Signaling Safety

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Like a seasoned ballplayer edging cautiously toward second, ever alert to a throw from the mound, a female "dancing" fiddler crab (*Uca terpsichores*) ventures uneasily from her burrow. Her ovaries ripe with eggs, she leaves the safety of her burrow to find a mate. As she moves—exposed—from one eager suitor to the next, the risk this little crab faces is vastly more serious than being thrown out at second base. Great-tailed grackles (*Quiscalus mexicanus*) and a variety of crab-eating shorebirds are nearly always within attack range on her home beach in Panama. Yet mate-searching females seldom become bird food for the simple and remarkable reason that males use signals, sometimes including hooded structures built in the sand, to help keep females safe.

Fiddler crabs, genus *Uca*, are relatively small, often colorful, daytime-active crabs. They are typically less than three-quarters of an inch (twenty millimeters) wide, but can be as wide as an inch and a half (thirty-five millimeters). With ninety-seven species worldwide, they are in the family of "swift-footed" crabs, the Ocypodidae, and are closely related to the larger, usually nocturnal, ghost crabs.

All species of fiddler crabs are sexually dimorphic (that is, males and females differ in their appearance). Females have two small claws, which they use to feed. In contrast, one of the claws of a male is greatly enlarged to form a "major cheliped" that is far too large for feeding. As a secondary sexual characteristic, this is a remarkable appendage.

The male fiddler crab has one greatly enlarged claw, used for fighting and for signaling during courtship. Photograph of *Uca stenodactylus* by Christian Lukhaup.

In larger species this oversized claw can account for more than 50 percent of the male's total mass, proportionately far more than the largest rack of a male elk or moose or the most extreme horns of a rhinoceros beetle. Males use their large claws as weapons to fight other males for territory or burrows and as semaphores to signal females during courtship. The similarity between the waving large claw and the movement of the bow-arm of a vigorous fiddle player gives this group of crabs its English name.

Fiddlers are found throughout the tropics and on temperate coasts where the water temperature is typically more than 68 degrees Fahrenheit (20 degrees Celsius) during the months each year when crabs reproduce. Fiddlers produce planktonic larvae that develop in coastal waters. Larvae develop more slowly in colder water. Mortality due to dispersal by currents and predation increases with the length of larval development, which may explain why most species are found on temperate coasts where water temperatures are warmer.

Typically, fiddler crabs prefer habitats with little or no vegetation and they are most abundant on muddy-sand sediments in salt marsh and mangrove estuaries. The somewhat flattened species *Uca panamensis* even squeezes into burrows in the sand matrix under stones on the blistering cobble beaches of Central America's eastern Pacific coast. A few species live in dense stands of marsh grass and deep in mangrove forests.

In the right habitat, fiddler crabs can be extremely abundant. A study done decades ago in a Georgia, USA, salt marsh found 170 crabs per square yard (205 per square meter). As abundant primary consumers, fiddler crabs contribute importantly to energy flow and nutrient cycling in coastal ecosystems.

Fiddler crabs may occupy beaches at great densities, emerging from their burrows after the tide recedes. Photograph by Christian Lukhaup.

The common name of the European fiddler crab (*Uca tangeri*) is a little misleading inasmuch as most of its range is along the Atlantic coast of South and West Africa. Photographed in Guinea by Piotr Naskrecki.

Fiddler crabs feed more by method than by selection of specific food items. They rapidly scoop up bits of sediment into their mouths, where they scour off the organic material—diatoms, bacteria, fungi—and spit out much of the inorganic material in the form of small balls. The organic matter is mixed with water drawn forward from their lateral gill chambers, making a slurry in their mouths that is then ingested, filtered, and passed to the digestive gland for chemical processing and absorption. Periodically, a feeding crab will tip forward onto the sediment and discharge a brownish-green fluid, which may contain digestive juices and larger material that did not pass the gastric filters.

The general abundance of fiddler crabs makes them a staple in the diets of many shorebirds. Currently, there are no known fiddler crab species that taste bad or are toxic. They are commonly eaten by raccoons and larger crabs, and occasionally by snakes, fish, and even humans. Fiddler crabs have evolved refined mechanisms for predator detection and avoidance. Much of what is known about these adaptations comes from research done by Jochen Zeil and his students at the Australian National University, and by John Layne at the University of Cincinnati.

