Hybridization and Extinction

In protecting rare species, conservationists should consider the dangers of interbreeding, which compound the more well-known threats to wildlife

Donald A. Levin

The world is awash in biological diversity. Yet even the least discerning observer will notice that the diversity of life is not a random sampling of all possible biological characteristics. You cannot find, say, organisms that are half sunflowers and half camels. Rather, nature blends only specific sets of traits, each tailored to enhance survival and reproduction. Other combinations are conceivable, but, like the sunflower-camel, they generally make no biological sense.

The well-defined sets of attributes one finds populating the natural world make up the fundamental units of biodiversity: species. Investigators have now described nearly two million species (millions more await attention) and placed them within an elaborate taxonomic hierarchy. But even the naturalists of antiquity realized that some organisms resemble one another so much that they ought to be classified in the same general group or genus. Only much later did Charles Darwin and Alfred Russell Wallace realize that species within the same genus share many traits because they evolved from a common ancestor. That is, what was once one type of plant or animal split into two or more species.

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Despite their overall similarity, different species in the same genera do not normally interbreed. They may be prevented from doing so because they have widely separated home ranges or different reproductive seasons. Indeed, that they do not freely exchange genes, for whatever reason, defines them as separate species. Yet in some circumstances separate species will mate, and if such a liaison is successful, a hybrid results.

Although such hybridization never takes place in the vast majority of genera, it is quite common in some. Botanists believe that hybridization between species happens in 6 to 16 percent of plant genera. Crossing between species is less common in animals, although it is not infrequent in some groups. For example, 9 percent of all bird species hybridize. Such a blurring of taxonomic lines also takes place within primate genera, including lemurs, gibbons and baboons. Anthropologists have even speculated that humans and Neanderthals may have once interbred.

With hybridization so rampant, one wonders how species ever maintain their distinctness. They do, in part, because the production of hybrids does not necessarily shift genetic material between species. For genes to traffic in this way, hybrids must cross with at least one of the parent species. In many instances that just doesn't happen. Why? As Darwin had observed, most hybrids are inferior to their parents: Some abort as embryos, others die as juveniles, and others still grow to adulthood but cannot reproduce. (Mules, for example, are vigorous but sterile: If you want to produce a mule, as people have been doing for more than 2,000 years, you have to mate a female horse and a male donkey. Getting it backward will result in a hinny, which is also sterile but less robust.) Hence many hybrids are unable to pass their genes back to members of their parent species.

That hybrids can survive at all is a reflection of the similarity between the parents. That they are usually weak and sterile is a reflection of the differences of the parents, whose two sets of genes were really not meant to work together. Hybridizing two species is like building a car with half GM and half Chrysler parts. It should be no great wonder that the product might not function so well.

Only in the mid-20th century did biologists recognize that, under some circumstances, hybrids can be superior to their parents. This realization stems from work of Edgar Anderson of the Missouri Botanical Garden in St. Louis, who believed that disturbance to habitat sometimes creates new conditions that are more suitable for hybrids than for the parents. He carried his argument one step further in his book *Introgressive Hybridization*, published in 1949, where he contended that, in areas of disturbance, fertile hybrids allow genes of one of the parent species to pass into the other. This process, which he dubbed *introgression*, could transform the species receiving the new genes enough to survive the environmental disruption.

Other botanists were slowly swayed over to Anderson's view and soon realized that habitats appropriate for hybrids—indeed where the hybrids outshine their parents—sometimes arise independent of any disturbance. In his 1997 book *Natural Hybridization and Evolution*, Michael Arnold of the University of Georgia provides a comprehensive analysis of this phenomenon. There he details the adaptive advan-

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Figure 1. Listed as "critically endangered" by the International Union for the Conservation of Nature, the Ethiopian wolf is now officially protected throughout its range in East Africa. Although loss of habitat accounts in part for its decline, this animal suffers also from a tendency to mate with wild dogs, which erodes its ever-diminishing genetic stock. The author surveys many such instances, where hybridization threatens rare plants and animals poised on the verge of extinction.

tage of hybrids in habitats where environmental conditions are intermediate between those of the two parent species. Biologists are aware of many such places, which often contain multiple types of hybrids (termed *hybrid swarms*) in addition to the parent species. Sometimes the hybrids constitute a majority, and crosses between them and one or both of the parents mongrelizes the pure species, that is, takes away their genetic distinctiveness. One yardstick of mongrelization is what the organisms look like, but easily observable traits are sometimes misleading. Hence biologists frequently choose to examine telltale genetic markers, which show clearly whether the species under investigation has been "infected" with alien genes. Such work has recently uncovered, for example, that introgressive hybridization has been blending two species of Atlantic redfish off the coast of Newfoundland.

