedly with males of any size. Sperm are stored for months, assuring females of a supply when eggs are ripe. The sexes do not fight for burrows and burrows are not apparently limiting. Turbid water may reduce predation on searching males and burrows in mud may be more difficult to defend against larger competitors than are cavities in coral. Both factors might favor male searches for additional mates rather than mate guarding.

The spearer *Lysiosquilla* lives in soft sediment (sand) but their burrows are elaborate and up to 10 m long. These shrimp have reduced armor and are particularly helpless on the surface. *Lysiosquilla* is monogamous. Shrimp are always found in pairs, some too small to be sexually mature (Caldwell, unpublished observation). Males have larger eyes and raptorial appendages

than do females, do most of the hunting by spearing fish that pass the burrow entrance, and provision their mates. The vulnerability *Lysiosquilla* and their extreme investment in elaborate burrows may preclude searching by either sex.

FIDDLER CRABS

Ecology and behavior

Fiddler crabs (genus *Uca*, about 80 species) burrow intertidally, usually in colonies of thousands, in soft sediments on open flats or under vegetation on protected shores in tropical to warm temperate regions (Crane, 1975). When covered by the tide, crabs occupy burrows that they usually seal with a plug of sediment. When their habitat is exposed by the receding tide, fiddlers emerge and feed on detritus, algae, bacteria and other organisms in surface sediment. Some species feed around burrows they defend while others, especially those that burrow higher on the shore, leave their burrows and forage in the lower zones.

Species in the genus can be divided roughly into two groups by the width of the space between the eye stalks (Crane, 1957). Broad fronts (BF) are more common in the New World and narrow fronts (NF) are more common in the Indo-Pacific, but both groups and intermediate forms occur world-wide. All fiddlers are highly sexually dimorphic; males grow larger than females, and only males have a large (major) cheliped which is used during courtship and aggressive interactions. There are a number of sex specific differences between BF and NF species. NF females may be as colorful as males and they typically defend burrows vigorously against intruders of both sexes. BF females usually are drab and devote little to burrow defense. Individual NF females typically produce small clutches each semilunar period while individual BF females produce larger clutches once every second or third semilunar period. The BF females in a population are not synchronized, however, with some females breeding each semilunar period. NF females commonly feed on the surface while their eggs develop, probably because their

clutches are small enough to be covered and protected by their abdominal flaps. To protect their larger, exposed clutches, BF females usually stop feeding and remain in burrows for about two weeks until their eggs hatch.

BF males usually (but see Zucker, 1978) exhibit semilunar cycles of reproductive activity. For several days twice each month, they become brightly colored and fight for, court from and defend "breeding burrows." These periods coincide with times when females are receptive, mate and produce eggs. Males wave their large claws and use other signals (see below) that attract receptive females into their burrow. Females enter and leave the burrows of several males ("sampling") before remaining with a male in his burrow (Christy, 1983, 1987). The male then plugs the burrow entrance with sediment. The pair mates and remains below for 1-3 days in the plugged burrow. After the female oviposits, the male opens the burrow and either leaves or stays and courts other females. If he stays, he digs a new terminal chamber on the burrow, leaving his first mate to incubate in the original chamber now separated from the burrow shaft (Christy, 1982). By contrast, NF males typically wander on the surface every day and court females which defend their own burrows (Salmon, 1984). Males court by plucking and stroking the female's front and carapace with their legs and small chelae. Mating occurs on the surface by the female's burrow, lasts only a few minutes and the male then leaves.

Mating systems

Resource-based mating systems in which males provide females with burrows suitable for breeding are typical of BF species. NF fiddlers exhibit resource-free mating systems in which females breed in their own burrows and males compete in ways that may maximize the rate with which they encounter and court females. In a previous review (Christy and Salmon, 1984), we discussed the major ecological and social selective forces that may account for the evolution of these two broad classes of mating systems in the genus *Uca*. Subsequent

studies (Nakasone *et al.*, 1983; Christy, 1987; Murai *et al.*, 1987; Salmon, 1987) have shown that elements of both kinds of mating systems are common within populations of some species. Revision of our explanatory scheme is indicated, but the comparative data do not yet suggest clearly new hypotheses about the selective processes that are generating the observed reproductive patterns.

Sexual communication

The courtship displays of fiddlers have been known for decades but their function in mate choice has not been well understood. Here we review modes of courtship signaling in BF fiddlers and speculate on the relationships between the form and function of their displays. Displays of NF fiddlers will not be discussed as so little is known how they affect mate choice.

