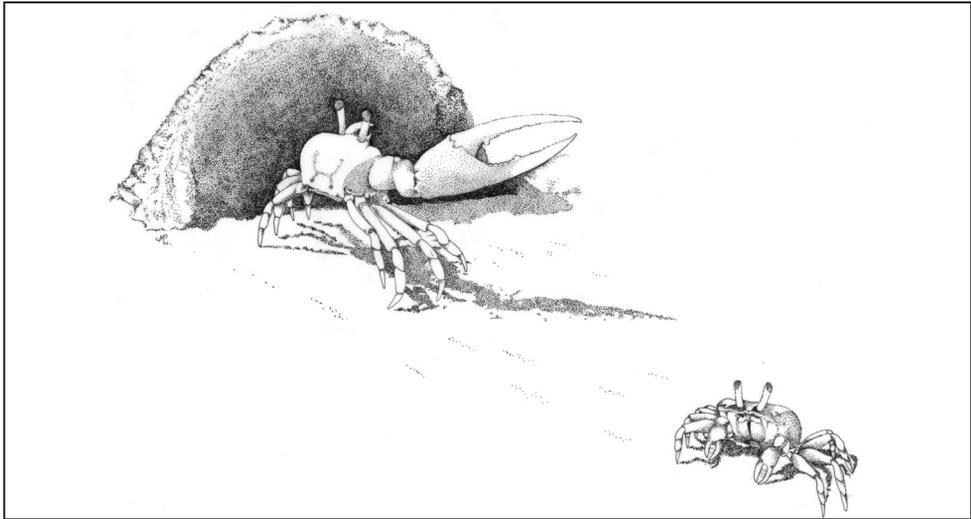


# Predation and the Reproductive Behavior of Fiddler Crabs (Genus *Uca*)

John H. Christy



*Males of some fiddler crabs (here *Uca terpsichores*) build structures of sand or mud at one edge of their burrow opening. Males attract females by waving their single large claw, and females use males' structures as landmarks to the exact location of the burrow.*

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Failure to avoid predators results in death, while failure to meet other challenges seldom is fatal. This may explain why predator avoidance behavior often compromises an animal's performance while engaged in nearly all other functional categories of behavior (Lima and Dill 1990, Magnhagen 1991, 1993, Sih 1994, Endler 1995). Behavioral responses to predation can be direct, such as escape elicited by the presence of a predator, or they can be indirect, such as habitat choice based on the presence of refuges. In the former, an interaction occurs in ecological time and is governed by the detection of a predator and decisions about the threat it poses (Helfman 1989). In the latter, the behavior is the result of differences in fitness between ancestral phenotypes that were predictably exposed to predation in past environments. Such antipredator adaptations often do not depend on predator detection and risk assessment. They can even result from selection on another life stage, such as parental behavior that reduces predation of young. Choice of habitat and activity period determine not only the rates and kinds of encounters between predator and prey (Endler 1995) but also the environments in which animals are active and hence the context-dependent expression of a broad range of behavior.

### Purpose and Scope of Discussion

Here I discuss some of the many ways that two kinds of behavioral responses to predation affect the reproductive behavior of fiddler crabs (genus *Uca*, about 97 species; Rosenberg 2001). My intent is to illustrate how research on this group has provided new insights or a different perspective on problems of general interest. Both sets of examples illustrate the multiple effects of adaptations to predation that do not depend on predator detection and risk assessment. First I show how variation in performance at one life stage can profoundly affect the behavioral phenotype of another (Podolsky 2003). I review the evidence for a functional link between avoidance of predators by newly hatched larvae and the timing of larval release by females relative to the tidal amplitude, tide height and diurnal light cycles, which together govern predator activity and hence predation risk (see Yamahira 2004 for an applicable fitness model). Cycles of larval release are produced by cycles in courtship and mating and are under endogenous control. Predation on larvae selects for precise timing of the reproductive behavior of both sexes, and it does so by affecting the phase of the crabs' endogenous rhythms. In contrast, in many other organisms, including crustaceans, temporal elements of reproductive behavior result not from endogenous clocks but from responses by individuals to current, variable, social, and ecological conditions, including their effect on an animal's internal state (e.g., anurans, McCauley et al. 2000; amphipods, Jormalainen 1998 [see also chapter 8]; lobsters, chapter 6).

In the second example, I show how the ecology of courtship and searching for a mate, and adaptations for predator avoidance can drive the evolution of courtship signals (Endler 1992). Adult fiddler crabs are relatively small, nontoxic, poorly defended morphologically, and highly conspicuous to their predators, primarily shorebirds, as they interact socially on the surface of open intertidal mud and sand flats. Research on fiddler crab visual and nonvisual systems for predator detection and avoidance and on male courtship signals and mechanisms of mate choice suggests that characteristics of these systems have strongly biased how females choose mates and which male signals are

attractive. This conclusion has important general implications for understanding sexual selection and signal evolution (Christy 1995, Dawkins and Guilford 1996, Endler and Basolo 1998).

There are other studies of how predation has shaped fiddler crab behavior that have general implications, including studies of predator detection and avoidance by hiding in refuges (Koga et al. 2001, Hugie 2004, Jennions et al. 2003, Pratt et al. 2005, Wong et al. 2005) and studies of risk reduction by aggregating in a "selfish herd" when individuals are far from safe sites (Viscido and Wetthey 2002). For lack of space, I do not review these topics here. I concentrate on how predation influences reproductive ecology and behavior.

Before I discuss (1) the effects of reproductive timing for predator avoidance by larvae on courtship and mating behavior and (2) how antipredator adaptations have biased courtship signal evolution, it will be useful to give a brief overview of the diversity, distribution, and general patterns of reproduction in the genus *Uca*.

