Submarine Beetles

When the tide comes in, they batten down the hatches

by Tristram Wyatt

One summer evening, I watched the tide as it flowed gently up the creek like a river in reverse, creeping slowly over the salt-marsh shore in Norfolk, England. Out of the corner of my eye I saw a flash of red. A small, shiny black-and-red beetle had run in and out of its burrow; then, moments later, it disappeared under the rising water. I had not expected to see a land beetle here, but remembered reading about a species that lives in intertidal zones. Was this the salt-marsh beetle? Yes, it was *Bledius spectabilis,* a staphylinid beetle about half an inch long. During the next low tide, I discovered hundreds of burrows among the *Salicornia*—stubby little plants with water-swollen stems—that follow a contour around the salt-marsh creeks. Each burrow had a characteristic little heap of tailings above its entrance. The beetle I saw had emerged to scrape algae from around the burrow's entrance; then it carried the morsels down below, to be stored and later eaten in safety.

The intertidal zone is a difficult habitat that few animals can exploit. It is between land and sea, and a creature adapted to one is often poorly adapted to the other. Most intertidal animals are essentially marine species, such as crabs, that colonize the land. Their major risk is drying out on a sandy beach or rocky shore. By contrast, muddy salt-marsh shores in northern Europe, with their wetland acres of mud and quiet creeks, can support such land animals as spiders and mites that have moved into intertidal zones. Some have evolved great tolerance for seawater and can pump excess salt from their bodies; others simply develop behaviors to avoid getting drenched. Insects' cuticles are already impermeable to prevent water loss on land, but their main challenge has been to adjust to the tides. Those that have adapted to life in this difficult environment can exploit a rich habitat. The only serious competitor of *Bledius* is the gray mullet, a fish that comes in at high tide and also feeds on shoreline algae, leaving its toothmarks in the mud.

Colonies of salt-marsh beetles may occupy hundreds of square yards in the intertidal zone, with densities of a thousand adults per square yard. Colony perimeters are abrupt; no beetles dig burrows outside its boundaries. Sometimes the muddy beach is covered with beetles; on a given shore, they can number in the millions.

How does this land beetle survive the twice daily tides without any special bodily adaptations? It lacks, for example, snorkel tubes that might allow it to breathe under water. The answer lies in its behavior: the salt-marsh beetle builds and maintains a snug, watertight burrow. And the females are good parents, protecting their eggs and larvae from predators as well as from the tides.

When I first dug up some burrows, I could see that they were made with care and were perhaps the key to understanding the beetles' adaptation. The mud is firm and will hold any shape into which it is sculpted; a pencil hole made in the surface will last for many weeks. To study the burrows' shapes and preserve the eggs in place, I filled a few burrows with clear silicone resin. When the clear, hardened resin cast was removed from the mud, the egg chambers, each containing an egg, resembled miniature table-tennis balls stuck to the burrow's characteristic "wine bottle" shape. The burrow is about two and one-half inches long, with a living chamber one-quarter of an inch in diameter; a narrow neck three-quarters of an inch long opens out to the surface. The individual egg chambers extend from the living space.

I saw no evidence that burrows ever become flooded, even at high tide. To find out why, I sculpted an artificial burrow in clear agar (the kind of gel used for bacterial plates) and then submerged it. At first the narrow neck seemed effective in keeping the water out, while artificial burrows with wider openings quickly became flooded. Eventually, however, even narrow-necked burrows took on water. Since this didn't happen in the field, I introduced a female beetle into one of my transparent burrows to observe her during my artificial "high tide." A few minutes after the "tide" began, the beetle suddenly ran up to the burrow neck and sealed the entrance with a neat plug of agar "mud," taken in mouthfuls from the walls. When I tested for the same behavior in the salt marsh, burrows from which I removed the female did indeed flood, while those with a female inside remained dry. Rather than anticipate the tide and block their burrows in advance, females can continue to feed until the very last moment, when the water reaches their doorstep.

