

EXTINCTION BY HYBRIDIZATION AND INTROGRESSION

Judith M. Rhymer

Department of Wildlife Ecology, University of Maine, Orono, Maine 04469

Daniel Simberloff

Department of Biological Science, Florida State University, Tallahassee, Florida 32306

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ABSTRACT

Nonindigenous species can bring about a form of extinction of native flora and fauna by hybridization and introgression either through purposeful introduction by humans or through habitat modification, bringing previously isolated species into contact. These phenomena can be especially problematic for rare species coming into contact with more abundant ones. Increased use of molecular techniques focuses attention on the extent of this underappreciated problem that is not always apparent from morphological observations alone. Some degree of gene flow is a normal, evolutionarily constructive process, and all constellations of genes and genotypes cannot be preserved. However, hybridization with or without introgression may, nevertheless, threaten a rare species' existence.

INTRODUCTION

Most attention to species extinction has focused on the "evil quartet" (45): overkill, habitat destruction, impact of introduced species, and chains of extinction. Introduced species, in turn, are seen as competing with or preying on native species or destroying their habitat (e.g. 19).

Introduced species (or subspecies), however, can generate another kind of extinction, a genetic extinction by hybridization and introgression with native flora and fauna. Habitat modification can also break down reproductive isolation between native species, with subsequent mixing of gene pools and potential

loss of genotypically distinct populations. These phenomena can be especially problematic for rare species contacting more abundant ones. Conservation geneticists have largely focused not on the loss of distinct gene pools by mixing but on the potential decreasing fitness of individuals in small populations who suffer inbreeding depression and on the possible difficulty of evolution in small populations that have lost alleles to genetic drift (129).

We define "hybridization" as interbreeding of individuals from what are believed to be genetically distinct populations, regardless of the taxonomic status of such populations (cf 127). "Hybridization" most commonly refers to mating by heterospecific individuals but has been applied to mating by individuals of different subspecies and even of populations that, though not taxonomically distinguished, differ genetically. Arnold et al (18) suggest restricting "hybrid" to matings between species and using "intergrade" for matings between subspecies and "cross" or "interbreed" for matings between individuals of geographically distinct populations. Although such distinctions might clarify future discussions, all these terms seem so widely used in the literature for matings at every taxonomic level that they are unlikely to be restricted. Instead one must depend on accurate taxonomic description of the entities between which mating occurs.

Introgression is gene flow between populations whose individuals hybridize, achieved when hybrids backcross to one or both parental populations. Beyond F1 hybrids, the point at which an individual is no longer viewed as a hybrid but rather as a member of one of the parental populations that has undergone introgression is arbitrary (9, 141). A hybrid swarm is a population of individuals in which introgression has occurred to various degrees by varying numbers of generations of backcrossing to one or both parental taxa, in addition to mating among the hybrid individuals themselves. Hybridization need not be accompanied by introgression; for example, offspring of hybrid matings might all be sterile. Introgression can be unidirectional, with backcrossing to one parental population only. But hybridization can pose a threat to small populations even if gene pools do not mix.

Botanists have paid more attention than zoologists to the evolutionary consequences of hybridization and introgression, apparently because these are much more common phenomena in plants than in animals, at least at the interspecific level (cf 72). Further, botanists have more frequently addressed the creative role of hybridization, although they have also pointed to such outcomes of potential conservation consequence as the role of introgressive hybridization in the evolution of aggressive weeds (e.g. 71). Zoologists, on the other hand, have generally been more exercised about the loss of distinct gene pools than about hybridization as a creative force. We show in our examples that the same sorts of conservation problems arise in both plants and animals.

It is often difficult to identify hybrids on morphological grounds alone, particularly after several generations of backcrossing. Morphological observations may suggest that hybridization or introgression has occurred, but introgression is not always reflected morphologically. Often individuals not previously identified as products of introgression can be shown by molecular techniques to be introgressed (115). With the advent of molecular genetic analyses, one can now often document not only the extent of hybridization and introgression between populations but also the gender of hybridizing individuals from each population. In this review, we primarily discuss studies for which some molecular analyses have been done.

With few exceptions, mitochondrial DNA (mtDNA) is maternally inherited (20). Thus a first approach to a study of hybridization in animals is to identify population-specific mtDNA haplotypes of the parental populations and to screen suspected hybrid individuals for those haplotypes. In studies of plant hybridization, chloroplast DNA (cpDNA) is more often used; it is maternally transmitted in most plants (20). These data reveal the direction of hybridization: Does it consist only of males of one population mating with females of the other, or does the reciprocal cross also occur? However, mtDNA or cpDNA alone allows an incomplete picture of the extent of hybridization and introgression (39). In order to identify unequivocally all hybrid individuals, one must also analyze biparentally inherited nuclear markers such as those revealed by studies of allozymes, microsatellite DNA, random amplified polymorphic DNA (RAPDs), and single-copy nuclear DNA. First generation (F1) hybrids will be heterozygous at all loci with population-specific alleles. Backcross individuals from crosses between hybrids and the parental populations will have various combinations of genotypes depending on the cross and the results of Mendelian segregation.

MODIFICATION OF GENE POOLS

Mixing Through Introductions

Mixing of gene pools of formerly distinct taxa by introgression has been called "genetic assimilation" (38, 52, 116), "contamination" (4), "infection" (48), "genetic deterioration" (B Heredia, in 144), "genetic swamping" (74, 80), "genetic pollution" (35), "genetic takeover" (68), and "genetic aggression" (71). The latter seven terms have pejorative connotations. They imply either that hybrids are less fit than the parentals, which need not be the case, or that there is an inherent value in "pure" gene pools. "Genetic assimilation" need have no such connotation, but this term is widely applied to an entirely different phenomenon (143). "Mixing" need not be value-laden, and we use it here to denote mixing of gene pools whether or not associated with a decline in fitness.

A well-known example of genetic mixing through introductions involves mallard ducks (*Anas platyrhynchos*), which have a holarctic breeding range. They have hybridized with several closely related, more narrowly distributed endemic species, with subsequent introgression. Hybridization has been facilitated by introductions of mallards into various localities (e.g. New Zealand, Hawaii, Australia, south Florida, eastern USA). For instance, hybridization with introduced mallards has been implicated in population declines of the New Zealand grey duck *A. superciliosa superciliosa* (115), and mtDNA evidence suggests that loss of this indigenous species through introgressive hybridization is a real possibility (115). Many populations are increasingly mallard-like in appearance (153). Hybridization with introduced mallards has contributed to the decline of the endangered, endemic Hawaiian duck (*A. wyvilliana*) and has hampered attempts to reintroduce this species to Oahu and Hawaii (63). Domesticated nonmigratory mallards that escaped or were released for hunting breed with the endemic Florida mottled duck (*A. fulvigula fulvigula*), and the resultant introgression threatens the existence of the latter subspecies (98). Introgression also occurs between domesticated introduced mallards and the native Australian (Pacific) black duck, *A. superciliosa rogersi* (92).

The North American ruddy duck, *Oxyura jamaicensis*, similarly threatens Europe's rarest duck, the white-headed duck (*O. leucocephala*) (14, 144). Formerly widespread in the Mediterranean region, the white-headed duck in Europe was reduced by habitat destruction and hunting to 22 individuals in southern Spain. Rigorous protection and captive breeding have resulted in growth of this Spanish population to nearly 800 birds. The ruddy duck was first bred in captivity in England in 1949 but quickly escaped; it now numbers some 3500 individuals (109, 144). They invaded the adjacent Continent and recently reached Spain, where at least ten fertile hybrids have hatched (144); the extent of backcrossing has not yet been determined. It is not inconceivable that the ruddy duck could expand its range to contact the only other white-headed duck population, in Kazakhstan.