### Systematics and Mating Systems

Rosenberg's (2001) comprehensive review and synthesis of the systematics and taxonomy of the genus *Uca* (see also Rosenberg 2006) produced a detailed and credible phylogeny for the group based on adult morphology, with tree branching constraints suggested by a coarser phylogeny based on 16S ribosomal DNA sequence (Sturmbauer et al. 1996). There are now 97 recognized species, compared to the 67 species and numerous subspecies described by Crane (1975), the previous authority. Especially pertinent for this chapter, *Uca musica*, the name I used previously for a species that has figured prominently in my studies of courtship and mate choice, becomes *U. terpsichores*. There are three major branches in the genus: (1) a basal clade of nine species, which includes one species, *Uca tangeri*, in the eastern Atlantic, the only *Uca* species in that region, and eight species in the Americas: six in the tropical eastern Pacific and two in the western Atlantic and Caribbean; (2) a "crown" American clade of 57 species, 21 in the western Atlantic and Caribbean and 36 in the eastern Pacific (nearly all tropical); and (3) an Indo-Pacific clade with 39 species (again, mostly tropical).

DeRivera and Vehrencamp (2001) summarized the ecological and social correlates of mating systems in fiddler crabs within a phylogenetic perspective. There are two general modes of mating in the genus. Males of many American species (but not those in the basal clade) court from and defend burrows to which they attract females for mating and in which females breed. Females search for mates and breeding burrows by leaving their own burrows, walking on the surface, and sequentially visiting from a few males (one or two minimum, *Uca pugilator*; Christy 1983) to many (up to 106! *U. crenulata*; deRivera 2005). This can take an hour or more, and the female may move many meters in short punctuated steps as she stops at one male's burrow after another (repeat visits are extremely rare). Mate choice is indicated when the female stays in a male's burrow, and he plugs the entrance, sealing himself and the female below. After mating, the female ovulates, fertilizes, extrudes, and attaches her eggs to her abdominal appendages ("oviposits") in an enlarged terminal chamber of the burrow. She typically will stay in this burrow for about two weeks until she releases her planktonic

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Table 10.1. Characteristics of the species of fiddler crab (genus *Uca*) discussed in this chapter.

Clade	Species	Predation <sup>a</sup>	Mating Location	Male-Built Structure
American	<i>beebei</i>	++	Male's burrow, surface	Pillar
	<i>crenulata</i>	-	Male's burrow	None
	<i>pugilator</i>	++	Male's burrow	Semidome
	<i>pugnax</i>	+	Male's burrow	Semidome (rare)
	<i>stenodactylus</i>	++	Male's burrow, surface	None
	<i>terpsichores</i>	++	Male's burrow	Hood
Basal	<i>stylifera</i>	+	Surface	None
	<i>tangeri</i>	+	Male's burrow	None
Indo-Pacific	<i>annulipes</i>	--	Male's burrow, surface	Semidome (rare)
	<i>lactea</i>	-	Male's burrow, surface	Semidome
	<i>paradussumieri</i>	-	Female's burrow	None
	<i>perplexa</i>	--	Male's burrow, surface	Lip, pillar (rare)
	<i>rosea</i>	-	Male's burrow, female's burrow, surface	None
	<i>tetragonon</i>	-	Male's burrow, surface	None

<sup>a</sup> ++, +, -, --: very frequent to very infrequent predation of adults based on personal observations and the opinions of other field researchers.

larvae. Most of the species showing this mode of mating are small to medium in size (typically <2 cm carapace width), and they live at high densities on well-drained sediment in the upper intertidal or supratidal zone. In contrast to this pattern of female searching, in many of the Indo-Pacific species and those in the basal clade in the Americas (with notable exceptions), it is the males that search for mates among nearby female burrow residents. Courtship may not include male claw waving but always includes (poorly known) tactile stimulation and possibly seismic signals transmitted through the substratum. The pair usually mates on the surface at the entrance of the female's burrow, and the female subsequently breeds alone. Many of the species with this male-searching behavior are relatively large (>2 cm carapace width) and live at lower densities in muddier sediment in the mid to upper intertidal zones. Several species in the Americas and in the Indo-Pacific mate both on the surface and in males' burrows (Table 10.1; *Uca beebei*, Christy 1987; *U. lactea* and its relatives, Backwell and Passmore 1996, Murai et al. 1987, Nakasone and Murai 1998; *U. tetragonon*, Murai et al. 1995, Goshima et al. 1996; *U. stenodactylus*, J.H. Christy, personal observation; and a few others, Murai et al. 1996).

### Temporal Patterns of Reproductive Behavior

Fiddler crabs have been the subjects of extensive research on physiological and behavioral rhythms, their endogenous properties and control, and their adaptive significance (for a review, see Thurman 2004). Because fiddlers live in the intertidal zone and

emerge from their burrows primarily when they are exposed to the air during the day, the diurnal and tidal cycles together determine when they are active. The phase relationship between these physical cycles varies in time and across tidal regions but predictably so. It is not surprising, then, that the daily activity and biweekly or monthly reproductive rhythms of fiddler crabs are governed by endogenous clocks. There is one clock with a 24 hour circadian period and a continuing debate whether there is but one other clock with a 12.4 hour circatidal period or two other clocks with 24.8 hour circalunidian periods that are 180° out of phase, each tracking one of the two semidiurnal tides. Thurman (2004) suggests that the two circalunidian clock model is more likely the correct one. The period of reinforcement of the circadian and one or the other of the two circalunidian clocks is about every two weeks. Hence, the interaction between these three clocks, set to local conditions, can flexibly govern the timing of reproductive cycles with respect to the spring-neap tidal amplitude cycle (14.8 day average period) on coasts with semidiurnal tides (e.g., western Atlantic and tropical eastern Pacific) and with respect to the tropic-equatorial tidal amplitude cycle (13.7 day average period) that dominates the tidal pattern on some coasts with mixed semidiurnal tides (e.g., eastern Gulf of Mexico).