The End of the Line

Although hybridization and the enhanced adaptability it provides is sometimes beneficial, it can also be detrimental, because it allows an abundant species to drive a rare relative to extinction. John Harper, a plant ecologist at University College in North Wales, first recognized this possibility in 1961. The actual threat of hybridization to some species became apparent during the 1970s, as investigators studied more rare species and began applying the tools of molecular biology.

It is easy to see why certain organisms are at risk. Rare species often flourish only because they are isolated from related ones and therefore cannot interbreed. As my son and I pointed out not long ago in these pages (*Macroscope*, January–February), modern civilization is carving up natural habitats, separating like organisms in a way that

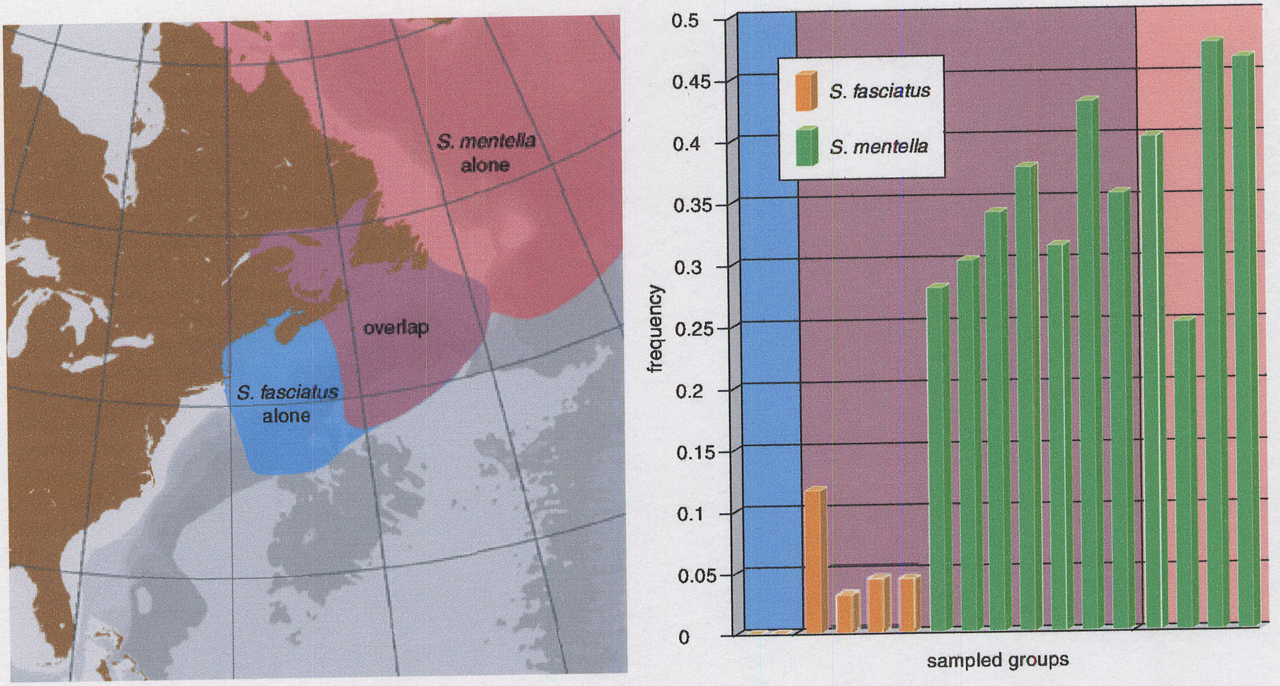

Figure 2. Introgressive hybridization has been shown to operate in two species of North Atlantic redfish: *Sebastes fasciatus* and *S. mentella*. The former typically prefers warmer waters, and in the southwestern part of its range *(blue zone on map)* does not come in contact with the other redfish. Similarly, *S. mentella* lives in isolation from its cousin throughout the more northerly portion of its range *(red zone)*. The two species do, however, overlap throughout a sizable region *(purple zone)*. Genetic analyses of these fish reveal introgressive hybridization in the region of overlap. For example, one genetic pattern found in an appreciable fraction of *S. mentella* sampled from 11 sites *(green bars, right)* does not appear at all in *S. fasciatus* obtained from two sites in the region where the two fish do not overlap; the telltale genetic marker for *S. mentella* does, however, appear in *S. fasciatus* sampled from four sites where the two species coexist (*orange bars*). (From the study of Roques *et al.* 2001.)

