EVOLUTIONARY ECOLOGY

Sex and the Single Killifish

Males seem to be superfluous in one fish species but may come in handy when genetic diversity is needed

Males—who needs them? Not the mangrove killifish. Made up primarily of hermaphrodites, the species reproduces just fine without the masculine touch. Yet male killifish do exist and can play a role in the species' survival, says John Avise, an evolutionary geneticist at the University of California (UC), Irvine. He and his colleagues have now shown that mangrove killifish are part of a select group of animals that use this unusual reproductive strategy, known as androdioecy.

This particular killifish "is the single species of any vertebrate that is doing this," says Stephen Weeks, an evolutionary ecologist at the University of Akron, Ohio.

Among androdioecious species, which include certain clam shrimp, barnacles, and nematodes, most individuals have a single gonad that produces both eggs and sperm, which meet internally before the eggs leave the body. But in each of these species, a few diehard males exist.

Until recently, evolutionary biologists considered androdioecy to be a transitory phase that occurs while a species, depending on its need for either genetic diversity or reproductive self-sufficiency, switches from two separate sexes to hermaphroditic, or vice versa. One reason is that "it's a high evolutionary hurdle" for males to persist among hermaphrodites, explains Loren Rieseberg, an ecologist at the University of British Columbia, Vancouver. "Males need twice the fertility of hermaphrodites."

Weeks has found that clam shrimp have no trouble jumping this hurdle, suggesting that for at least some species androdioecy is a viable, long-term solution. He recently added nine new species of clam shrimp to the list of androdioecious shrimp, for a total of 13. Moreover, the phylogeny and biogeography of these species indicate that this male-hermaphrodite strategy has lasted between 24 million and 180 million years, Weeks and his colleagues reported online in the 6 December 2005 *Proceedings of the Royal Society B*.

Avise is just beginning to piece together the story of the mangrove killifish. It lives in the muck around the roots of mangroves in the Caribbean and along the coasts of South Florida and northern South America, hanging out in crab burrows and dead logs. Self-fertilization by the hermaphrodites yields offspring that are virtual clones of the parent, which is why researchers once expected to see little genetic diversity among killifish at any particular location.

Going it alone. Neither the mangrove killifish (*bottom*) nor the clam shrimp (*top*) needs a male to reproduce.

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But 15 years ago, ichthyologist Bruce Turner of Virginia Polytechnic Institute and State University in Blacksburg discovered that certain populations had unexpectedly high levels of genetic diversity. He proposed that these fish might have unusually high mutation rates or that fish immigrating from other populations were the source of this variation. "Turner had it wrong," says Avise.

Working with colleagues, including Mark Mackiewicz of the University of Georgia, Athens, Andrey Tatarenkov of UC Irvine, and Turner himself, Avise collected killifish from along the Florida coast and analyzed their DNA. The group focused on 35 markers, DNA sequences called microsatellites, along the genome. In each population, the researchers found some individuals whose microsatellites were virtually identical. But, as they reported online 5 July in the *Proceedings of the Royal Society B*, some samples contained a few individuals whose DNA differed at so many markers that it raised suspicions that there was a second parent somewhere in the picture.

As far back as the 1960s, ichthyologists had demonstrated that they could, in the lab, produce male mangrove killifish by keeping self-fertilized eggs cool, for instance, or by growing immature hermaphrodites at high temperature. But little was known about what conditions produced males in the wild.

Avise and his team found very few males among the killifish collected in Florida or the Bahamas. But when they repeated the study with fish from Belize, 10% to 20% of the catches were male. And DNA analyses revealed dramatic differences in diversity among killifish from the various locations. Those from any one spot in the Bahamas or Florida were genetically similar, whereas members of Belize populations varied in their genetic makeup about as much as would be expected had they been following the typical male-female reproductive strategy, the researchers reported in the 27 June *Proceedings of the National Academy of Sciences*. More recently, Avise's group has confirmed in lab experiments that these males mate with the hermaphrodites and produce viable young that spice up the genetic diversity. They will report these results in an upcoming issue of the *Journal of Heredity*.

The existence of androdioecy in species as different as killifish and shrimp indicates that "there must be underlying biological commonalities in the kinds of selection pressures … and the evolutionary responses involved," says Avise. Weeks and other researchers think this strategy has worked so well—and for so long—in clam shrimp because they live in ephemeral pools and often find themselves trapped in new places sans partners. The widespread distribution of killifish suggests that it, too, is a good colonizer and that hermaphroditism may facilitate that skill, Avise adds.

But David Bechler, an ichthyologist at Valdosta State University in Georgia, suspects that hermaphrodites won't always have the upper hand among these killifish. Both he and Avise agree that mangrove killifish were once a two-sex species. And although conditions now favor hermaphrodites, the high proportion of males in Belize suggests that the low genetic diversity is becoming a handicap. "What we are seeing is male evolution reoccurring," Bechler suggests.

–ELIZABETH PENNISI

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