#### ***Timing of Larval Release***

Biweekly or monthly cycles of larval release have been described for 10 species of fiddler crabs (family Ocypodidae), and numerous species of intertidal crabs in several other families (e.g., Grapsidae, Gecarcinidae, Xanthidae; for reviews, see Morgan 1995, Morgan and Christy 1995, Christy 2003, and Thurman 2004). Intra- and interspecific comparative studies indicate that these cycles result from the hierarchical expression of diel (circadian clock), tidal (circalunidian clock), and tidal amplitude (circadian  $\times$  circalunidian clock interaction) rhythms (Morgan and Christy 1994, Morgan 1996, Kellmeyer and Salmon 2001). Most intertidal crabs release larvae at night, close to the time of high tide on the days of the month with larger amplitude tides, typically during the spring or tropic tides. As a result, newly hatched larvae move rapidly on nocturnal ebb currents from shallow habitats where they are released, to the deeper coastal ocean where they grow and develop. Since small planktivorous fish are numerically most abundant in shallow water, and most feed primarily during the day (Morgan and Christy 1995), emigration, a consequence of the timing of larval release, allows crab larvae to escape many predators. Several weeks later fiddler crab megalopae (postlarvae) immigrate into estuaries, primarily on nocturnal flood tides, and settle in adult habitats (Christy and Morgan 1998). The predator avoidance hypothesis as an explanation for the reproductive timing of intertidal crabs has received strong support from comparative studies; larvae that are protected by spines or cryptic colors do not emigrate from shallow waters and adults of the species with these larvae lack the strong temporal patterns of reproduction that characterize species with vulnerable larvae (Christy 1986, Morgan and Christy 1995).

#### ***Timing of Courtship and Mating***

Precise timing of larval release, a female behavioral trait that promotes larval survival, is known in several species to be preceded by cycles of female sexual receptivity and

male investment in courtship (e.g., *Uca pugilator*, Christy 1978, 1983; *Uca terpsichores*, Zucker 1976, Christy et al. 2001, Christy 2003; *Uca perplexa*, Murai and Backwell 2005). Little is known about the hormonal control of crab reproductive behavior or the role of endogenous rhythms in hormone production. However, since larval release ends a sequence of reproductive events that begins with courtship and mate choice, and since larval release is under endogenous control, it is likely that the earlier stages of breeding are, as well.

Temporal patterns of investment in courtship by male *U. terpsichores* additionally suggest that endogenous rhythms govern the early stages of the reproductive sequence. Courting males of this species sometimes build sand hoods at the entrances of their burrows; these structures attract mate-searching females (Christy et al. 2002; see also below). Hoods are destroyed by the tide and must be built anew daily. On the hourly scale, during the tidal activity period, most males build their hoods before females begin to search for mates (Fig. 10.1); hence, males do not adjust their investment in courtship signaling according to their perception of the number of females that are receptive on a given day, for example, through encounter rates with mate-searching females. On the biweekly temporal scale, the mating rate of hood builders is about 9% per day and does not vary with the number of hoods built each day (Christy et al. 2001). This constant proportional relationship between the male hood building cycle and the female cycle of receptivity and mate choice indicates that these two cycles

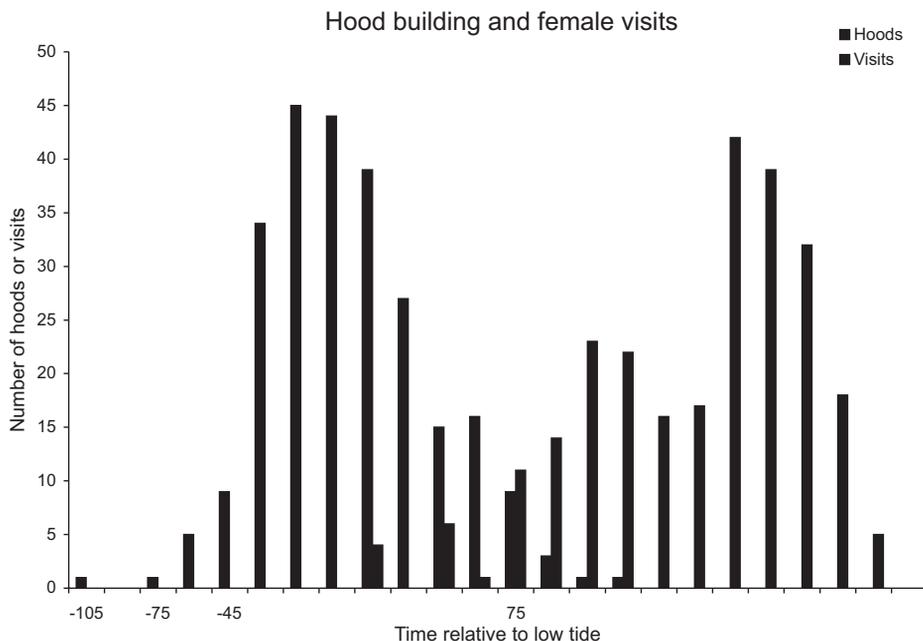


Figure 10.1 Timing of hood building (open bars) by male *Uca terpsichores* and female visits to courting males (solid bars) during the tidal activity period. The counts of newly appearing hoods and visits each 15 minute interval were summed across three consecutive days at the beginning of a biweekly reproductive cycle.

are coincident. Expression of a behavior in anticipation of or coincident with favorable conditions are the classic characteristics of endogenous rhythms. The daily number of hoods is an accurate proxy (by a factor of 0.09) for the daily number of females seeking mates, for the number of females that begin incubation about 1.5 days later, and for the number that release larvae about 15 days later. If males adjusted their tendency to build hoods according to the number of mate-seeking females the preceding day, the number of hoods would have proportionately lagged and overshoot the number of receptive females early and late in the reproductive cycle, respectively.

