The Species Problem

Everyone from politicians to population biologists uses the notion of a species. Geneticists compare different species to understand how genes evolve, ecologists use them to define the boundaries of ecosystems, and policy-makers use endangered species to argue for protecting lands. Yet biologists have not been able to agree on what a species is, exactly. And the definitional muddle has made it difficult, for instance, to classify organisms or show how a new species forms. "The definition of species is a constant thorn in the side of progress in speciation research," says University of British Columbia ecologist Dolph Schluter, who studies speciation in what may or may not be two species of stickleback fish.

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One species or two? These sticklebacks may be separate species—or not, depending on the species definition.

By the leading textbook definition, the sticklebacks probably don't count as two species. The two groups of fish interbreed occasionally and produce viable offspring, which disqualifies them from species status under a strict interpretation of the "biological species" concept, published by Harvard University biologist Ernst Mayr in 1942. Says Mayr, "I've always defined species as a reproductive community that is isolated ... from other such species" by "isolating" mechanisms. Those mechanisms are biological differences among individuals that prevent the populations from interbreeding. Even though individual pintail and mallard ducks, for example, can mate to produce offspring, the hybrids don't do well enough to establish a new group, so the two parent populations stay distinct and are usually recognized as separate species.

But other biologists say this rigorous standard isn't always realistic. "Reproductive isolation is a kind of mystical definition, in that you know it when it's absolutely complete, but actually there are plenty of examples of species that do hybridize in the wild," says evolutionary biologist James Mallet at University College in London. Coyotes interbreed with wolves and dogs, blue whales interbreed with fin whales, and many species of Protozoa, lower Metazoa, and plants do as well. "Are we going to say those aren't species?" asks Mallet.

The shortcomings of this concept have sent biologists looking for alternatives. Systematists, who classify organisms, often do so based on obvious differences in populations' morphology and genes. Mallet has tried to formalize this practice with his "genotypic cluster definition." It requires populations to fall into two distinct clusters based on differences in their genes or morphology if they are to qualify as separate species. His definition tolerates interbreeding as long as the genetic traits being studied stay distinct in two clusters.

But this is hardly the only alternative to Mayr's classical species concept. Ecologists often rely on an "ecological species" definition, for example, which defines species as groups that occupy different ecological niches—populations of identical-looking multicellular organisms called rotifers that live in different kinds of ponds or puddles, for example. Evolutionary biologists trying to trace the origins of species often use the "evolutionary species" concept, which says that a species is a single lineage of ancestral-descendant populations that remains separate from other such lineages in an evolutionary tree. Biologists using a classification scheme called cladistics identify these distinct branches on the evolutionary tree from unique "derived" characters: traits that appear in a descendant population but not among its ancestors or any contemporary relatives. The black-and-white markings on the tail of the Ethiopian wolf, for instance, separate it from the gray wolf, the species it is thought to have evolved from.

Others have tried to bring some of these ideas together under a conceptual big tent, such as the "cohesion species concept," proposed by geneticist Alan Templeton of Washington University in St. Louis. But scientists would still like to winnow the definitional diversity, so that when researchers such as Schluter publish on stickleback speciation, others won't voice doubts that he was looking at separate species in the first place. "Perhaps the best we can do is to agree to disagree in a rational manner" and agree on a limited set of concepts, says entomologist Stewart Berlocher of the University of Illinois, Urbana-Champaign.

–Ann Gibbons

Arnold, an evolutionary biologist at the University of Georgia. "[Harvard biologist] Ernst Mayr has said that hybridization isn't important in the speciation process; that hybrids will never get off the ground," he notes. "But, in fact, natural hybrids are produced that are very fit, and sometimes they lead to new evolutionary lineages."

Take the case of two species of finches on the island of Daphne in the Galápagos, which Princeton University biologists Peter and Rosemary Grant and their team have studied since the early 1970s. The cactus finch (*Geospiza scandens*) and the medium-beaked ground finch (G. *fortis*) "are kept apart by their songs. They are a barrier to gene flow," explains Rosemary Grant. The songs are passed down within a family, from father to son, as the Grants learned by recording the songs of fathers and sons in both species. Properly imprinted birds show no interest in the trills of the other species (and consequently do not mate with them).

But there are the occasional natural mishaps. The Grants observed cases when a G. *scandens* father died and his sons subsequently overheard a male G. *fortis* singing. They learned his song and ended up attracting and mating with G. *fortis* females. The G. *scandens* daughters also learned the wrong mating song and like their brothers chose the wrong mate.

Until 1983 such mishaps went nowhere, for the resulting hybrids always died, apparently because their beaks were unlike those of either parent and so weren't suitable for the available food supply. Because of their "intermediate bill size," the hybrids needed an "intermediate diet," says Rosemary Grant. But the small, soft seeds they required did not last much beyond the beginning of the island's dry season, and so the hybrids starved to death.

But in 1983, the island's weather changed, thanks to the arrival of a warm El Niño current. Suddenly, the parched landscape became "almost like a meadow," says Rosemary Grant, "with masses of annual plants." These