Among birds, such problems are hardly restricted to ducks. The Seychelles turtle dove (*Streptopelia picturata rostrata*) has so massively hybridized with *S. p. picturata*, introduced from Madagascar, that a hybrid swarm now inhabits the Seychelles, and the average phenotype resembles that of the invader (38). In South Africa, the endemic red-eyed dove, *S. semitorquata australis*, whose populations had waned because of deforestation, has hybridized with introduced *S. s. semitorquata* from Mozambique with introgression to the extent that there is now a hybrid swarm (32). Even the most publicized threatened species of the United States, the northern spotted owl (*Strix occidentalis caurina*), may be at risk from this process. Although destruction of its old growth habitat

has been the main cause of its decline (137), the recent invasion of the Pacific Northwest by the barred owl (*S. varia*) is ominous. It is gradually expanding its range and numbers (13), and nest observations already show that it hybridizes and produces fertile offspring with the spotted owl and that there has been productive backcrossing in one direction (67).

There are several well-documented mammalian examples as well. Feral housecats (*Felis catus*) threaten the existence of the wildcat (*F. silvestris*) through hybridization (77). Remote areas of northern and western Scotland were believed to harbor among the purest wildcats in Europe, but 80% of individuals studied by a number of genetic analyses had domestic cat traits. An identical problem is occurring even in remote areas of southern Africa as feral housecats breed with the African wildcat, *F. libyca* (133).

The attempt to reintroduce the red wolf (*Canis rufus*) into the eastern United States (146) may already be doomed. mtDNA analysis of individuals from much of its current and historical range indicate that all of them have either gray wolf (*C. lupus*) or coyote (*C. latrans*) haplotypes, suggesting the red wolf may be a species of hybrid origin (148). Red wolves have also hybridized with coyotes as the latter increased in density and range in the East in this century. The continued increase in Eastern coyote populations bodes ill for the red wolf, as the coyote will ultimately be far more numerous wherever captive-reared red wolves can be released. Hybridization between coyotes and red wolves or gray wolves has probably also affected coyote genotypes in the East (89). Whether the red wolf has a hybrid origin remains controversial (47, 106, 111, 147), but recent microsatellite DNA analysis (122) supports this hypothesis. Either way, it is difficult to be optimistic that genes of individuals released now will not mix extensively with those of coyotes. Such a hybridization between an introduced red wolf and a coyote was recently reported (R Wayne, personal communication).

In Europe, what had been considered pure wolf (*C. lupus*) populations have turned out to be largely hybrids between wolves and domestic and feral dogs (*Canis familiaris*), leading to the formation of a "Wolf Federation" to protect wolves from "genetic pollution" from dogs (35). By contrast, the identical hybridization in the United States has led to recent calls to protect humans from the hybrids (76) and also to delist the wolf because it no longer satisfies the criteria of the Endangered Species Act (ESA) (75).

In Britain, the European polecat (*Mustela putorius*) had declined nearly to extinction because of predator control to enhance gamebird shooting (30). As this pressure is easing, the polecat is recovering, but there is widespread concern (30, 94) for its genetic integrity because of hybridization with domesticated, escaped, and feral ferrets (*M. furo*). The ferret is itself a domesticated form of *M. putorius*, *M. eversmanni*, or both.

Simien jackals (*Canis simensis*) in Ethiopia were so greatly reduced by habitat destruction and hunting that they are now restricted to habitat fragments (105) and are outnumbered by domestic dogs by about 10:1 (60). Introgression occurs through matings between male dogs and female jackals (60), as demonstrated by mtDNA and microsatellites. As in the red wolf example, the great disparity in the population sizes of the two parental taxa puts the genome of the rare one at risk far more than that of the common species.

In Scotland, sika deer (*Cervus nippon nippon*) introduced from Japan about 80 years ago hybridize with native red deer (*C. elaphus*), and allozyme, microsatellite DNA, and mtDNA analyses show extensive introgression (1). A broad, non-equilibrium hybrid zone is moving, and the genetic integrity of Scottish red deer is threatened (1).

A unique genetic threat has recently been described among amphibians. The hybridogenetic hybrid frog *Rana esculenta* and its two parental species *R. lessonae* and *R. ridibunda* have been introduced to sites in central Spain (15). There is a substantial threat that *R. esculenta* will outcompete the native *R. perezi*, which has a restricted distribution, and there is also concern that *R. ridibunda* will hybridize with *R. perezi*. This cross has occurred in nature in northern Spain and produced a hybridogenetic taxon whose presence has affected the genetic structure of the local *R. perezi* populations and whose individuals may be expected to be more vigorous than those of the latter species (15).

Genetic mixing occurs among fish species because of the prevalence of introductions for sport or commercial fishing, biological control, or through accidental introductions of bait species. Smallmouth bass (*Micropterus dolomieu*) introduced into the Guadalupe River system in central Texas have hybridized with endemic Guadalupe bass (*M. treculi*), threatening the continued survival of the latter species (50); allozyme analysis confirms backcrossing (151).

Extensive, multiple introductions of rainbow trout (*Oncorhynchus mykiss*) and cutthroat trout (*O. clarki*) in western US watersheds have resulted in loss of diversity of native species because of massive introgression (2, 46, 90). Rainbow trout hybridize extensively with threatened Apache trout (*O. apache*) and endangered Gila trout (*O. gilae*) in the southwestern United States (46). Of Apache trout populations, 65% contain individuals with rainbow trout alleles, and one native population is now completely composed of rainbow trout. Similar molecular studies in northern Italy show that stocking of domestic forms of brown trout (*Salmo trutta*) has resulted in introgression of domestic strains with unique native forms (*S. fario*, *S. marmoratus*, and *S. carpio*) (59). In Poland, hybridization and introgression of the introduced *Coregonus peled* with the native *C. lavaretus* is so extensive that only hybrids occur in about 70% of lakes; pure forms are difficult to find (156).

The arctic char (*Salvelinus alpinus*) in Sweden hybridizes with the introduced American lake trout (*S. namaycush*) (28), a cross that occurs with introgression confirmed by allozyme and mtDNA analysis in Canada, where the two species's native ranges overlap (69, 154). Similarly, arctic char have been shown by allozyme electrophoresis to hybridize with brook trout (*S. fontinalis*) where their native ranges overlap in Labrador, raising concern that char gene pools will be modified in numerous parts of its range where brook trout have been introduced (70).

Casual release of bait fish by sport fishermen, even without a stocking program with tens or hundreds of thousands of fishes, sufficed to generate a hybrid swarm through introgression between introduced sheepshead minnows (*Cyprinodon variegatus*), a bait fish, and the endemic Pecos pupfish (*C. pecosensis*) in less than five years. This occurred over a 430-km stretch of the Pecos River in Texas, about one half of the original geographic range of *pecosensis* (49). Massive introgression was demonstrated by allozyme analysis.

Interspecific gene flow is a major problem in plant conservation because so many plant species, occasionally even heterogeneric ones, can hybridize (52, 62). For example, many endangered sunflower (*Helianthus*) species are threatened by hybridization with the weedy *H. annuus* as the latter has spread with human sowing and disturbance (121). A measure of the problem can be gleaned from the fact that more than 90% of all threatened and endangered plants in California occur sympatrically or parapatrically with at least one congener (12). Consider the Catalina Island mountain mahogany (*Cercocarpus traskiae*), now consisting of 11 adult trees and some 75 seedlings. Allozyme and RAPD analyses show five of the adults and some of the seedlings to be of hybrid origin with the more widely distributed and much more common *C. betuloides* var. *blancheae* (117).