Male *Uca terpsichores* evidently invest in courtship exactly according to the expected payoff. This may be true generally for fiddler crabs (*U. pugilator*, Christy 1978; *U. crenulata*, deRivera 2003; *U. pugnax*, Greenspan 1982; *U. perplexa*, Murai and Backwell 2005) because the sexes share the same endogenous mechanism governing biweekly reproductive cycles (but see Kim and Choe 2003). Biweekly (semilunar) reproductive rhythms, whether endogenous or not, are common among shallow-water marine organisms presumably because selection affecting adults or young varies predictably with the light and tidal cycles across the geographic range of a species (e.g., Warner 1997, Yamahira 2004). In contrast, in terrestrial animals, with the exception of seasonal cycles, temporal patterns in sexual competition usually are thought to reflect day-to-day assessments and strategic decision making rather than the expression of underlying rhythms. Hence, the terrestrial and marine realms may differ in the predictability of predation and, conversely, safe periods on longer (>24 hours) but subseasonal time scales. This may account for a fundamental difference in the mechanisms that regulate the expression of antipredator behaviors and their diverse effects on the rest of the behavioral phenotype.

### **Timing of Aggressive and Coercive Elements in Courtship**

Cycles of mate choice by females may not perfectly anticipate ovulation and fertilization cycles (Christy 1978, deRivera 2003, Murai and Backwell 2005), and this may affect male courtship tactics. It is not known whether such tactics are endogenously controlled or reflect male assessment of the reproductive state of individual females (e.g., Goshima et al. 1996, Murai et al. 2002). Early in a breeding cycle, after choosing a mate, some females take longer to ovulate compared to females that mate at or after the peak of the cycle. Since males usually guard their mates until they oviposit, a male who attracts a mate early in a cycle will guard longer, feed less, and miss more future mating opportunities than a male who attracts a mate later. This lag between female behavioral receptivity and ovulation may create a conflict between the sexes over whether to commit to pairing in a plugged burrow (Jormalainen 1998; see also chapter 8). On the one hand, due to the male-based sex ratio, mating opportunities per male are rare, and males should accept any sexually receptive female. Guarding time is lost feeding time for the female, too, so the lag between mate choice and oviposition should never be large, even when a female chooses a mate early. In addition, one might expect "early" females to be well fed and to produce relatively large clutches, which would additionally favor their acceptance and guarding by the male. On the other hand, sexual selection should always favor males that increase their mating rate by decreasing the time they spend with each mate. Male *U. pugilator* can mate with up to three females in a single breeding cycle while at the same burrow

(each in a separate incubation chamber; see Christy 1982), and the record is four for *U. crenulata* (deRivera 2003). Males always should prefer receptive females who are ready to ovulate so that they can return quickly to the surface and attract additional mates. On balance, a conflict seems likely; how is it resolved?

Males of several other mate-guarding crustaceans that mate when the female molts distinguish among potential mates on the basis of time to molting, which they probably assess after contact and reception of chemical cues (e.g., Jormalainen 1998). Although a male fiddler crab may chemically assess a female's readiness to ovulate (Murai et al. 2002) after she has entered his burrow, it would be more efficient for the male to screen the female at an earlier stage in courtship. One possible method may be to include threats in the courtship sequence. Threats (e.g., chela flicks, lunges, short chases) are commonly given by males during courtship in species in which males attract females to their burrows. In *U. pugilator* (Christy 1983), *U. beebei* (Christy 1987), *U. terpsichores* (Christy et al. 2002), *U. lactea* (Murai et al. 1987), *U. tetragonon* (Goshima et al. 1996, Koga et al. 2000), and *U. rosea* (Murai et al. 1996), females that are not receptive nevertheless leave their burrows and move on the surface, perhaps in search of a better burrow or feeding area or to escape aggression from neighboring males (Murai et al. 1987). Males court these females and females visit these males, perhaps as a way to reduce their predation risk while changing burrow locations. Clearly, it is not in a male's interest to court a female who will not mate. As a female nears ovulation, her tendency to approach courting males may increase (decreasing response threshold; Murai and Backwell 2005) while her tendency to feed may decline. Nonreceptive female *U. beebei* (Christy 1988b) and *U. terpsichores* (Christy et al. 2002) feed, sometimes extensively, and they do not respond as quickly or directly to courting males as do receptive females. Males who readily switch from an attracting wave to a threat upon the slightest hesitation from the female may most effectively repel nonreceptive females and receptive females that are several days from ovulation. If true, males should less often threaten females as the breeding cycle advances and proportionately more wandering females become ready to ovulate. At the same time, the costs of failing to exclude a female that requires a longer mate guarding time will diminish because the chance of attracting an additional mate after emerging from guarding will decline quickly as the cycle wanes. This will additionally favor eliminating threats from courtship on and after peak mating days.