might ultimately foster speciation for some groups of plants and animals. But people's activities are also eroding physical and ecological barriers, allowing once-isolated species to make contact locally or even over large regions. In Louisiana, for example, farmers' pastures and irrigation ditches brought distinct species of *Iris* together over wide areas. Herbert Riley of the University of Kentucky and Anderson studied the resultant hybrid swarms more than 50 years ago.

Similar changes to the natural environment have spurred the hybridization of animals. For example, the alteration of water courses for flood control and irrigation affords easy avenues for the intermingling of certain aquatic species. Or consider the settlers who planted trees on the Great Plains during the 19th century. They inadvertently provided stepping stones for the westward expansion—and subsequent hybridization—of several species of birds, including grosbeaks and jays. In the Northeast, people's meddling with the environment has led to hybridization between golden-winged and blue-winged warblers and between the American black duck and mallards.

Indeed, mallards have been spreading their genes far and wide. Brought to Hawaii in the early 1900s as game birds, they have been mating with the Hawaiian duck. And since being introduced to New Zealand in the 1930s, European mallards have been hybridizing with the native grey ducks there. Although it is not impossible for a species to hop over geographical or ecological barriers on its own and land in the neighborhood of a relative, such jumps seldom happen naturally. Even an Olympic-class mallard, for example, would be hard pressed to make it across the Pacific. But since the time of Columbus (and even before), people have routinely transported plants and animals—either purposefully or accidentally—all over the globe.

Not surprisingly, hundreds of different organisms brought from distant continents have escaped and crossed with indigenous species. That process affects, for example, the plant *Lantana depressa*, which is endemic to Dade County, Florida. There *L. depressa* is hybridizing with the introduced *L. camara*, a species common in southern gardens. The hybrids, which combine the local adaptations of the native and vigor of the alien, have thrived and are spreading.

Elbowing Out the Cousins

The proliferation of an exotic species need not in itself spell trouble for native species, but it often does. One problem is *reproductive interference*: when the introduced organism leads to failed matings (ones that produce no progeny) or matings that yield only hybrids. One illustrative example of this process involves female European minks, which can mate with their kind as well as with introduced American minks. After linking up with their Yankee cousins, the Europeans are averse to mating with males of their own species. Accordingly, the number of European minks born in areas where these two species are in contact is much reduced from normal levels. For the tsetse fly and certain bird parasites, reproductive interference is even more dramatic. The very act of mating with a different species results in the death of the females through a mechanical incompatibility between genitalia.

Even when the failure to mate is not a major issue, the process of hybridization itself can threaten a species simply because it leads to fewer pure progeny. If the parents of a particular species have, on average, just one pure offspring each, the population will just be able to maintain its numbers over time. Hybridization can then tip the balance, so that each organism produces less than one pure offspring. When this happens, the population declines in size. The fewer the number of pure offspring, the faster the slide to extinction.

Simple arithmetic explains why when two species hybridize, the less abundant one usually suffers the most: All else being equal, the minority species sustains a proportionally greater decline in its reproductive rate. Harlan Lewis, a botanist from the University of California, Los Angeles, showed how this mechanism worked in artificial mixtures of the annual plants *Clarkia biloba* and *Clarkia lingulata*, where the former outnumbered the latter by a ratio of five to two. These species cross readily, and their hybrids are sterile. To no one's surprise, in Lewis's experiment *C. lingulata* was hybridized out of existence through the loss of reproductive capacity. These results bear directly on wild *C. lingulata*, which is known only from two sites in the Sierra Nevada of California, one of which is separated by only 100 meters from a population of *C. biloba*. The continued existence of *C. lingulata* is clearly in jeopardy.

A rare plant or animal can be driven to extinction even when the hybrids are not sterile. The abundant relative just overwhelms it. That is, the fertile hybrids provide pipelines for the movement of genes from the abundant species into the rare one, contaminating its gene pool. Soon all of the rare organisms are tainted with alien genes, and eventually the rare species no longer exists as such. It is first mongrelized, then fully assimilated.