Male BF fiddlers wave their large claws rhythmically while they defend burrows. Males increase waving rate and often the amplitude of each wave when a female is near and when neighbors wave vigorously. It is likely that waving attracts wandering females since females approach waving males and follow them into their burrows. BF males use a variety of other visual signals and tactics to induce females to enter their burrows. For example, immediately after a female has emerged from sampling the burrow of a male sand fiddler crab (*Uca pugilator*), the male may dash 50 cm or more from his burrow, raise his major chela to its highest extent and then dash back toward the female and burrow (Christy, 1980). The female responds to the "dash-out-back" display as if she were startled—she often runs rapidly back into the empty burrow. The male then follows immediately, the reverse of the usual order of entry. Males of other species may block the movements of females and "herd" them to their burrows (Salmon, 1967; Crane, 1975) or even capture and carry females below (Crane, 1975; Zucker, 1983).

BF species also use acoustic signals during courtship. "Rappers" strike or vibrate their major chelae against the substrate, "honkers" vibrate their claws or legs, and some species stridulate, all mechanisms

producing substrate vibrations to which crabs are sensitive (Salmon, 1983). Acoustic signals are presented as series of rapid "pulses" separated from the next series or "sound" by a pause. Males produce sounds at night and during the day when dense vegetation obscures vision or when they are just inside the entrances of their burrows and can not wave or use other visual signals to attract females. Fiddlers detect acoustic signals with receptors on each leg (Salmon *et al.*, 1977). Crabs are most sensitive to the species-typical temporal components of sounds which are conveyed to vibration-specific brain areas by several types of acoustic interneurons (Hall, 1985). Crabs may locate sound sources by time-of-arrival cues (Salmon, 1983).

Sequential sampling by females of BF males that court at high densities in open two-dimensional habitats creates ideal conditions for intense competition among males to attract or otherwise cause females to enter their burrows. Differential attractiveness of certain male morphological and behavioral traits could evolve because attracted females gain immediate ecological or ultimate genetic benefits by mating with males bearing those traits—an adaptive choice hypothesis (*e.g.*, Kodric-Brown and Brown, 1984). Alternatively, as illustrated by a recent study of the courtship behavior and mate choice of the fiddler *Uca beebei* (Christy, 1987, 1988), certain signals may be attractive because they exploit female sensory systems, the design of which reflects strong selection in other contexts—a sensory exploitation hypothesis (West-Eberhard, 1984; Ryan, 1990).

Uca beebei court at high densities (up to 65/m²) on sandy mud flats seaward of the mangrove fringe in the tropical East-Pacific. During each low tide some males feed little, spend most of their time courting, and build mud pillars about 2 cm high next to their burrow entrances ("P" males). Other males feed more, court vigorously only when a wandering female is near and do not build pillars ("NP" males). Records of the behavior of 51 wandering receptive females revealed that females sample up to 12 males and burrows before choosing a mate. Typically, females sample P males

and their burrows 1.5 times more often per courtship than they do NP males. However, once a female enters a burrow she is as likely to stay, mate and breed whether or not the burrow has a pillar. Female choice appears to be based on structural features of burrows that do not differ between burrows of P and NP males. The presence of a pillar is useless as a predictor of female choice. Why are P males and their burrows so attractive to females if pillars do not provide cues either of male or burrow quality?

Predation on fiddlers away from the safety of their burrows usually is very intense. For example, at a study site in Panama (100 m² area), about three *U. beebei* wandering on the surface are eaten by birds (usually grackles) every 5 min; birds hunting crabs are nearly always present. Predation by birds that run after and catch crabs on the surface probably has led to strong selection for eyes best able to detect moving objects on the horizon, and for rapid orientation to cover, typically vegetation or other structures that project vertically from the surface. Indeed, fiddler crab eyes are best able to resolve objects in the vertical plane (Zeil *et al.*, 1986) and they use this ability to orient flight responses toward vertical structures (Langdon and Herrnkind, 1985). Pillars appear to function as guideposts that provide cues to the location of males' burrows and thus serve to orient the movements of receptive females when they are wandering away from the safety of their own burrows (Christy, 1988). It seems likely, then, that P males exploit characteristics of the female visual sensory-response system that have evolved under selection from intense predation.