The diminishing cost to males of committing to mate guarding as a cycle peaks and then wanes also should favor more frequent use of coercive behavior later in each breeding period. Males of some species (Crane 1975) cut off, push, herd, capture, carry, and otherwise directly and aggressively attempt to force females into their burrows (Zucker and Denny 1979). Males of other species in which the female usually follows the male into his burrow sometimes use tactics that get the female to enter his burrow first (Murai et al. 1996). A female always has ultimate control over mating because she must lower her abdominal flap to allow the male access to her gonopores for intromission and sperm transfer. However, by forcing a female into a burrow and keeping her there shortly before she will ovulate, the male may leave the female no choice but to mate with him if she is to produce a clutch and begin incubation on time. Hence, as the reproductive cycle peaks and wanes, aggressive elements may become less frequent in courtship sequences that function to attract females into males' burrows, and coercive interactions may become more frequent.

### ***Staying on Time by Choice of Breeding Site***

In species that breed in male-defended burrows, selection for precise timing of larval release to promote larval escape from predators may affect not only when but also where females choose to breed. Comparisons of features of the burrows females enter and leave with those in which they stay and mate indicate that burrow structure affects mate choice in *U. pugilator* (deep, stable burrows; Christy 1983), *U. annulipes* (deep but compact burrows of moderate size; Backwell and Passmore 1996), and *U. crenulata* (longer burrows of a specific shaft diameter; deRivera 2005). Indeed, burrow features are more important than male size as criteria for mate choice in these species, at least during mating peaks. There are several possible ways that burrows may affect female reproductive success (Christy 1983, Christy and Salmon 1984), but until recently, there has been no experimental demonstration of such effects. DeRivera (2005) has published an exciting study of *U. crenulata* showing experimentally that the diameter of the burrow relative to the size of the female critically affects (how is not known) the timing of larval release and that females choose burrows that allow them to release larvae on time. Thus, predation on newly hatched larvae may select for female choice of breeding sites where they can incubate their eggs and release their larvae during safe periods. Choice of breeding sites should affect male–male competition for the burrows that females prefer. Linkage between mortality of young, female breeding site preference, and male–male competition has been demonstrated in *Uca pugilator* (Christy 1983).

### **Antipredator Behavior Biases Signal Evolution**

Predation on adult fiddler crabs appears to be far more common in the Americas (Backwell et al. 1998, Iribarne and Martinez 1999, Ribeiro et al. 2003) than in the Indo-Pacific (P. Backwell, M. Murai, and others, personal communication). Hence, most of my examples of how predation may bias signal evolution are of American species, but I include a few Indo-Pacific species to illustrate behavioral patterns where predation evidently is relatively infrequent. At best, these comparisons are only suggestive because species in the two regions diverged long ago (Rosenberg 2001), making it difficult to separate the effects of history and predation.

### **Theory**

Female mating preferences are thought to evolve primarily due to selection that is a consequence of mate choice (Kokko et al. 2003, Fuller et al. 2005). In this nearly universal view, preferences are adaptations for choice of a mate that will contribute the most to female or offspring fitness. However, it has become increasingly apparent that preferences are based on features of female sensory-response systems that evolve for a variety of reasons unrelated to mate choice (Endler and Basolo 1998). Research on fiddler crab courtship, mechanisms of mate choice, and mating preferences has contributed to this view as expressed in the sensory trap model of signal evolution (West-Eberhard 1984, Christy 1995). A sensory trap occurs during courtship when a signal elicits a response that has an ecological or social function other than mate

choice. The receiver responds to the signal because it mimics stimuli that elicit the response for the other function. The words “mimicry” and “trap” are sometimes thought to imply that sensory trap preferences must be costly and maladaptive (e.g., Marcías and Ramirez 2005, Stuart-Fox 2005). This implication does not follow from the sensory trap model (Christy 1995, 1997, Dawkins and Guilford 1996); the preference may or may not be costly. Most important, the net effect of a sensory trap response on fitness, across all the contexts in which the response is made, must be positive or the response will be eliminated (Christy 1995).

In courtship, sensory trap preferences may often be beneficial because they increase the efficiency (by decreasing time or energy expenditure) of mate localization and because they reduce predation risk during mate searching. Research on the function of the behavioral mechanism that governs the female preference for sand hoods built by courting male *Uca terpsichores* has provided a detailed example of a sensory trap preference that is based on an antipredator behavior. I begin this example with a brief overview of fiddler crab orientation and antipredator behavior and the contexts in which they function. This will help show how a behavior that reduces predation risk has come to play a role in mate choice.

### ***Predator-Escape Behavior, Vision, and Orientation Mechanisms***

When a fiddler crab detects a predator, it runs quickly back to the burrow it most recently left (Zeil and Layne 2002). Crabs can do this at night, if they are experimentally blinded, and if the burrow entrance is covered; they do not need to see their burrow entrance to find it. Indeed, if a crab is more than about seven to eight body lengths from its burrow (Ribeiro et al. 2006), the opening becomes invisible due to perspective foreshortening and the relatively poor resolution of the ventral portion of the crab's eye that “looks” at the ground. With vision of limited use, crabs rely on a remarkable mechanism, probably based on leg odometry, to construct a path map to their burrow and safety (Layne et al. 2003a, 2003b). The operation of this mechanism is revealed by the near alignment between a crab's transverse axis and the bearing back to its burrow.

Crabs that leave a burrow eventually abandon their path map to it and use other means to reduce their predation risk when a predator comes near. Perhaps most often, the crab will visually move to where a nearby resident disappeared and thereby gain access to a burrow. If for any reason these cues to safety are unavailable, crabs will run to a nearby stone, shell, piece of wood, plant part, or even a lump of sediment and remain motionless at the base of the object. Although critical studies have not been done, this presumably reduces the crab's risk of predation because it makes the crab more difficult for the predator to detect. Landmark orientation, this tendency to orient to objects projecting from the surface, seems to be widespread in the genus *Uca* (Herrnkind 1983, Christy 1995) and is also expressed in other semiterrestrial crabs (Diaz et al. 1995).