The Role of Habitat Change

Several kinds of habitat change can increase the probability and rate of hybridization. First, local habitat modification can lead to the mixing of previously distinct gene pools, and this mixing can occur between two native populations as well as between a native and an introduced one. Wiegand (152) and later authors have noted that local anthropogenic habitat disturbance promotes introgressive hybridization in plants (references in 118). Anderson (7) refers to "hybridization of the habitat" by disturbance as the means by which interfertile taxa, formerly reproductively isolated by different habitat requirements, achieve close enough spatial proximity for hybridization to occur. For example, in the Ozark Mountains, zigzag spiderwort (*Tradescantia subaspera*) typically grows in rich lime soil at the bases of bluffs, while another native spiderwort (*T. canaliculata*) grows in rocky soil on exposed cliff edges. Hybrids

in nature are very rare, but when bottomlands are cleared, leaf cover erodes and the sunlight increases; hybridization then becomes common, and a hybrid swarm can replace both parental species (9, 104). Hybridization and subsequent introgression between *Iris fulva* and *I. hexagona* in Louisiana have been similarly facilitated by human disturbance (16).

Local habitat change has similarly broken down reproductive isolation between the Chatham Islands subspecies of the yellow-crowned parakeet (*Cyanoramphus auriceps forbesi*) and the red-fronted parakeet (*C. novaezealandiae chathamensis*), although the exact habitat features that formerly separated these taxa are not well understood (38). Further, the general change in the habitat has been in favor of the red-fronted parakeet, and the growing disparity in numbers must exacerbate the probability that individual yellow-crowned parakeets will hybridize. A hunting effort has been mounted against hybrids and red-fronted birds (38). The yellow-crowned parakeet is similarly threatened on other islands, a situation exacerbated by release of hybrids reared in captivity (138).

Construction of artificial ponds and the disturbed nature of their surroundings have fostered hybridization between the native tree frogs *Hyla cinerea* and *H. gratiosa* in Alabama (88, 125). The latter species calls while floating or partially submerged near pond banks. In undisturbed areas, the former species calls from an elevated position on shrubbery near pond edges or from emergent vegetation. In disturbed areas, such emergent vegetation is absent, and *H. cinerea* calls from the banks or occasionally from trees overhanging the water. In these positions, most hybridization takes place when *cinerea* males intercept *gratiosa* females. Backcrossing occurs, generating introgression, although hybrids and backcrosses may have somewhat reduced fitness. Hybridization is not observed in undisturbed habitat.

A second form of habitat modification that can lead to hybridization is regional habitat change that allows geographic range expansion of one taxon into the range of another. The blue-winged (*Vermivora pinus*) and golden-winged (*V. chrysoptera*) warblers were allopatric in North America before European settlement but have long been sympatric over wide areas because of the abandonment of old fields and reforestation in the northeastern United States (38, 56). Both birds use shrubby stages of old field succession. Hybridization has been frequent wherever *pinus*, which is expanding its range northward, encounters *chrysoptera*, and the latter species has declined greatly (38, 51, 56, 57). The hybrids are fertile, and backcrossing and introgression have occurred (41, 58). The extent to which the *chrysoptera* decline is due to direct competition with the blue-winged warbler, habitat change favoring the latter species, hybridization, or a combination of these factors is unknown (41).

In North America, range extensions of mallards with habitat changes wrought by agriculture have facilitated high levels of hybridization and introgression with Mexican ducks (*A. platyrhynchos diazi*) in the Southwest (78). The Mexican duck in the United States was delisted as an endangered species, and the American Ornithologists' Union declared it to be conspecific with the mallard in 1983, because introgression was so extensive throughout northern Mexico and the southwestern United States (5). Similarly, habitat change associated with agriculture and urbanization has greatly increased the possibility of introgression between mallards and American black ducks (*A. rubripes*) in the Northeast (11, 74, 81). This potential has also increased because of massive releases of game-farm mallards for hunting on the Eastern Shore of Maryland (over one million birds in recent years—J Serie, personal communication).

Several bird subspecies on the Great Plains may disappear as distinct entities because of regional habitat modification (87, 124). The allopatry that resulted from forests spreading westward through grasslands and retracting during warmer interglacials left specifically and subspecifically distinct populations on either side of the prairie. Fire control and planted trees on the Great Plains have formed stepping stones and movement corridors exploited by at least six eastern taxa with subsequent hybridization: eastern and western races of the rufous-sided towhee (*Pipilo erythrophthalmus*), yellow shafted (*Colaptes auratus auratus*) and red-shafted (*C.a. cafer*) flickers, Baltimore (*Icterus galbula galbula*) and Bullock's (*I.g. bullocki*) orioles (cf 75), blue (*C. cristata*) and Steller's (*C. stelleri*) jays, indigo (*Passerina cyanea*) and lazuli (*P. amoena*) buntings, and rose-breasted (*Pheucticus ludovicianus*) and black-headed (*P. melanocephalus palpago*) grosbeaks. For the flickers and orioles, at least, morphological analysis suggests introgression (6, 102). The spread of the barred owl across North America, noted above, might well have been facilitated by the same tree plantings on the Great Plains plus opening and fragmentation of old growth forest in the Pacific Northwest (R Gutierrez, personal communication).

A third kind of habitat change that can engender hybridization is simply the construction of a permanent corridor allowing the continual movement of a taxon into the range of another. For example, several fish species native to the Sumjin River in Korea were introduced to the Dongjin River when two power plants were constructed on the Dongjin, diverting water from the Sumjin (86). One of these species, the loach *Cobitis tainia striata*, hybridized with the endemic subspecies *C.t. lutheri*. High levels of hybridization and introgression have occurred over a 20-km length of the Dongjin River, an area comprising half the historic range of the endemic subspecies.

Outbreeding Depression and the Loss of Locally Adapted Genotypes

Our examples to this point have not discussed whether the new, mixed genotypes are inferior in any way to the original native ones. Sometimes they are not. For example, experimental evidence suggests that hybrid and backcross individuals resulting from hybridization between mallards and North American black ducks and between mallards and New Zealand grey ducks are as fertile and viable as pure parental individuals (65, 110). Also, the formation of a hybrid swarm (e.g. the Pecos pupfish example) suggests that hybrids are not at a substantial disadvantage, particularly when pure parentals disappear and are replaced by hybrids.

Some authors (e.g. 92) would view genetic mixing as a tragedy even if the new genotype were better adapted than the original one to the ambient environment. However, there is every reason to think that hybridization sometimes leads, at least initially, to a population less well-adapted to the local environment. Outbreeding depression is lowered fitness in offspring, or later generations, of crosses between genetically different sources (135). Occasionally the decline in adaptation to the local environment is dramatic, as when the Tatra mountain ibex (*Capra ibex ibex*) population in Czechoslovakia was eliminated through interbreeding with introduced ibexes of different subspecies (135, 136).

Anadromous salmonid fishes have numerous genetically determined adaptations to local environments, including orientation behavior of newly emerged fry and timing of spawning (3). Because of the migratory life cycles of these fishes, these adaptations are crucial to survival and reproduction. Widespread transfers of artificially propagated salmon within the native ranges of these species may cause outbreeding depression through both loss of local adaptation and breakdown of coadapted gene complexes (3).

In another example, widespread introductions of two clam species, *Merccenaria mercenaria* and *M. campechiensis* into one another's ranges, of cultured hybrids into pure single-species populations, and of both species together into previously uncolonized locations have provided many opportunities for hybridization (29). Hybridization between these two species in a Florida coastal lagoon has contributed to a chronic, epizootic incidence of gonadal neoplasia there. Hybrids are more susceptible to the disease, resulting in reduced hybrid fitness through increased mortality and reduced reproduction.

Outbreeding depression is known in several other animals (references in 135) and many plants (references in 52), and observed decreases in fitness are often substantial. However, because the demographic data required to establish a decline in fitness are so scarce, it is likely that other examples, such as some of

those cited in the section Mixing through Introductions as instances of simple mixing, also entail a loss of fitness. However, as we discuss in the section Introgressive Hybridization as an Evolutionary Constructive Process, hybrid vigor or heterosis, with exactly the opposite outcome as outbreeding depression, has been far more frequently documented.