The study of how the pillars of *U. beebei* function to attract females suggests a new avenue for interpretation of the relationship between the form and function of courtship signals of fiddler crabs. The waving displays of fiddlers show species specific temporal and spatial features but all have strong vertical components. Could it be that the vertical components of waves, like the vertical profile of pillars, are attractive because they exploit female visual sensory-

response systems, causing females to orient to the signaler and his burrow? Alternatively, and unlike the presence/absence of pillars, variation in male wave displays may provide reliable cues to females about the quality of the signalers and their defended resources; if so, the attractiveness of male waves may evolve via an adaptive choice mechanism. Studies of the effects of male courtship on female behavior and patterns of female choice are needed to test the adaptive choice versus sensory exploitation explanations for the evolution of waving and other elements of fiddler crab courtship behavior. At present, however, a number of observations seem either consistent with a sensory exploitation hypothesis or inconsistent with an adaptive choice hypothesis.

1) In species with indeterminate growth, male size may be correlated generally with male quality, yet a female preference for large males has not been found in any species of *Uca* in which it has been studied (Greenspan, 1980; Christy, 1983, 1987).

2) Waving may attract females but it is not essential for mate choice in some species and circumstances. Female *U. lactea* (Yamaguchi, 1971; Murai *et al.* 1987) and *U. beebei* (Christy, 1987) may mate on the surface with neighboring or wandering males that do not wave prior to copulation. Males lacking a major chela may mate in *U. lactea* and female *U. pugilator* may "choose" a male and burrow when the male is not courting on the surface (Christy, 1980). If an adaptive choice hypothesis applies, one might expect waving to be an essential element of courtship, especially in surface matings when cues to variation in male quality would be most important, since only sperm are transferred to females.

3) Courting male *U. pugilator* and *U. stenodactylus* appear to exploit startle responses of females. When startled by predators or other stimuli, crabs near a burrow they have entered recently use a "memory," established through proprioception, of the location of the burrow and flee rapidly below. Crabs moving away from burrows either run to nearby cover or "freeze" and rely on the match between their color pattern and the sediment for protection. A male

U. pugilator usually uses the dash-out-back display only after a female has sampled his burrow, precisely when the female's startle response and last memory of the location of a refuge will lead her into the male's burrow. With this claw raised high, a male *U. stenodactylus* runs toward and intercepts the path of a wandering female causing her to change direction rapidly. The male quickly follows this and subsequent movements of the female, racing in a tightening spiral around her until she stops running. The male then captures the female and carries her to his burrow where he attempts to push her below. The initial approach of the male appears to elicit the "run response" to a moving object but the "circus" display effectively cuts off escape routes for the female and may elicit the "freeze response" just before the male captures the female.

4) The probable origin of some displays can be derived easily from their putative function as attractors independently of their possible value as cues of male or resource quality. For example, a male *U. beebei* will stop waving and raise his carpus and flexed major cheliped to a nearly vertical position when a female approaches him and his burrow. The "raised carpus" display reveals the dark melanic ventral surface of all segments of the appendage and probably functions, like pillars, as a visual guidepost to the location of the male and his burrow. The display likely arose from the incidental attractiveness of the natural elevation of a male's major chela as he rotates his body to enter his burrow (nearly always with the side lacking the large claw entering first) during the final stages of courtship. Selection for improved signal function could have led to the dark color (better contrast?) of the ventral surface of the appendage, and performance of the movement while the male is still a few cm away from the burrow entrance as females approach. Similarly, acoustic signaling by rapping at the burrow entrance in male *U. pugilator* and other "rappers" could have evolved from incidental contact of the major chela with the sand as a male waved and entered his burrow. Females would have been able to use the substrate vibra-

tions so produced to find the burrow entrance when the male could no longer use visual signals to attract and guide the female to his burrow.

CONCLUDING REMARKS

We have shown what comparative ethological studies have revealed about the reproductive behavior of two crustacean groups. For stomatopods we reviewed studies that identify broad correlations between species' ecology and mating systems and we suggested explanations for why the correlations exist. We focused on more detailed comparisons of sexual signals in fiddler crabs and showed how such comparisons are useful in evaluating ideas about the function and evolution of sexual signals in the genus. Both comparisons produced incomplete vignettes because so much more empirical work needs to be done. We hope that students of terrestrial organisms may find these comparisons informative and broadly applicable in their own studies. Our most general goal, however, was to emphasize the importance of comparative ethological studies. In the past, comparisons have advanced our understanding the adaptive value of natural patterns of behavior. For ethologists today, as for all fields of biological inquiry, the comparative approach remains an essential tool of the trade.

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