The Catalina Island mountain mahogany, *Cercocarpus traskiae*, provides an illustrative example of this process. This species, California's rarest tree, is confined to a single canyon on Santa Catalina Island, which lies roughly 60 kilometers off the coast of southern California. The 40 mature trees noted when this species was first described in 1897 have now dwindled to 12 adult plants and some 75 seedlings. The principal cause of this precipitous decline is clear: The sheep, cattle and other animals brought to the island over the past 150 years have grazed on too many of the seedlings. This tree also suffered from hybridization with the birch-leaf mountain mahogany, *Cercocarpus betuloides*, which is more abundant on the island. In 1995, Loren Rieseberg and Daniel Gerber of Indiana University showed that nearly half of the adults and some seedlings of *C. traskiae* contain alien genes. Assimilation seems likely unless drastic steps are taken.

Another prime example of this phenomenon involves a plant named *Argyranthemum coronopifolium* (a relative of chrysanthemum), which is restricted to the Tenerife, one of the Canary Islands. This plant has been found at only seven sites, three of which are in various stages of hybridization with its more prolific cousin, *A. frutescens*. Roads built in the past 50 years hastened the spread of *A. frutescens* to the restricted habitats of *A. coronopifolium*. At one site, contact first took place in 1965. By 1985 only a few pure examples of the rare daisy remained, and they were embedded in a hybrid swarm. Now there are only hybrids and the invading *A. frutescens*. At another site on the island, the beleaguered species has been reduced to a few individuals, now far outnumbered by the hybrids and attackers. Similar encounters with *A. frutescens* also threaten the survival of two other species of *Argyranthemum* on Tenerife.

Such assaults on rare plants are not uncommon. As Judy Rhymer of the University of Maine and Daniel Simberloff of the University of Tennessee pointed out a few years ago, some of the plant species on the Nature Conservancy's vulnerable list are apparently at risk because they are hybridizing with numerically superior relatives. Included on that tally is the white firewheel *(Gaillardia aestivalis)* of Texas, which is hybridizing with the Indian blanket *(Gaillardia pulchella)*, a flower the Texas Department of Transportation likes to plant along roadways. Also, the last population of the Bakersfield saltbush *(Atriplex tularensis)* seems to be mongrelized by the widespread *A. serenana* in Kern Lake Preserve of California. Similarly, the California sycamore *(Platanus racemosa)*, which grows along the Sacramento River and its tributaries, is being amalgamated with the London plane tree, and the California black walnut may have been infused with genes of several other walnuts. Oddly enough, the London plane tree is itself a hybrid of the oriental plane *(Platanus orientalis)* and the

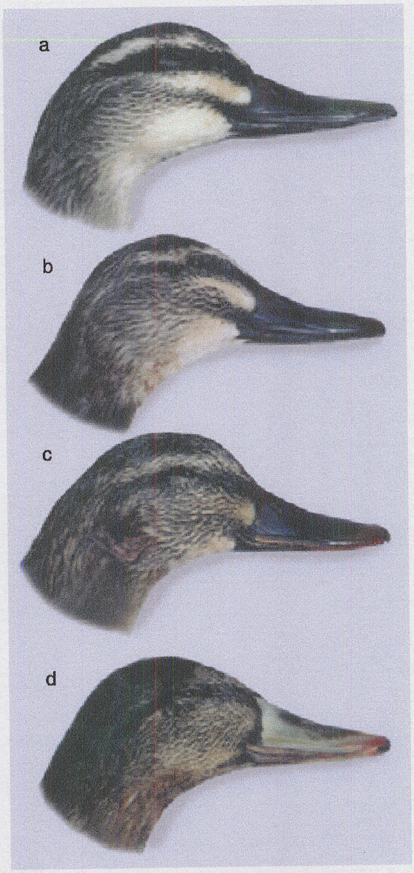

Figure 3. Introduced to New Zealand in the mid-1800s, European mallards *(Anas platyrhynchus, a)*. have mated freely with the local grey ducks *(A. superciliosa, d)*, and genetic studies reveal that more than half of the nominally native ducks found now are, in fact, products of hybridization—which is sometimes apparent from their intermediate appearance *(b, c)*. (Images courtesy of Murray Williams, New Zealand Department of Conservation).

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Figure 4. Tough evergreen shrub native to the West Indies, *Lantana camara* grows up to six feet high and eight feet wide. It has escaped cultivation and encroached on native plants in more than 40 countries. In the U.S., this weedy invader has hybridized with a native shrub of the same genus *(L. depressa)*.