Implications of Mixing for Translocation, Reintroduction, and Stock Enhancement Programs

The fact that genetic mixing can occur suggests that certain conservation programs, though promising to solve one problem, may generate others. As is clear from the ibex example, a well-meaning reintroduction project, aiming to reestablish a species now locally extinct or to prevent inbreeding depression in a small isolated population, can produce catastrophic results even if the hybrids are fertile. The salmon example suggests that stock enhancement programs can be similarly disastrous. The threat posed to marine turtles by recently detected hybridization is not known, but it is possible that well-meaning captive-rearing and transplantation activities are the cause (85). In the section Conservation Implications of Hybrid Sterility and Unidirectional Introgression, we give an example of ungulate hybridization, but one in which the hybrids are sterile and nevertheless the hybridization threatens the parental populations. Hybrid sterility in that instance is caused by segregational difficulties during meiosis, in part owing to differences between the parental species in diploid number of chromosomes. Geographic chromosomal variation may not even correlate with variation in phenotypes within some species of mammals and should be taken into account in translocations of animals among populations, lest wasted reproductive effort doom an entire project (119).

Numerous stock enhancement programs for freshwater fishes such as trout or salmon release fry produced in hatcheries; generally the fry are not obtained from broodstock originating from the population to be enhanced (91). This fact leads to concern that fitness in the local environment will be compromised even if the genotypes of added individuals adapt them to some other environment, because coadapted gene complexes may be destroyed (3, 18). Similar questions have been raised (40) about enhancement programs for sea turtles. Likewise, marine fish stocks such as those of cod in the north Atlantic and invertebrates such as shrimp in Italy, Japan, and China are replenished from hatcheries, and the hatchery strains used for these purposes generally differ genetically from the target populations; they are often also somewhat domesticated by culture conditions (91). Frequently, genetic diversity and effective population size of hatchery stock are low because of inbreeding and/or because relatively few males are used or certain pairs are more successful (23). Mixing of hatchery

stock with wild populations may also lead to increased variance in reproductive success and a decrease in genetic diversity in the wild.

Domesticated stock—individuals selected for survival and reproduction in culture conditions rather than in the wild—may have characteristics that are maladaptive in the target environment. Captive propagation may select for very different traits than nature would (cf 3, 64), and the net result may be lower average fitness in the target population. Additionally, captive propagation in small populations may increase the frequency of correlated traits that are not under selection in the stock but could be maladaptive in the wild.

CONSERVATION IMPLICATIONS OF HYBRID STERILITY AND UNIDIRECTIONAL INTROGRESSION

The fact that individuals of two different taxa mate (hybridization) does not automatically mean that introgression occurs. The hybrids might all be sterile. One might imagine that, if mixing is not an issue, the consequences for conservation are nil, but wasted reproductive effort can threaten a population. For example, the red hartebeest (*Alcelaphus buselaphus*) and the blesbok (*Damaliscus dorcas*) produce viable hybrid offspring in nature, but the male hybrids are sterile and the female hybrids are probably sterile (120). Though gene pools are not mixed in this example, the reproductive effort expended on hybrids is wasted. This loss is not inconsequential because these species are both declining; they are often found in small, isolated populations. The gestation period for both species is eight months, and only a single calf is normally born (105).

The European mink (*Mustela lutreola*) is threatened and declining almost throughout its range. A chief cause is its interaction with the introduced and more numerous American mink (*Mustela vison*). Where they are sympatric, the larger American mink males mate with European mink females, which then do not permit other males to approach them. But the embryos resorb at an early stage, and the female leaves no offspring for that year, while the American mink females are productively mated by conspecific males (123).

Introduced brook trout (*Salvelinus fontinalis*) are displacing resident bull trout (*S. confluentus*) in areas of northwestern North America (90). According to mtDNA analysis, males of each species mate with females of the other, yet allozyme data indicate that about 97% of detected hybrids are F1 individuals. The apparent meagre amount of introgression may result from near sterility of hybrids, their poor mating success, and/or low survival of their progeny. However, even without substantial mixing, this hybridization can have conservation consequences. The more numerous introduced brook trout may have an

advantage because a smaller fraction of the reproductive effort is wasted in the production of hybrids.

Ellstrand (52) describes several examples in plants in which hybrid progeny are either sterile or have such reduced vigor that mixing of either parental gene pool is unlikely. However, if either species is rare, the burden of producing such progeny may threaten its populations with extinction. The fitness costs associated with hybridization of this sort may be severe enough to select for the evolution of secondary isolating mechanisms, but a rare species will often lack the genetic variation necessary for such evolution (52). In any event, several theoretical considerations argue against selection of isolation by this means (37).

Even if introgression occurs, it can be limited in various ways. For example, it can be unidirectional. Either hybrids can fail to mate with individuals of one parental taxon, or such matings can be sterile. Further, hybridization itself can be unidirectional (i.e. males of one species breeding with females of the other species, but not the opposite cross). For example, mtDNA analysis shows that, in the blue-winged/golden-winged warbler example cited above, blue-winged genes are moving into golden-winged populations, but not vice versa (58). Similarly, in the mixing of native Apache trout genomes with those of introduced rainbow trout noted above, rainbow genes have moved into Apache populations, but the reverse introgression has not occurred (46). Even if hybridization is fertile in both directions, it is possible that such hybridization can produce fertile offspring of only one sex. Biased introgression of mtDNA indicates a partial barrier to gene flow, possibly owing to assortative mating or selection against hybrids of one of the crosses (46). In short, the existence of hybridization and even introgression need not mean that there are no barriers to gene flow.

Reduction of the frequency of alleles from introduced species could be attained by elimination of populations or individuals based on morphological or allozyme evidence of introgression. In the absence of such data, culling is presently used to contain hybridization between ruddy and white-headed ducks (144) and between yellow-crowned and red-fronted parakeet hybrids (38). However, culling of hybrids may also result in the loss of locally adapted (nuclear) genetic variation and unique mtDNA haplotypes. If the number of individuals in a population is so low that it is possible that the population could disappear entirely from causes other than introgression, culling could eliminate the very individuals whose genomes might permit the partial "reconstruction" of the species. Extensive genetic data (including mtDNA analysis) are therefore sometimes required to make informed management decisions about the possible eradication of hybrids.

ARE HYBRIDIZATION AND INTROGRESSION MAJOR CAUSES OF EXTINCTION?

What is Important?

If introgression is the perceived threat, there is likely to be disagreement about how concerned we should be. What should we be worried about the extinction of? No one would argue that every individual genome should be protected, although almost all individuals carry a certain amount of genetic variability (genotypic if not allelic) not found elsewhere. A huge gray area—subspecies, races, populations—generates controversy. To adherents of the biological species concept, species are reproductively isolated, although the degree of isolation required for specific status differs among authors. Given this view of species, particularly its most extreme interpretation, introgression would, by definition, be intraspecific. One might then argue that concern over possible outcomes of genetic mixing by introgression is misguided. Why should we worry about loss of such infraspecific entities as subspecies, races, and local populations? On the other hand, often one of the major components of genetic variation in a species is among populations, and so, to conserve genetic variation in a species, one should at least aim to save different populations (20).

There should be no such disagreement about cases in which hybridization without introgression threatens the existence of intersterile taxa (see section on Conservation Implications of Hybrid Sterility and Unidirectional Introgression), since these are clearly not infraspecific units.

Conservation scientists have agreed that entities that do not qualify as species can undergo extinction and that we need to worry about them. The existence of genetically distinct populations, whether or not the differences among them are adaptive, has fostered widespread concern for the conservation of infraspecific entities. Even the ESA allows endangered or threatened status for “subspecies” and “distinct population segments” (75, 140). Such concern leads directly to unease at the prospect of loss of such entities to introgression. The National Research Council Committee on Scientific Issues in the Endangered Species Act (CSIESA) advocates the concept of the “evolutionary unit,” “a group of organisms that represents a segment of biological diversity that shares evolutionary lineage and contains the potential for a unique evolutionary future,” to replace “distinct population segment” in a future ESA (103). A similar concept, the “evolutionarily significant unit,” has been proposed by the National Marine Fisheries Service for managing anadromous salmonids (145). Neither concept forbids gene flow between the units, although the latter emphasizes a substantial (but not absolute) degree of reproductive isolation.