A dry, sealed burrow poses other dangers, however. Salt-marsh beetles usually burrow into "blue" mud, which is so tightly compacted that it allows no oxygen into the burrows. (This mud is unlike the surrounding, looser, aerobic "brown" mud, which is tinged by iron oxides.) During low tide, when the burrows must be re-

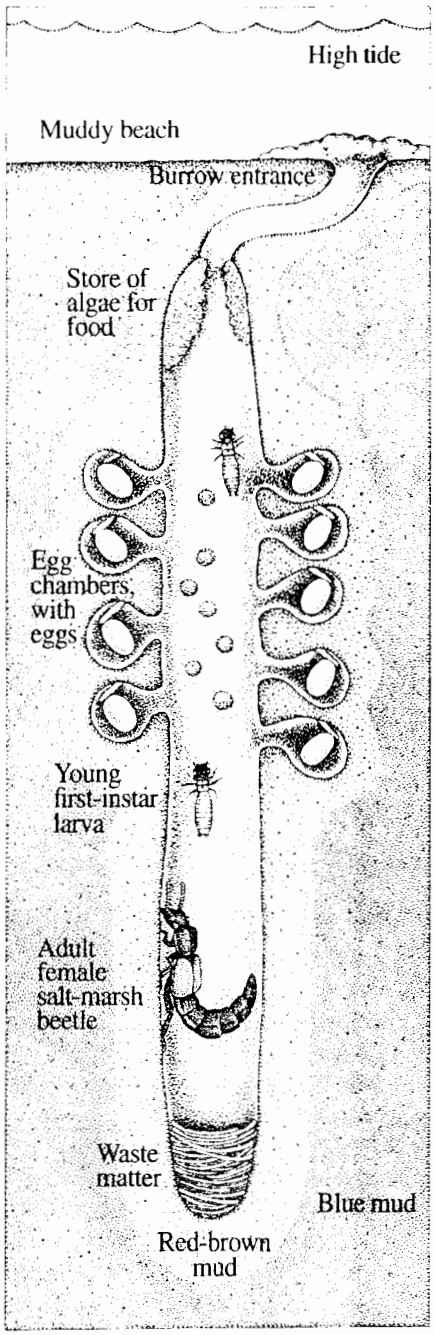
opened to allow oxygen replenishment, each beetle pushes up a new heap of tailings as it clears the entrance of washed-in debris. Only by plugging and unplugging her home in sync with the tides can a female salt-marsh beetle rear eggs and larvae in the airless mud—a life style very much like that of fiddler crabs.

For most of the year, male *Bledius* dig burrows very similar to those of females, but without the egg chambers. During the spring, they walk the marsh surfaces in search of mates, pausing at burrow entrances. If caught by the tide during their search, males grip the mud and flip their abdomens over their heads to create an air bubble. After the tide subsides, those that remain continue their search, but many have been washed away. When he finds a female that allows him access, the male stays with her for some hours underground, where copulation takes place. Right after mating, the male leaves and goes in search of another female.

After fertilization, the female lays an egg every other day in an individual chamber off the main burrow. After about twenty-seven days, the first-instar larva hatches, crawls into the main living chamber and begins to feed on its mother's algae collection. Eight days later, it leaves to dig its own burrow. After six more days, it molts into a second instar; then into a third, thirteen days later. It remains in its third and final instar stage for twenty-eight days. Finally, it spends about fifteen days as a pupa. A beetle's development from egg to adult takes about a hundred days during a British summer.

Since older larvae were found alone in their own burrows, I wondered at what stage they venture above ground. William Foster, of Cambridge University, and I went to the salt marsh about midnight with red flashlights to observe the tiny first instars. They come out only at night and walk over the beach exploring every crevice and dimple in the mud. (They were very interested in a hole I made with a pencil point.) If a larva ventures into an occupied burrow, the owner chases off the intruder, which continues to search for a home. Within dense colonies, the young larvae roam in tight circles during their search, but run quickly in straight lines through areas without burrow entrances. These movement patterns (also used by parasitoid wasps hunting for hosts) tend to keep the larvae within the colony.

For the dispersing larvae, survival is a race against two clocks. They have to find or dig a burrow before the next tide washes



The watertight burrow made by the female salt-marsh beetle enables her to raise a brood in intertidal zones. During high tides, she seals the entrance with mud, uncovering it later to admit air.
Patricia J. Wynne, after Poul Winter

them away or before the sun rises, whichever comes first. At night most predatory shorebirds are asleep. The mud is cool and damp, making burrowing easy. The air is relatively humid, so the larvae (accustomed to high humidity below ground) do not risk drying out. On a summer day, the salt-marsh surface is a baking desert covered with salt crystals.