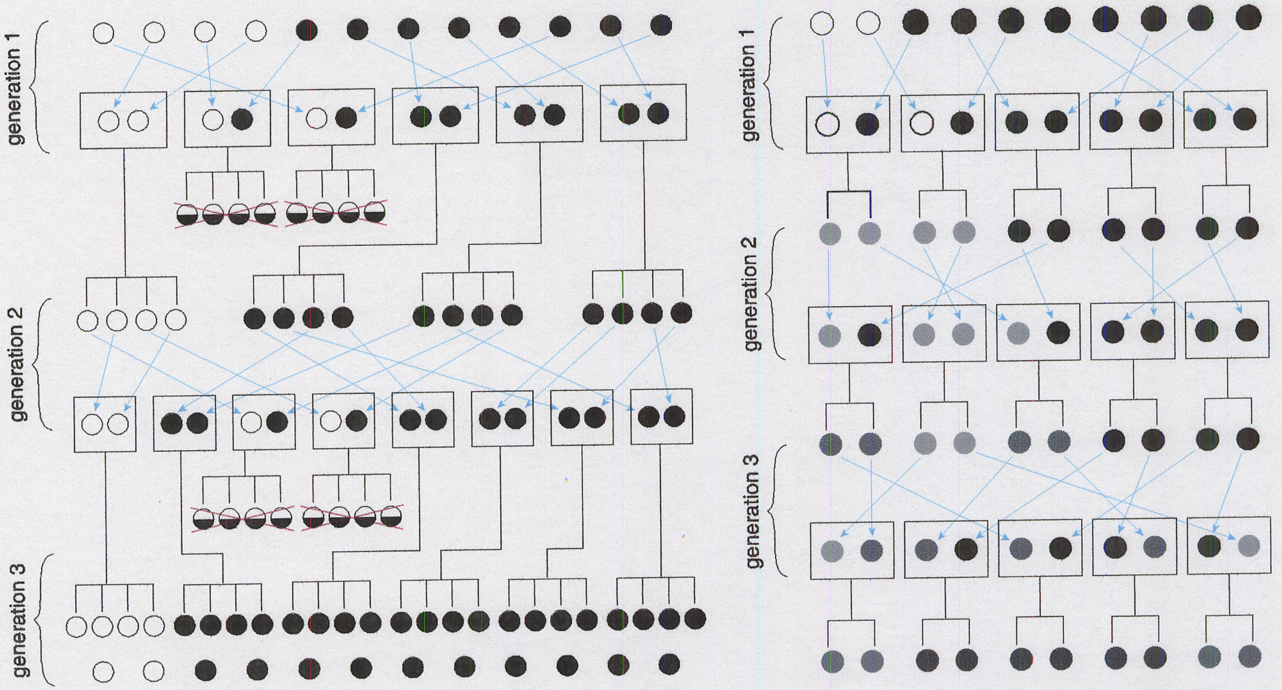

Figure 5. Hybridization causes a rare species to disappear over time, as can be seen in these hypothetical examples, where the white dots represent a rare species and the black dots a more abundant relative. The chart at left shows the changes that might take place over the course of three generations when the parent species pair up at random *(boxes)* and hybrids do not survive long enough to reproduce (or are sterile). In this simple simulation, each pair of breeders produces four progeny, but in the end the burgeoning population is halved, representing the natural limit imposed by the environment. Although total numbers are the same at the start and finish, the proportion of rare individuals declines. Continuation of this process would eventually drive the rare species to extinction. The same holds true for the situation depicted on the right, but in a different manner. Here the rare *(white)* and abundant *(black)* species again pair at random *(boxes)*, but all progeny are fertile, allowing genes to mix between the parental species through the process of introgressive hybridization. In this example, population numbers remain stable over time, but with each passing generation the diagnostic attributes of the rare species become diluted, represented here by the blending of shades.

American sycamore *(Platanus occidentalis)*, and was imported from Europe.

In each of these cases, a rare species suffers at the hands of a more abundant relative, but this imbalance is not a prerequisite. For example, on the shores of San Francisco Bay, the native California cordgrass *(Spartina foliosa)* is hybridizing with smooth cordgrass *(S. alterniflora)*, which was introduced in the 1970s. Despite its small numbers, the exotic species is at an advantage because it produces 21 times as much pollen as the native. Moreover, the pollen of smooth cordgrass is superior: Some 23 percent of the flowers will set seed with it, whereas only about 4 percent will do so with pollen of the native. As a result, San Francisco Bay has a large population of hybrids, which are spreading at the expense of the native and may ultimately replace it.