The ESA does not confer protection on hybrids (53), a fact that led to proposals to delist such taxa as the wolf (75) and the Florida panther (53) on the grounds that they have undergone introgression. In fact, the Fish and Wildlife Service (FWS) withdrew its policy that hybrids cannot deserve protection in 1990, but they have not replaced it and are operating on a case-by-case basis (53, 75, 107). The CSIESA proposes that a modified ESA should protect, as evolutionary units, taxa that undergo introgression so long as they remain phenotypically much like the endangered parent taxa, whatever the taxonomic level of the latter (103).

How Common Are These Phenomena?

Just how common is extinction by hybridization and/or introgression? As noted in the introduction, these processes are not usually listed among the major extinction threats. Most general discussions of extinction problems omit any mention of hybridization and introgression, with a few exceptions (e.g. 95, 104). However, there are grounds for thinking these phenomena are more important than is commonly realized. For example, 24 animal species listed under the ESA are now extinct; of these, at least 11 were in fact extinct before the Act was passed (99). Of those 24, introgression was thought to be at least a substantial contributing factor for three taxa, all fishes—the Tecopa pupfish (*Cyprinodon nevadensis calidae*), the Amista gambusia (*Gambusia amistadensis*), and the longjaw cisco (*Coregonus alpenae*) (99).

It is also suggestive that many of the most famous “poster children” among endangered vertebrates are perceived as potentially threatened or irrevocably “contaminated” by hybridization and introgression. In addition to species already cited—the gray and red wolves, the European mink, the Hawaiian, New Zealand, and white-headed ducks, the northern spotted owl, several genera of marine turtles—one can mention the Florida panther (53), Przewalski’s horse (112), orangutan subspecies (10), both mountain zebra subspecies (31–33), wisent (54), wood bison (101), black robin (36), and black stilt (113).

We believe that the examples cited are probably the tip of the iceberg. Because of the complexity and extent of the genetic techniques that are the major tools for detecting introgression, for most populations, even those where introgression might be suspected, genetic analysis has been insufficient or non-existent. There is every reason to think that the great majority of introgression has been undetected (8, 118), and the advent of molecular tools is just beginning to redress this situation. Detecting effects of hybridization where introgression does not occur may be equally difficult. For example, assessing the extent to which American mink mate with European ones (123) is no mean feat, and, of course, cannot be aided by post facto genetic analyses.

The only comprehensive massing of literature reports of hybridization and introgression is of fishes (141). Of 42 interspecific hybridizations suspected on morphological grounds, all but two were confirmed by molecular techniques, while backcrossing was demonstrated by molecular techniques in 22 of these cases. The majority of these examples come from North America. Twenty-four new cases of hybridization not previously suspected on morphological grounds were reported as confirmed by molecular techniques, and backcrossing was demonstrated in 19 of these.

At the intraspecific level, examples are legion. For example, among African ungulates of conservation concern, habitat fragmentation and deliberate introduction and translocation have caused hybridization among various taxa of wildebeest, springbok, impala, blesbok, oryx, and zebra (32).

We appealed to Nature Conservancy land stewards in their internal informational bulletin (*Stewardship Newsletter*) for information on suspected threats from hybridization and introgression. This query elicited numerous examples in which introgression was believed to be threatening a vulnerable taxon. Striking was that most of these were unpublished or "gray literature" reports by experts in the field working on threatened taxa, with minimal or no laboratory support.

Just among plants, for example, at the Lanphere-Christensen Dunes Preserve (California), a native lupine (*Lupinus littoralis*) is hybridizing with an aggressive introduced species, yellow bush lupine (*L. arboreus*), as confirmed by morphology and pollination experiments, with backcrossing less firmly determined (149). No molecular tests have been conducted. In the Roy E. Larsen Sandyland Sanctuary (Texas), it is feared that the candidate endangered white firewheel, *Gaillardia aestivalis* (Walt.). Rock var. *winkleri*, is hybridizing with Indian blanket (*G. pulchella* Foug.), widely planted on roadsides by the Texas Department of Transportation (W Ledbetter, personal communication). No molecular evidence is available. At the Kern Lake Preserve (California), the last population of the candidate endangered Bakersfield saltbush (*Atriplex tularensis*) is suspected through morphological evidence of disappearing in an introgressed hybrid swarm with the widespread *A. serenana* (55; T Kan, personal communication). The process is engendered by anthropogenic habitat change. Along the Sacramento River and its tributaries, the California sycamore (*Platanus racemosa*) appears in the process of being lost to introgression with the London plane (*P. acerifolia*), while the California black walnut (*Juglans hindsii*) may have been hybridized with numerous congeners imported from all over the world for commercial purposes (FT Griggs, personal communication). In neither instance is molecular evidence available.

In Oregon, the federally endangered western bog lily (*Lilium occidentale*) is suspected of hybridizing with the Columbia lily (*L. columbianum*); the federally

threatened Nelson's sidalcea (*Sidalcea nelsoniana*) is suspected of hybridizing with the rose checker-mallow (*S. virgata*); and the candidate endangered peacock larkspur (*Delphinium pavonaceum*) is suspected of hybridizing with the Columbia larkspur *D. trolliifolium* (L Gooch, personal communication). Evidence on introgression is lacking in all three of these cases, and all three may result from natural or anthropogenic range expansion.

It is a common perception that both hybridization and introgression are more frequent in plants than in animals (72) and among freshwater fishes than among other vertebrates (3). For both these groups, we have cited numerous examples of potential conservation consequences. However, it is striking that we found numerous cases of conservation interest, some noted above, among birds and mammals, and a few among reptiles and amphibians. We know of far fewer examples among invertebrates. However, this lacuna may not reflect a smaller incidence of such problems among invertebrates. It may not be coincidental that the problem is well known among the higher vertebrates and poorly known among invertebrates; this disparity exactly mirrors a difference in attention paid by conservation biologists to the different taxa. In general, much more is known about threatened mammals and birds—about which species of both are threatened, and why they are threatened—than about invertebrates (66).

Finally, the key forces conducing to hybridization—anthropogenic species (and subspecies) introductions and habitat modification—are increasing with burgeoning human populations and mobility (139, 150). Habitat modification, in addition to juxtaposing previously disjunct habitats as noted above, leads to fragmentation and isolation of many populations; this phenomenon has been a main theme of conservation biology for over a decade (100). Individuals in small, isolated populations in contact with other taxa are much more likely to hybridize if only because of the difficulty of finding mates of the same species (subspecies, variety, etc). This situation even obtains when the different population is also small, as in the hybridization of blesbok and red hartebeest discussed above. But it is greatly exacerbated when the other population (whether native or introduced) is much larger, as for the European mink, Simien jackal, red wolf, yellow-crowned parakeet, and bull trout. When introgression occurs, barring specific mechanisms opposing interbreeding, a relatively greater fraction of the small population will hybridize each generation, leaving an ever-smaller fraction that has undergone no genetic mixing. Thus, the very factors that threaten extinction by hybridization and introgression—habitat destruction, fragmentation, and species introductions—are all increasing and often act synergistically. The problem is especially likely on islands, on which there are frequently disproportionate amounts of habitat destruction and relatively more introduced species, many of which are more common than the natives (130). Island plants

are often at still greater risk because they tend more than mainland species to be reproductively isolated by habitat rather than by genic or chromosomal barriers (117).