Fiddler crab visual systems have three features that are well designed for predator detection and avoidance (Zeil and Hemmi 2006): (1) they have a zone of high vertical resolution in a band around the equator of their eyes (Zeil and Al-Mutairi 1996), (2) they keep this zone aligned with the horizon through fine muscular control of all three axes of rotation of their long eyestalks (Nalbach et al. 1989), and (3) they

classify as threatening nearly all moving objects they see above their visual horizon (Layne et al. 1997). Crabs look for, detect, classify, and avoid even small predators that are many meters away. These features of crab visual systems and orientation mechanisms operate during mate search producing preferences that shape male courtship signals and signaling behavior.

### **Structure Building by Courting Males**

Courting males of 18 species of fiddler crabs are known to build structures at the openings of their burrows to which they attract females for mating (listed in Christy 1988a, Christy et al. 2001, plus *Uca uruguayensis*, P. Ribeiro, personal communication). Most structure builders are in the crown American clade, but *U. lactea* and its relatives in the Indo-Pacific also sometimes build structures. Structure building and structure size and shape vary considerably. Male *U. terpsichores* build sand hoods (Fig. 10.2a), the largest structures relative to male size in the genus, and they do so following a biweekly or monthly (upper intertidal populations only) cycle. Male *U. beebei*, a species that is sympatric with *U. terpsichores* (but with little spatial overlap) and is about the same size, build narrow mud pillars (Fig. 10.2b) that are as tall as hoods. Both structures attract females to males' burrows for mating (Christy et al. 2003a).

We studied how hoods attract female *Uca terpsichores* by recording the responses of females to courting hood-building and nonbuilding *U. terpsichores* males with and without natural and replica hoods. These experiments controlled for differences between builders and nonbuilders that might affect their attractiveness (Christy et al. 2002). Female *U. terpsichores* significantly more often approached the males that courted them if they had hoods (or replicas) at their burrows. Hoods did not attract females from a distance, nor did they affect female mating decisions after they reached males' burrows. We placed hood replicas about 3 centimeters to the side of males' burrow entrances and found that females sometimes moved to the offset replicas, not to the courting males as the males led the females to their burrows.

Why do females preferentially move to hoods when they leave one burrow and go to the next? Sexually receptive and nonreceptive female *U. terpsichores* both preferentially approach males with hoods (Christy et al. 2002), suggesting that they use the same orientation mechanisms. As they leave one male's burrow and move to the next, females must abandon their path maps and move on. This sometimes is clearly evident in a "break" in the transverse orientation of the female toward the burrow she is leaving. At this point, the female quickly moves to the next burrow by either following a male or moving to a hood. The results of several experiments with and without model predators support the hypothesis that hoods elicit landmark orientation (Christy 1995, Christy et al. 2003a, 2003b). The most telling experiments showed that receptive and nonreceptive females, when not given burrows, moved spontaneously to hoods (replicas), shells, stones, and pieces of wood. We added these objects to courting males' burrows and found that receptive females did not prefer hoods over the other natural objects that are common on the beach (Christy et al. 2003b).

Comparative studies also support the idea that the female preference for hoods is based on landmark orientation. Males and females of species that do not build structures run to hoods and pillars when they are chased by a model predator (Christy 1995, Christy et al. 2003a). Using cast replicas, we switched structure types between