This type of exposure to introduced plants is particularly strong when crops are grown in the vicinity of rare wild relatives. Even if only a tiny fraction of the pollen from the sown fields reaches the native plants, significant hybridization can result. As Norman Ellstrand of the University of California, Riverside, and his associates recently noted, 12 of the world's 13 most important food crops hybridize with wild relatives in some part of their ranges. These include wheat, rice, maize, soybeans and barley. Sometimes this process endangers the wild stock, as is the case for Hawaiian cotton and some African rices. In most other situations, when the wild type is relatively common, the species is not put at risk. The reason is simple: When crop genes infiltrate a natural population, they are not apt to spread far, because they are typically detrimental. But this generalization need not hold in all cases.

One of the best studied exceptions is with sunflowers. Domesticated and wild varieties of the common sunflower *(Helianthus annuus)* grow side by side in many locations. Honeybees pollinate both types, and the two interbreed readily, producing fertile hybrids. Randal Linder, one of my departmental colleagues, analyzed the extent to which three populations of wild sunflowers shifted their genetic makeup in the direction of a domestic variety growing nearby in much larger numbers. The wild populations and domesticates he investigated have been in contact for between 20 and 40 years. In that time, the genetic constitution of the wild plants shifted about 35 percent in the direction of the cultivated variety.

The danger domesticates pose for their wild cousins is even more evident for some animals. Consider our greatest friend, the dog. All members of the dog genus, *Canis*, can, in principle, interbreed and produce fertile offspring. So the potential for gene swapping between domesticates and wild relatives is quite real. Indeed, the work of Carles Vilà and Robert Wayne of the University of California, Los Angeles, suggests that dogs and wolves (*Canis lupus*) have exchanged genes repeatedly since domestication began, some tens of thousands of years ago (if not longer). Hence most taxonomists now regard dogs and wolves as members of the same species.

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Figure 6. Native species can slowly disappear when they mate with close relatives that exist in higher numbers. One example is the California Sycamore *(Platanus racemosa, left)*, which ranges from Baja California to the foothills of the Sierra Nevada and is hybridizing with the London plane tree in some locales. Another example can be found in wetlands: When smooth cordgrass *(Spartina alterniflora, middle)* was transplanted from South Carolina to the San Francisco Bay area in the 1970s, it quickly overtook the native cordgrass, *Spartina foliosa*. Wild populations of sunflowers *(Helianthus annuus, right)* readily interbreed with domesticated varieties, and in some locales this process is making the wild type resemble nearby cultivars. (Sunflower photograph courtesy of C. R. Linder, University of Texas at Austin.)

The most threatened canid is the Ethiopian wolf, which is known from fewer than 500 individuals in six small isolated populations. Hunting and destruction of their natural habitat have devastated these animals. Wild dogs now outnumber them by 10 to 1. Genetic studies by Vilà, Wayne and their colleagues revealed that from 8 to 17 percent of the wolves in one of the six groups are of hybrid ancestry, the result of matings between female wolves and male dogs. (Because females normally leave their pack to copulate with male wolves from neighboring territories, they often encounter dogs and mate with them.)

The housecat *(Felis catus)* is another domesticated culprit polluting the gene pools of wild animals. Like the dog, this species has in many parts of the world established feral populations, which can interbreed with their local relatives. In Europe, for instance, hybridization between wild and domestic cats is pervasive. Such interbreeding is thought to be the least prevalent in northern and western Scotland; yet even there approximately 80 percent of the wildcats *(F. silvestris)* show genetic markers that are characteristic of their domesticated cousins.

Solving the Problem

Environmentalists have focused considerable attention on protecting rare species from the destruction of their habitat and from hunting and predation, as well as from the disease and outright competition for resources they often face when encountering introduced species of a like kind. Clearly, hybridization needs to be added to this list of threats.

Preservationists should recognize that what some endangered species

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Figure 7. Experts believe that the European wildcat *(Felis silvestris)* may no longer exist in pure form. Through the years, frequent matings with feral and domestic cats have diluted the gene pool of this animal so much that one would be hard pressed to identify a pure example now. These shy, nocturnal felines used to range over Britain, but clearing of their preferred wooded habitats drove them out of most locales. They can now be found only in Scotland, where they enjoy legal protections.