Under what circumstances will introgressive hybridization lead to the genetic extinction of one or both parental taxa as opposed to simply a stable hybrid zone? Although some hybrid zones may be maintained in habitat mosaics that include patches to which hybrids are more suited than parental individuals, broadly speaking, lack of fitness of F1 hybrids, later generations, or backcrosses is evident in many stable hybrid zones (72). This is a form of outbreeding depression. The lack of fitness may result from chromosomal differences, the breakdown of coadapted gene complexes, or both (126). In any event, selection against the hybrids stabilizes the zone and prevents mixing. In this instance, there is an inherent weakness in recombinants of the two parental taxa, independent of the habitat. Hybrid zones also form at boundaries or narrow gradients between distinct habitats, so that each habitat favors one parental taxon, and hybrids are selected against in both (7, 72). There is an equilibrium between increasing dispersal of hybrid individuals away from this "tension zone" and increasing selection against them (24). However, lack of fitness of hybrids is far from a universal phenomenon, and many recent studies of particular taxa show various hybrid classes to have fitness greater than or equal to that of parentals (17). It does not appear possible yet to predict which introgressive hybridizations will lead to stable zones and which to massive introgression and even hybrid swarms; many more empirical studies, particularly those assessing fitness of hybrids of various classes, may lead to such generalizations (17).

What Should Conservationists Do?

The less the genetic distinctness, the less concern is merited, and this is independent of the fact that some conservation "poster children," like the Florida panther and red wolf, that are probably not very distinct genetically may be useful emblems for a larger conservation effort. The amounts of natural gene flow at low taxonomic levels are probably often simply too great to allow optimism that we can maintain segments of the gene pool as distinct entities, whatever ethical considerations might dictate. If natural gene flow is sufficiently great, it is hard to imagine that it should be an ethical concern at all. To some extent, subspecific designations are arbitrary, and most systematists stopped naming subspecies in the 1960s or earlier (18); this tendency was encouraged by the recognition that different traits often show different patterns of geographic variation within species (155). Conservationists are loath to abandon a concept that might be seen as a useful way to save populations, and, as noted above, the ESA allows protection of subspecies. However, modern systematics and molecular techniques cast doubt on the validity of such taxonomy.

Also, it is important for conservationists to choose their fights carefully. One cannot be exercised over every situation in which new genes are flowing into a distinctive population, or economic and emotional resources will be insufficient to win most of these battles. Concern over introgression can lead to absurd situations (79). The dusky seaside sparrow (*Ammodramus maritimus nigrescens*) was listed as an endangered subspecies by the FWS as its population declined because of habitat change. Although the Service spent \$5 million to purchase remaining habitat, the decline continued and five of the last six individuals, all males, were captured (82, 84). A proposal to salvage part of the gene pool of this subspecies by breeding these males with females of another subspecies was stymied for two years by the FWS on the grounds that such hybridization would dilute the dusky seaside sparrow gene pool and would, in any event, create birds not covered by the ESA because they would not be duskies (38, 44, 79, 82). In the end, the Service washed its hands of the affair, allowing the project to proceed with private funds at a Disney World facility (44, 83), but the Service slashed funding to protect habitat for reintroducing the fertile hybrids, on the grounds that the hybrids were not duskies (51).

In retrospect, the FWS could have chosen less controversial grounds for withdrawing from the attempt to salvage the dusky seaside sparrow gene pool. An mtDNA analysis showed no basis for distinguishing the last dusky seaside sparrow population as a subspecies distinct from other Atlantic coastal populations of *A. maritimus* (22) and indicated that the main concern, in terms of genetically distinct entities, should be to preserve representatives of Atlantic coastal populations on the one hand and of Gulf Coast populations on the other (21). This tempest in a teapot illustrates an important point. What does it mean to speak of saving the gene pool of a tiny population, whether subspecifically distinct or not? After all, the population is an evolving entity, and its gene pool will change even without human intervention, if not by gene flow then by mutation, selection, drift, etc.

The Florida panther (*Felis concolor coryi*) is a subspecies of the cougar listed as endangered by the FWS. Fewer than 40 individuals are believed to remain in the wild, all in south Florida, leading to enormous concern about the viability of this taxon (128). Of the two largest groups, one, in the Everglades, consists exclusively of hybrids between the Florida panther and individuals of other subspecies recently introduced from South or Central America (108). The other, in the Big Cypress swamp, appears to be primarily composed of "pure" Florida panthers, although several individuals have morphological and/or mtDNA traits suggesting a hybrid origin with South or Central American cats. Occasional migration is believed to occur between the two groups. These findings led some to question as to whether the Florida panther should be delisted (53).

Ironically, before the introgression with Latin American cats was known, the prospect of deliberately using other subspecies in a captive breeding program as part of a recovery plan was denounced because "such miscegenation would contaminate the *F. c. coryi* bloodlines" (42, p. 9), its status under the ESA would be jeopardized (27, 42), and *F. c. coryi* is believed to be the subspecies best adapted for survival in the Florida environment (27). For this reason, feasibility studies for translocation of Florida panthers into northern Florida were carried out with sterilized Texas mountain lions (*F. c. stanlevana*) (26).

Now the general thinking has turned completely around. Arnold et al (18) cautiously asserted that it may be a good idea to introduce individuals from Texas or possibly other subspecies so that hybridization will occur. This stance was largely rationalized by arguments that 1. hybridization has already occurred anyway, and the hybrid population appears cursorily to be less plagued than others with possible indications of inbreeding depression; 2. the numbers of Florida panthers are so low and signs of possible inbreeding depression so ominous that the subspecies will become extinct without the proposed introduction; and 3. the Florida panther is not genetically very different from other subspecies anyway, so that outbreeding depression is unlikely. Thus, eight female Texas cougars were released into south Florida in 1995, prompting a claim that the evidence of an important role for inbreeding depression is inconclusive and that the possibility of outbreeding depression was not sufficiently studied (96).

This case also seems to be a tempest in a teapot; there is so much evidence of ecological threats to the Florida panther (128) and so little evidence of either inbreeding or outbreeding depression (96) that it is difficult to believe that introduction of Texas cougars is crucial one way or the other to the survival of this population.

INTROGRESSIVE HYBRIDIZATION AS AN EVOLUTIONARILY CONSTRUCTIVE PROCESS

If one is at pains to conserve the processes of evolution, as well as its products (e.g. 100), it is also important to recall the constructive roles played by hybridization. Hybridization can allow for rapid evolutionary change by producing novel gene combinations (25, 93) even in small, fragmented populations (84a). Botanists recognize that it may lead to increased genetic variation at both the genic and genotypic levels, increased fitness, and adaptation to new environments in existing taxa (52, 116, 118).

Hybrid vigor, or heterosis, is a well-known phenomenon (e.g. 73) and has been documented more frequently than outbreeding depression has. Perhaps the relative importance or likelihood of outbreeding depression and hybrid vigor

is correlated with the degree of genetic differentiation of the parent taxa. In any event, sometimes particularly vigorous hybrids thrive in habitats inimical to both parental taxa, in ways that would normally be construed as benefits to conservation. The London plane tree (*Platanus x acerifolia*) is a hybrid of the American sycamore (*P. occidentalis*) and oriental plane (*P. orientalis*), both of which were introduced to England in the seventeenth century, and it is well known as a majestic tree particularly tolerant of coal dust, smoke, compacted soils, and other aspects of the urban environment (132). It is found in many large cities both inside and outside the ranges of both parental species, often where neither parental species can survive. If a tree grows in Brooklyn, it is most likely a London plane (34). That it threatens another taxon in California with introgressive extinction, as noted above, is ironic.