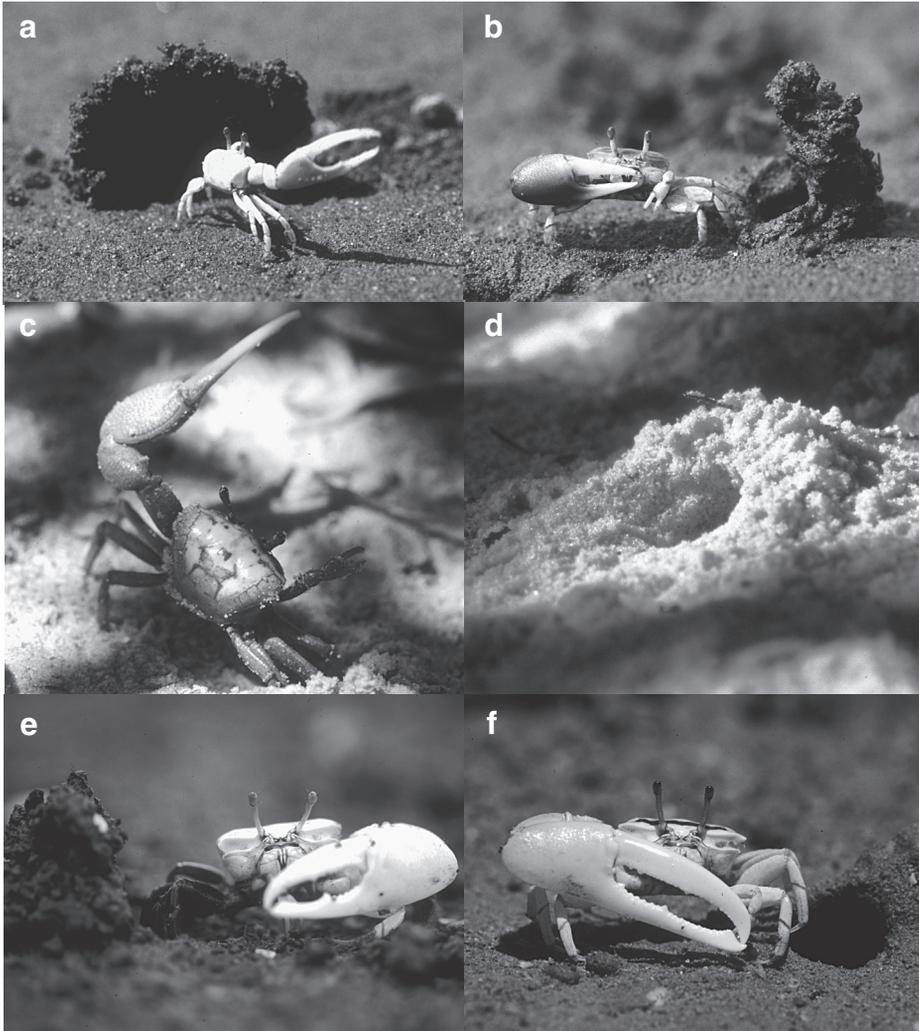


Figure 10.2 Male fiddler crabs and their structures: (a) *U. terpsichores*, hood, Rodman, Panama; (b) *U. beebei*, pillar, Rodman, Panama; (c) *U. pugilator*, Cayo Pelau, Florida; (d) massive semidome of *U. pugilator*, Cayo Pelau, Florida; (e) *U. lactea*, semidome, Aitsu, Japan; (f) *U. perplexa*, lip, Okinawa, Japan. All photographs by the author.

*U. beebei* and *U. terpsichores* and found that mate-searching females of both species preferred hoods; structure preferences are not species specific as they should be if they have evolved for mate choice. Female *U. stenodactylus*, a species that does not build structures, show a significant but relatively weak tendency to move to hoods, pillars, and other objects. Perhaps the tendency for females to orient to structures is enhanced in structure-building species. In these species, male-built structures may be the most abundant objects for landmark orientation (at least during courtship peaks), and they may indicate especially safe sites because, unlike other objects, they nearly always lead to an open burrow.

I know of no other example of a sexual signal that is attractive because it elicits an antipredator orientation response. Females of many species are at an increased risk of predation when searching for a mate and many modify their behavior to reduce this risk (Jennions and Petrie 1997, Hazlett and Rittschof 2000), suggesting that signals allowing safe searching should be common. Warner and Dill (1999) proposed that the bright sexual colors and vigorous displays of some male reef fish indicate to attentive females that it is safe to visit these males. And it seems likely that properties of signals that improve efficacy are favored in part because they facilitate detection (Fleishman 2000) and localization of the courting male, perhaps allowing the females to approach directly and with less risk. Either signals that elicit predator escape behavior are truly rare, or they have gone unnoticed.

### **Origins of Structure Building**

We have demonstrated current sexual selection by a female preference for structure building in two species that build tall structures. Recent observations and experiments indicate that hoods have a second function. Male *U. terpsichores* that had hood replicas placed beside their burrow entrance sometimes led females to these objects instead of to their burrows. Experiments (Ribeiro et al. 2006) have shown that male *U. terpsichores* that have had errors introduced experimentally in their path maps significantly more often and more quickly relocate their burrows if they have hoods at the entrance. Courting males without hoods sometimes fail to relocate their burrows and become wandering rogues (Christy et al. 2002). Thus, structure building in *U. terpsichores* may currently be under sexual selection by indirect male–male competition for resource-holding ability and by a female preference, and both may be mediated by landmark orientation, an antipredator behavior.

Some species build structures that are too low to be imaged in the acute zone of the eyes of adults, so they may not elicit landmark orientation. Male *U. pugilator* make massive but low semidomes (Fig. 10.2c,d; Christy 1982). *U. lactea* make more delicate low semidomes (Fig. 10.2e; Kim et al. 2004), and *U. perplexa*, a close relative, makes low asymmetrical lips on their burrows (Fig. 10.2f). Presumably, structure building evolved from sediment manipulation behavior that produced at first only simple low ridges or lips around the burrow entrance. How do males benefit from making low structures? Semidomes and even lips tilt the image of the burrow opening up from the horizontal. This will reduce perspective foreshortening and should make the opening visible from a greater distance, at least when seen from the front. Discriminating this oblate image from the visual background noise would be a formidable task (Zeil and Layne 2002) that might be made easier if the crab knew where to expect the image. Recent research has shown that fiddler crabs can use their nonvisual path map to project the location of their burrow in visual space (Hemmi and Zeil 2003). They use this ability to determine when an approaching crab is on a trajectory toward their burrow so they can defend their ownership. They could also use it to identify the area in their visual field where the image of their burrow opening should be if it were large enough to be seen. This would be useful to a male if spatially complex courtship interactions far from his burrow produce errors in his path map causing him to lead a female to the wrong place or to err when running back to his burrow to escape a predator. This function for lips and

semidomes is entirely conjectural, but it is consistent with the dual function of hoods in *U. tepsichores* that we are just beginning to understand.

Finally, it also is possible that both lips and semidomes allow females to see and more easily orient to the burrow entrance when they are close to it at the end of an approach. When approached by a female, courting male *U. perplexa* (lips) sometimes do not enter their burrows first. Instead, the male briefly and partially enters, sometimes repeatedly (J.H. Christy, personal observations), and then steps to the other side of the opening and waits for the female to go into the burrow first (Nakasone and Murai 1998). Perhaps this stimulates the female to find the burrow by orienting to where the male appears to enter the ground. The tilted image of the opening would only enhance her ability to locate the entrance by presenting an additional visual cue. Avian predation on this species and *U. lactea* is very infrequent. Landmark orientation may not bias sexual selection for tall structures in these species, leaving their architecture to be shaped by other orientation mechanisms used by both sexes to find the male's burrow.