By emerging at night, the instar larvae are protected from some hazards, but are exposed to others. During our nocturnal prowls, we noticed hundreds of carabid beetles, whose numbers on the muddy beach peak about midnight. Before long, we saw one bump into a first-instar salt-marsh beetle and eat it. Soon we realized that all over the marsh, *Bledius* larvae were being gobbled up. As though in a game of "blindman's bluff," the predators lunged in the direction of larvae as soon as their antennae touched one. Sometimes larvae escaped by suddenly running backward or forward (they can move just as fast in either direction) or by jerking their heads. With such tactics, they were able to escape about half the encounters with carabids. But when we plucked newly hatched first instars from maternal burrows and placed them on the beach, they were always caught. And when we removed females, we found that the burrows were soon invaded by carabid adults that fed on newly hatched larvae.

Once a larva has successfully emerged, run the midnight gauntlet on the beach, and dug itself a home, it may be safe. Most predators are too large to descend into a larva's burrow, which is very similar to that of an adult. For the rest of its life, the larva does not travel again, coming up to the burrow's entrance only to collect algae as adults do, and enlarging its burrow as it grows. Unlike adults, the larvae leave their feces neatly at the side of the burrow, instead of at the bottom.

One summer, we were fascinated to see a female parasitoid wasp walking along the flat mud, stopping at each heap of beetle tailings. We marked each one she visited with a little numbered flag. Within ninety-nine minutes she had visited sixty-two heaps, walking a total of fifty-nine feet, but there was more to the story. After investigating some heaps with her antennae, she quickly moved on. At others she patted the little mound with her antennae and then vigorously probed with her ovipositor to find the hole hidden below. If successful, she lifted up her wings and, ovipositor first, disappeared down the burrow for up to six minutes. Underground, we learned later, the wasp had attempted to paralyze the resident larva with its sting in order to lay a pearly white egg inside its body. Why did she behave so differently on different heaps? To find out, we dug up the burrows beneath each heap she had touched. When a burrow contained a lone larva, the wasp had usually entered, but if an adult female was present, in thirteen out of fourteen cases the wasp did not enter.

When the female beetle is with her

young, she defends them vigorously. Her good-sized jaws can nip, and she also lifts her poison-tipped abdomen over her head to jab at an intruder. Glands in the tip emit noxious chemicals, some of which smell strong even to humans. Perhaps the pungent odor of adult females alerts the wasps to stay away from guarded burrows.

A parasitoid wasp that hatches out of a beetle larva must emerge from its pupa, mate, and find salt-marsh beetle larvae to parasitize, all between tides. Once inside the unfortunate beetle larva, the wasp's egg is protected from saltwater and predators. After depositing her eggs, a female wasp is swept up in the next tide and ends as lifeless flotsam. When mature, the wasp larva bursts out of its living larder and spins a cocoon. It will overwinter in the chamber its host dug as its last act, emerging as an adult wasp the next summer.

Parental care appears to have evolved independently in several groups of beetles in similar environments. Ecologist Ellinor Larsen, working in Danish salt marshes in the 1930s, found two other species in which the mother digs narrow-necked burrows and remains with her eggs. (The three species belong to unrelated beetle families: the Staphylinidae, Carabidae, and Heteroceridae.)

When she compared close relatives of the salt-marsh beetles, Larson found one species that lives a few yards below them on the shore and also cares for its eggs and larvae. However, other closely related species that inhabit the high marsh or sand dunes, rarely covered by tides, do not show any parental care at all. Apparently, species that burrow in fast-draining, aerated, sandy beaches can also safely leave their eggs. So parental care seems to be an adaptation to the combined dangers of tidal flooding and airtight burrows. Additional advantages, such as foiling predators and reducing larval parasitism, were secondary gains.

After some years, beetle burrows honeycomb the muddy shore, increasing aeration and drainage. Now the soil is just right for bushy salt-marsh plants that move in and proliferate, shading and killing the algae on which beetles feed. Soon, only abandoned burrows remain under these bushes, and the beetles must find a new young marsh to colonize. Neither time nor tide waits for these beetles.

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