In animals, most of the closely studied examples come from domestic or laboratory species because of the difficulty of measuring fitness differences in the field. However, there is every reason to believe the phenomenon is common in nature. For example, a genetically depauperate sexual topminnow species, *Poeciliopsis monacha*, with consequent low heterozygosity, was consistently outcompeted in a stream for many generations by an asexual congener. Laboratory studies showed reduced developmental stability and resistance to anoxic stress associated with reduced heterozygosity, but the mechanism of competition in the field was not determined. However, addition of a few pregnant *P. monacha* from another, genetically variable population led rapidly to a great increase in genetic diversity and relative frequency of *P. monacha* and a great decrease in relative frequency of the asexual form (142).

In addition, as many as 70% of angiosperm species may have arisen through the formation of polyploid species by hybridization (97), and introgressive hybridization can foster speciation in plants even without the production of polyploids (16). Hybrid speciation may also have played an important role in the evolution of birds (61, 114), fishes (43, 134), mammals (122), and insects (131).

CONCLUSIONS

Hybridization, with or without introgression, frequently threatens populations in a wide variety of plant and animal taxa because of various human activities. Probably cases reported in the literature do not adequately convey the magnitude of the problem. Increased use of molecular techniques reveals examples not manifest from morphological analysis. Further, the increasing pace of three interacting human activities—habitat modification, fragmentation, and the introduction of exotic species—that contribute to this problem suggests it will worsen. It is thus surprising that most conservation texts and reviews barely mention it as a general problem.

If there is no introgression, but reproductive effort lost to fruitless hybridization threatens a species' existence, management actions may frequently be warranted. Introgression may also be a concern, but conservationists need not raise an alarm every time that populations exchange genes. First, some degree of gene flow is a normal and evolutionarily constructive process. Second, as a practical matter it is difficult to detect and often costly or impossible to prevent some gene flow. Third, particularly at the level of local populations, alleles and genotypes will be lost (and others will arise) even without gene flow; it is fruitless to have as a goal the long-term preservation of every constellation of genes and genotypes. However, often introgression between an introduced and native taxon may lead to less fit populations, perhaps even to a threat of extinction (as in the anadromous salmonids). Even where there is no evidence of fitness decline, it is surely worth attempting to prevent deliberate introductions from causing introgression into a morphologically well-defined, evolutionarily isolated taxon, such as the New Zealand grey duck.

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Literature Cited

1. Abernethy K. 1994. The establishment of a hybrid zone between red and sika deer (genus *Cervus*). *Mol. Ecol.* 3:551–62
2. Allendorf FW, Leary RF. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. *Conserv. Biol.* 2:170–84
3. Allendorf FW, Waples RS. 1996. Conservation and genetics of salmonid fishes. In *Conservation Genetics: Case Histories from Nature*, ed. JC Avise, JL Hamrick. New York: Chapman & Hall. In Press.
4. American Ornithologists' Union. 1979. Resolutions. *Auk* 97 (1, suppl.):10AA
5. American Ornithologists' Union. 1983. *Check-list of North American Birds*. Washington, DC: Am. Ornithol. Union. 6th ed.
6. Anderson BW. 1971. Man's influence on hybridization in two avian species in South Dakota. *Condor* 73:342–47
7. Anderson E. 1948. Hybridization of the habitat. *Evolution* 2:1–9
8. Anderson E. 1949. *Introgressive Hybridization*. New York: Wiley
9. Anderson E, Hubricht L. 1938. Hybridization in *Tradescantia*. III. The evidence for introgressive hybridization. *Am. J. Bot.* 25:396–402
10. Angier N. 1995. Orangutan hybrid, bred

- to save species, now seen as pollutant. *New York Times*, Feb. 28, pp. B5, B9
11. Ankney CD, Dennis DG, Bailey RC. 1987. Increasing mallards, decreasing American black ducks: coincidence or cause and effect? *J. Wildl. Manage.* 51:523–29
 12. Anonymous. 1989. *1988 Annual Report on the status of California's state listed, threatened, endangered plants and animals*. Sacramento: State of Calif. Dep. Fish & Game
 13. Anonymous. 1992. *Recovery Plan for the Northern Spotted owl—Draft*. Washington, DC: USGPO
 14. Anonymous. 1993. UK ruddy duck working group. Information. Peterborough: Joint Nature Conserv. Com.
 15. Arano B, Llorente G, García-Paris M, Herrero P. 1995. Species translocation menaces Iberian waterfrogs. *Conserv. Biol.* 9:196–98
 16. Arnold ML, Bennett BD. 1993. Natural hybridization in Louisiana irises: genetic variation and ecological determinants. See Ref. 72a, pp. 115–39
 17. Arnold ML, Hodges SA. 1995. Are natural hybrids fit or unfit relative to their parents? *Trends Ecol. Evol.* 10:67–71
 18. Arnold SJ, Avise JC, Ballou J, Eldridge J, Flemming D, et al. 1991. Genetic management considerations for threatened species with a detailed analysis of the Florida panther (*Felis concolor coryi*). Washington, DC: USFWS
 19. Atkinson I. 1989. Introduced animals and extinctions. See Ref. 151, pp. 54–75
 20. Avise JC. 1994. *Molecular Markers, Natural History and Evolution*. New York: Chapman & Hall
 21. Avise JC. 1994. A rose is a rose is a rose. See Ref. 100, pp. 174–75
 22. Avise JC, Nelson WS. 1989. Molecular genetic relationships of the extinct dusky seaside sparrow. *Science* 243:646–48
 23. Bartley D, Bagley M, Gall G, Bentley B. 1992. Use of linkage disequilibrium data to estimate effective size of hatchery and natural fish populations. *Conserv. Biol.* 6:365–75
 24. Barton NH, Hewitt GM. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16:113–48
 25. Barton NH, Hewitt GM. 1989. Adaptation, speciation and hybrid zones. *Nature* 341:497–503
 26. Belden RC, Hagedorn BW. 1992. *Feasibility of Translocating Panthers into Northern Florida*. Tallahassee: Fla. Game & Freshwater Fish Comm.
 27. Belden RC, Hines TC, Logan TH. 1986. *Florida Panther Re-establishment: A Discussion of the Issues*. Tallahassee: Fla. Game & Freshwater Fish Comm.
 28. Bernes C, ed. 1994. *Biological Diversity in Sweden—A Country Study*. Stockholm: Swedish Environ. Protect. Agency
 29. Bert TM, Hesselman DM, Arnold WS, Moore WS, Cruz-Lopez H, Marrelli D. 1993. High frequency of gonadal neoplasia in a hard clam (*Mercenaria*) hybrid zone. *Mar. Biol.* 117:97–104
 30. Birks J. 1995. Recovery of the European polecat (*Mustela putorius*) in Britain. *Small Carnivore Conserv.* 12:9
 31. Breytenbach G. 1986. Impacts of alien organisms on terrestrial communities with emphasis on communities of the southwestern Cape. See Ref. 95a, pp. 229–38
 32. Brooke RK, Lloyd PH, de Villiers AL. 1986. Alien and translocated terrestrial vertebrates in South Africa. See Ref. 95a, pp. 63–74
 33. Brown CJ, Gubb AA. 1986. Invasive alien organisms in the Namib Desert, Upper Karoo and the arid and semi-arid savannas of western southern Africa. See Ref. 95a, pp. 93–108
 34. Bumiller E. 1995. Go out, go forth and count. *New York Times*, July 29, p. 16
 35. Butler D. 1994. Bid to protect wolves from genetic pollution. *Nature* 370:497
 36. Butler D, Merton D. 1992. *The Black Robin. Saving the World's Most Endangered Bird*. Auckland: Oxford Univ. Press.
 37. Butlin R. 1989. Reinforcement of premating isolation. In *Speciation and Its Consequences*, ed. D Otte, JA Endler, pp. 158–79. Sunderland, MA: Sinauer
 38. Cade TJ. 1983. Hybridization and gene exchange among birds in relation to conservation. See Ref. 126, pp. 288–309
 39. Compton DE. 1990. Application of biochemical and molecular markers to analysis of hybridization. In *Electrophoretic and Isoelectric Focusing Techniques in Fisheries Management*, ed. DH Whitmore, pp. 241–64. Boca Raton, FL: CRC
 40. Carr AF III, Dodd CK Jr. 1983. Sea turtles and the problem of hybridization. See Ref. 125a, pp. 277–87
 41. Confer JL. 1992. Golden-winged warbler. In *The Birds of North America*, ed. A Poole, P Stettheim, F Gill, No. 20. Philadelphia: Acad. Nat. Sci. Washington, DC: Am. Ornithologists' Union
 42. Cristoffer C, Eisenberg IF. 1985. *On the captive breeding and reintroduction of the Florida panther into suitable habitats*.