Figure 8. Hybridization is saving the Florida panther *(Felis concolor coryi)*, which numbered in the tens of individuals and thus was on the verge of extinction. Excessive inbreeding within the small population of panthers caused serious health and reproductive problems. So conservation managers transported eight Texas cougars to Florida in a program designed to instill some new blood, and that effort has helped to boost the number of panthers.

need most is to be isolated from their close relatives, whether indigenous or introduced. This measure is simple enough to take in some settings, for example, in botanical gardens. Yet even at these bastions of conservation, I have been surprised to find collections of rare plants growing within pollination range of their close relatives. Another way to save rare plants and animals is to remove pure individuals from threatened populations and relocate them to a place where related species are absent.

But what do you do if an organism is on the verge of extinction, when only a few individuals are left anywhere? Do you breed it with a relative with the hope of salvaging some of its distinctive characteristics, or do you let it expire? You would probably choose to breed it, because, after all, something is better than nothing. So if only a handful of survivors remain, or if they are all of one gender, then hybridization with a relative is the only logical course of action. But what should your strategy be if, say, 30 or 40 individuals remain in the wild?

This very situation confronted those struggling to save the Florida panther, *Felis concolor coryi*, a subspecies of cougar (or, equivalently, puma). Restricted to south Florida, one of the two largest groups lives in the Everglades; the other inhabits Big Cypress Swamp. Although it has been protected from hunting for more than three decades, the Florida panther remains in decline, in part because of reduced male fertility. Indeed, these panthers have the worst sperm observed in any animal: About 95 percent of their sperm cells are malformed. Also, the incidence of cryptorchidism, a defect that causes one or both testicles to remain undescended, has risen from negligible levels to 80 percent since 1980. To make matters worse, these panthers have enormous parasite loads, which cause debilitating disease or even death.

The plight of the Florida panther stems in part from its low level of genetic variation, a direct result of its small numbers and the inbreeding that has gone on. To address this genetic impoverishment, conservation managers hatched a plan in 1992 to introduce the Texas puma *(Felis concolor stanleyana)* into Florida. Although this step compromises the Florida panther's very identity as a distinct subspecies, the experts concluded that the animal's critical status demands it. They decided that the Texas puma was a good source of new genes because the two cats formerly had overlapping ranges and probably once interbred in the wild.

Thus far this program appears a success. Crosses between the two types of cats have resulted in a few dozen progeny, and some of those hybrids have themselves procreated. So the number of panthers in Florida is on the upswing.

This experience suggests that forced cross-breeding is an excellent strategy, at least when closely related subspecies can be paired up. But the value of this approach becomes less clear if the endangered animal must be bred with an entirely different species. In that case, even specialists may be challenged to determine the biological compatibility between the species and to judge the vigor of their progeny. What is more, crossbreeding separate species muddies the legal waters and may dilute the safeguards afforded to the animal under the Endangered Species Act. As it stands, the U.S. Fish and Wildlife Service has no established policy for hybrids, and because the Act defines only vaguely what species warrant protection, hybridization truly complicates matters.

Another problem—for both biologists and lawyers—is that one doesn't always know whether an endangered species is pure. Consider the red wolf of the southeastern U.S. In the late 1970s, ecologists noted that the count of red wolves was frighteningly low and that these animals were increasingly interbreeding with coyotes. Responding to this crisis, scientists found a small number of "pure" red wolves and started a captive breeding program to save the animals from extinction. More than a decade later, Wayne and Susan Jenks of Sage College in Albany, New York, scrutinized DNA evidence and uncovered that the red wolf wasn't a distinct species at all. Rather, it appears to be a hybrid—part coyote, part gray wolf.

In light of these findings, should the government have spent millions of dollars protecting the red wolf? And should the programs continue? Wayne believes that they should, because preserving the red wolf could maintain characteristics no longer found in nature. (The original red wolf may have come from a match between a coyote and a now-extinct subspecies of gray wolf.)