### ***Claw Waving and Other Visual Signals***

Fiddler crabs are best known for their extreme sexual dimorphism, which is most apparent when males wave their single greatly enlarged cheliped, usually toward passing females, at least in American species (Pope 2000). Claw waving would seem to be a classic example of signaling behavior that is selected by female choice. Remarkably, there is no experimental evidence that females are attracted by claw waving (but see Oliveira and Custódio 1998). The best evidence, based on an analysis of videotapes of courtship (Backwell et al. 1999), is correlative, making it difficult to isolate which features of the wave or waving context are most important. Murai et al. (1996) noted that females of several species mate on the surface with males that do not direct claw waving toward them. Male *U. lactea* (Yamaguchi 1971) and *U. beebei* (J.H. Christy, personal observations) without large claws nevertheless can mate on the surface. Christy and Salmon (1991) suggested that the vertical components of the claw wave may be especially stimulatory given the female's highly structured perceptual field. Perhaps claw waving serves simply and primarily to attract the female's attention and reveal the location (and perhaps the species) of the male (Land and Layne 1995). Just as structures may elicit landmark orientation, claw waving and other male visual signals, such as the raised-carpus display of *U. beebei* (Christy 1985), may play to the tendency for crabs to follow residents to their burrows.

### **Future Directions**

Predictable selection favoring precise timing of larval release for predator avoidance and equally precise timing of female receptivity and male investment in courtship have apparently led to their control by endogenous timers, one with a circadian period and perhaps two with circalunidian periods running in antiphase. Definitive experimental demonstration of the roles of these timers in the biweekly behavioral cycles that are so apparent in the field is unlikely to be forthcoming for obvious practical reasons. However, indirect evidence may be sought in long-term monitoring studies

with an eye toward the predictive, rather than the reactive, nature of variation in these temporal patterns. For example, species that live in the upper intertidal zone experience an approximately seven-month cycle in which one of the two spring tides is higher and larger in amplitude. This cycle is a consequence of the changing phase relationship between the perigee and apogee cycle (varying distance of the moon from the earth, due to the moon's elliptical orbit) and the syzygies (approximate alignment of the sun, earth, and moon). If only one of the two spring tides is suitable for larval release, courtship and mating should be relatively more intense about two weeks prior to those tides, during the lunar phase with relatively low tides. Where in an estuarine or associated coastal system a species lives may also affect reproductive timing and synchrony. We have found that *Uca terpsichores* releases larvae on the two to three morning high spring tides just before dawn, skips a day, and then releases larvae on two to three subsequent evening tides, producing a relatively drawn out six to eight day hatching period (J. Christy and P. Backwell, unpublished observations). This species often lives on medium-energy sand beaches near or just inside the mouth of an estuary. Because oceanic waters are nearby, nighttime seaward migration of newly hatched larvae may be less important, permitting larval release on spring tides just before dawn, an atypical pattern for estuarine species. Differences in the temporal variance of reproduction will affect the operational sex ratio, perhaps also mate guarding tactics, and as suggested here, the use of aggressive and coercive elements in courtship. Finally, the tidal regimes on the coasts where fiddler crabs live vary considerably (see Thurman 2004); so, too, do the times best for larval release (Morgan and Christy 1994), yet the effects of this variation on the timing of courtship and mating, mating modes, and courtship behavior have hardly been explored.

We are just beginning to understand the structural and functional organization of the fiddler crab visual system and how it interacts with the nonvisual orientation mechanism to keep crabs safe from predation as they feed, defend their burrows, change locations, and court or be courted. I have argued here for a dominant role for predator detection and escape behavior in the courtship (signals and responses) of smaller fiddlers that live in open habitats in the Americas where predation is frequently seen. Some of these ideas could be tested by comparing the visual systems, orientation mechanisms, courtship signals, and responses of these species with those that experience less frequent predation, including larger species in the Americas (less preferred prey; Backwell et al. 1998), and species in the Indo-Pacific, where predation appears to be infrequent. For example, coercive courtship tactics that stimulate predator detectors and elicit escape responses would not be expected in species that are not frequently startled to their burrows by predators, while coercive behavior that elicits burrow defense mechanisms would be. Systematic comparisons of fiddler crab courtship signals and displays that may operate as sensory traps based on antipredation and burrow defense behavior would be informative.

## Summary and Conclusions

Predation affects fiddler crab reproductive timing, male competition for females, visual systems and orientation mechanisms, mechanisms and patterns of female choice, and the kinds of signals males use to attract females for mating. Predation is

pervasive in the lives of these animals as both larvae and adults; so, too, are adaptations to avoid being eaten, and these adaptations strongly influence how crabs communicate and compete for mates. The bulk of theoretical and empirical research on courtship signal evolution considers predation to be a constraint on signaling behavior, signal elaboration, mate sampling, and choice (e.g., Koga et al. 1998, Acharya and McNeil 1998, Jones et al. 2002). Fiddler crab courtship shows how predation can also be a creative force in signal evolution. Male-built structures and even the well-known waving display of these animals may be selected by preferences that allow females to better detect, locate, and visit males safely. The number of examples of sensory traps in animal courtship is increasing (Christy 1995, Sakaluk 2000, Córdoba-Aguilar 2002, Fleishman 2000, Rodd et al. 2002, Stålhandske 2002, Zimmer et al. 2003, Marcías and Ramirez 2005). These studies show that it is not sufficient to ask what a courtship signal may indicate about the benefits a female and her young receive as a consequence of mating with males that use that particular signal. To understand the origin and maintenance of a mating preference and how it shapes signal evolution, it is necessary to ask how the sensory and behavioral mechanism on which it is based evolves, particularly how the mechanism functions and is selected in other social and ecological contexts (Stuart-Fox 2005).

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