The first line of defense for a fiddler crab is cryptic coloration, which is especially well developed in females of species in the Americas, where, for reasons that aren't well understood, predation on fiddler crabs is particularly intense. If seen by a predator, a crab associated with a burrow has an effective means of escape. It uses a non-visual memory (probably based on information from leg movements) of where the burrow is located to make a straight-line sideways dash back to safety from as much as forty inches (a meter) away. The existence of a non-visual "path map" to safety is easily demonstrated by moving a crab on a piece of sandpaper when it is away from its burrow. When it runs back, it goes to where the burrow should have been if it too had been moved. This forced error also shows that crabs do not easily see their burrow openings. Recent experiments with *Uca* *terpsichores* in Panama showed that a crab can't see its burrow opening if it is more than about four to four and three-quarters inches (ten to twelve centimeters) away. Part of this visual limitation is due to the structure of crabs' eyes. They have a zone on the equator of their eyes that they keep directed toward the true horizon. Here they can see vertical objects easily, but their eyesight above and below their visual horizon is poor. In addition, surface irregularities and reflections create a "visual noise" that makes it difficult for a crab to see the narrowing dark slit of its burrow opening as it moves away from it.

Crabs that are close to a burrow are relatively safe. But what about the sexually receptive female (*Uca terpsichores*) trying to find a mate? When a male or female crab moves between burrows, at some point it must ignore its path map back to the burrow it last visited. Briefly, as the crab moves to the next burrow, it is at an elevated risk of falling prey to a shorebird. Crabs in this situation can reduce their predation risk in two ways. They can watch where a nearby crab disappears from the surface and follow it for a sure means to a burrow and safety. Or they can orient to shells, stones, and pieces of wood, and hide temporarily against them while danger is near; this is called landmark orientation.

By waving their claws high and moving repeatedly back to their burrows during courtship, male fiddler crabs of many species give females the first cue that can help them find a safe haven from predators. But such behavioral cues aren't always sufficient. In eighteen species of fiddler crabs, courting males sometimes make structures of mud or sand by their burrows called mud pillars or sand hoods. Studies over the past decade have shown that hoods are very attractive to females not because they advertise that the male could be of exceptional quality as a prospective mate but because they elicit risk-reducing landmark orientation. Working in Panama, Tae Won Kim of Seoul National University has provided new, strong evidence in support of this con-

Male European fiddler crabs (*Uca tangeri*) place mudballs around their burrows to defend their territories and attract females. Photographed in Guinea by Piotr Naskrecki.

After each tide, a male "dancing" fiddler crab (*Uca terpsichores*) constructs an elaborate hood over its burrow as a way of signaling to roving females a place of safety. Photographed in Panama by John Christy.

clusion. He experimentally attracted great-tailed grackles to where *Uca terpsichores* females searched for mates and found that, with increasing predation risk, the hoods were more attractive. Studies of fiddler crab courtship have helped decode these sexual signals.

Living on exposed mudflats and beaches around the world, fiddler crabs are particularly vulnerable to predation by a number of birds and mammals. Fiddler crabs on the surface are constantly monitoring for threats and are always aware of where the nearest safe shelter lies. These instincts manifest themselves both in impressive homing abilities when close to the home burrow and in remarkable behaviors while searching for a mate.

Unlike many females, who choose a mate based on his physical prowess, dancing fiddler crabs are more interested in the safety offered by their prospective mate's burrow. But this is not entirely surprising. When a runner rounds second base and tries to beat the throw to third, it is always better to pay attention to the third-base coach than to the cheering fans. Likewise, a female fiddler crab is more likely to make it safely home by being alert to the signals provided by the conspicuous hood over the male's burrow or by his waving claw.

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Patricia R. Y. Backwell is a senior lecturer at the Australian National University, Canberra. She also began her research career studying vertebrates—at night, in the rain. After a single visit to the mud flats in Panama, she put down her studies of frog communication to watch fiddler crabs in the warm sun instead.