Others might argue that "contaminated" species should not have government protection, but the question remains on the table. Hybridization should be promoted when it is necessary to maintain deteriorating populations, and it should be prevented when it threatens rare species. Thankfully,

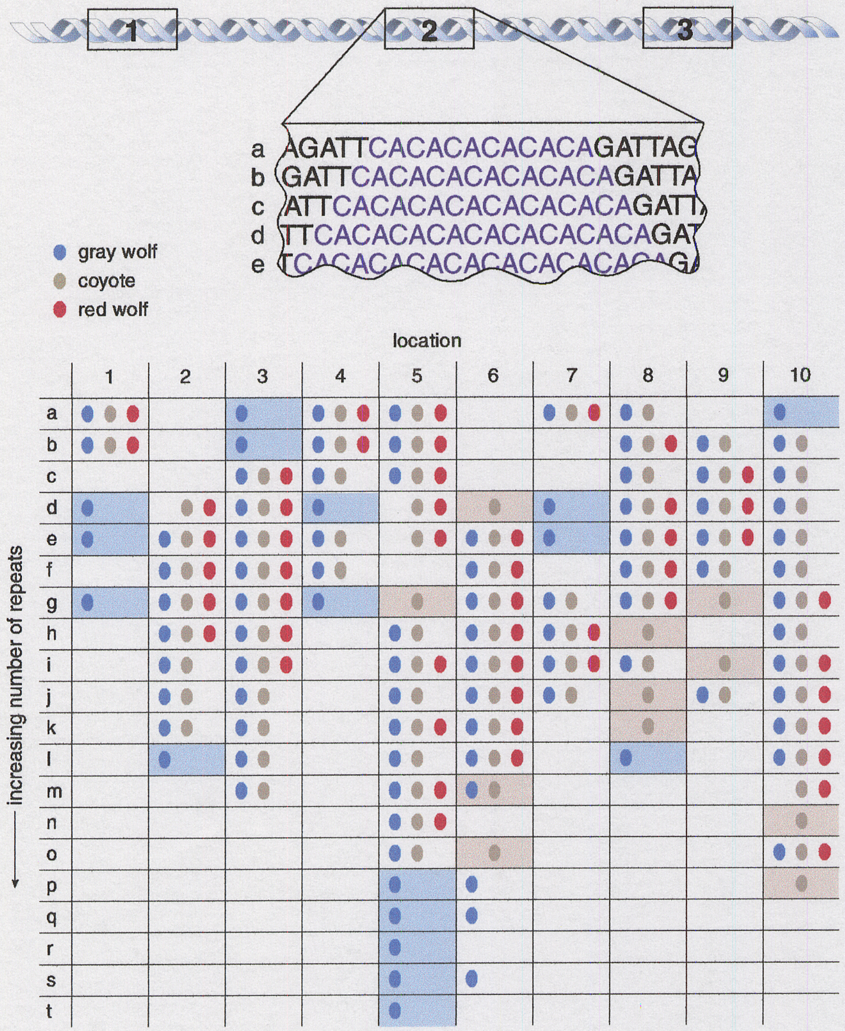

Figure 9. Conservationists sprang into action when the numbers of red wolves dwindled in the late 1970s. A captive breeding program attempted to save a few pure animals and separate them from coyotes, which hybridize with red wolves in the wild. But in the 1990s, some biologists began to suspect that the red wolf is not a distinct species at all. Rather, it appears to be a hybrid between the gray wolf and the coyote. Genetic evidence for that assertion comes from the examination of DNA "microsatellites" (also called single-sequence repeats). Many locations in the genome *(schematically denoted 1, 2, 3... above)* show a variable number of distinctive sequence repetitions in different species. (In the example depicted above, the nucleotide pair CA is repeated several times.) The shortest repeated sequence found in the studied canid populations (which included the golden jackal, although those results are not shown here) is labeled a, the next shortest sequence b and so forth. Red wolves *(red dots)*, gray wolves *(blue dots)* and coyotes *(brown dots)* share the same number of repeats for many genetic locations *(chart)*, but some repeat patterns are found only in gray wolves *(blue shading)*, and some are found only in coyotes *(brown shading)*. Red wolves, however, do not show any genetic patterns unique to them, which strongly suggests that they are merely the product of recent hybridization between gray wolves and coyotes. (Chart summarizes the genetic results of Roy *et al.* 1994).

people are becoming increasingly aware of these problems. For example, the Hawaiian duck's race toward extinction prompted both U.S. and international agencies to address the problem of its hybridization. In 1992, the Rio convention of biological diversity discussed the dangers of hybridization and the safeguards that need to be put in place before an exotic species is released into a new environment. And in 1999 an executive order of President Bill Clinton created the National Invasive Species Council expressly to deal with such issues. These are good first steps, but as I have tried to show here, conservationists must think about hybridization between native species, too.

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Links to Internet resources for further exploration of "Hybridization and Extinction" are available on the American Scientist Web site:

http://www.americanscientist.org/articles/02articles/levin.html