- Tallahassee, FL: Fla. Game & Freshwater Fish Comm.
43. DeMarais BD, Dowling TE, Douglas ME, Minckley WL, Marsh PC. 1992. Origin of *Gila seminuda* (Teleostei: Cyprinidae) through introgressive hybridization: implications for evolution and conservation. *Proc. Natl. Acad. Sci. USA* 89:2747–51
 44. Diamond JM. 1985. Salvaging single-sex populations. *Nature* 316:104
 45. Diamond JM. 1989. Overview of recent extinctions. See Ref. 151, pp. 37–41
 46. Dowling TE, Childs MR. 1992. Impact of hybridization on a threatened trout of the Southwestern United States. *Conserv. Biol.* 6:355–64
 47. Dowling TE, Minckley WL, Douglas ME, Marsh PC, DeMarais BD. 1992. Response to Wayne, Nowak, Phillips and Henry: use of molecular characters in conservation biology. *Conserv. Biol.* 6:600–3
 48. DuRietz GE. 1930. The fundamental units of biological taxonomy. *Svensk Bot. Tidsskr.* 24:333–428
 49. Echelle AA, Connor PJ. 1989. Rapid, geographically extensive genetic introgression after secondary contact between two pupfish species (Cyprinodon, Cyprinodontidae). *Evolution* 43:717–27
 50. Edwards RJ. 1979. A report of Guadalupe bass *Micropterus treculi* x smallmouth bass *Micropterus dolomieu* hybrids from 2 localities in the Guadalupe River, Texas USA. *Tex. J. Sci.* 31:231–38
 51. Ehrlich PR, Dobkin DS, Wheye D. 1992. *Birds in Jeopardy*. Stanford, CA: Stanford Univ. Press
 52. Ellstrand NC. 1992. Gene flow by pollen: implication for plant conservation genetics. *Oikos* 63:77–86
 53. Fergus C. 1991. The Florida panther verges on extinction. *Science* 251:1178–80
 54. Fisher J, Simon N, Vincent J. 1969. *Wildlife in Danger*. New York: Viking
 55. Freas KE, Murphy DD. 1988. Taxonomy and the conservation of the critically endangered Bakersfield saltbush, *Atriplex tularensis*. *Biol. Conserv.* 46:317–24
 56. Gill FB. 1980. Historical aspects of hybridization between blue-winged and golden-winged warblers. *Auk* 97:1–18
 57. Gill FB. 1987. Allozymes and genetic similarity of blue-winged and golden-winged warblers. *Auk* 104:444–49
 58. Gill FB. 1994. Rapid, asymmetrical introgression of mitochondrial DNA in hybridizing populations of the blue-winged and golden-winged warblers. In *Proc. XXI Int. Ornithol. Congress*, August 20–25, Vienna, Austria
 59. Giuffra E, Bernatchez L, Guyomard R. 1994. Mitochondrial control region and protein coding genes sequence variation among phenotypic forms of brown trout *Salmo trutta* from northern Italy. *Mol. Ecol.* 3:161–71
 60. Gotelli D, Sillero-Zubiri C, Applebaum GD, Roy MS, Girman DJ, et al. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf *Canis simensis*. *Mol. Ecol.* 3:301–12
 61. Grant PR, Grant BR. 1992. Hybridization of bird species. *Science* 256:193–97
 62. Grant V. 1981. *Plant Speciation*. New York: Columbia Univ. Press. 2nd ed.
 63. Griffin CR, Shallenberger RJ, Fefer SI. 1989. Hawaii's endangered waterbirds: a resource management challenge. In *Proc. of Freshwater Wetlands and Wildlife Symp.*, ed. RR Sharitz, IW Gibbons, pp. 155–69. Aiken, SC: Savannah River Ecol. Lab.
 64. Gross MR. 1991. Salmon breeding behavior and life history evolution in changing environments. *Ecology* 72:1180–86
 65. Haddon M. 1984. A re-analysis of hybridization between mallards and grey ducks in New Zealand. *Auk* 101:190–91
 66. Hadfield MG. 1993. Introduction to the symposium: the crisis in invertebrate conservation. *Am. Zool.* 33:497–98
 67. Hamer TE, Forsman ED, Fuchs AD, Walters ML. 1994. Hybridization between barred and spotted owls. *Auk* 111:487–92
 68. Hammar J. 1989. Freshwater ecosystems of polar regions: vulnerable resources. *Ambio* 18:6–22
 69. Hammar J, Dempson JB, Sk'old E. 1989. Natural hybridization between Arctic char (*Salvelinus alpinus*) and lake char (*S. namaycush*): evidence from northern Labrador. *Nordic J. Freshw. Res.* 65:54–70
 70. Hammar J, Dempson JB, Verspoor E. 1991. Natural hybridization between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*): evidence from northern Labrador. *Can. J. Fisheries Aquatic Sci.* 48:1437–45
 71. Harlan JR. 1983. Some merging of plant populations. See Ref. 126, pp. 267–76
 72. Harrison RG. 1993. Hybrids and hybrid zones: historical perspective. See Ref. 72a, pp. 3–12
 - 72a. Harrison RG, ed. 1993. *Hybrid Zones and the Evolutionary Process*. New York: Oxford Univ. Press
 73. Hartl DL, Clark AG. 1989. *Principles*

- of *Population Genetics*. Sunderland, MA: Sinauer. 2nd ed.
74. Heusmann HW. 1974. Mallard-Black Duck relationships in the Northeast. *Wildl. Soc. Bull.* 2:171-77
 75. Hill KD. 1993. The Endangered Species Act: What do we mean by species? *Environ. Affairs* 20:239-64
 76. Hope J. 1994. A wolf in pet's clothing. *Smithsonian* 25(3):34-45
 77. Hubbard AL, McOrist S, Jones TW, Boid R, Scott R, Easterbee N. 1992. Is survival of European wildcats *Felis silvestris* in Britain threatened by interbreeding with domestic cats? *Biol. Conserv.* 61:203-8
 78. Hubbard JP. 1977. *The biological and taxonomic status of the Mexican duck*. Bull. New Mexico Dep. Game & Fish, No. 1 Albuquerque, New Mexico: New Mexico Dep. Game & Fish
 79. James FC. 1980. Miscegenation in the dusky seaside sparrow? (letter). *BioScience* 30:800-1
 80. Johnsgard PA. 1961. Evolutionary relationships among North American Mallards. *Auk* 78:3-43
 81. Johnsgard PA. 1967. Sympatry changes and hybridization incidence in mallards and black ducks. *Am. Midl. Natur.* 77:51-63
 82. Kale HW II. 1981. Dusky seaside sparrow—Gone forever? *Fla. Naturalist* 54(4):3-48
 83. Kale HW II. 1983. Dusksies transferred to Discovery Island. *Fla. Naturalist* 56(4):3
 84. Kale HW II. 1987. The dusky seaside sparrow: Have we learned anything? *Fla. Naturalist* 60(3):2-3
 - 84a. Kaneshiro KY. 1995. Evolution, speciation and the genetic structure of island populations. In *Islands, Biodiversity and Ecosystem Function*, ed. PM Vitousek, LL Loupe, H Adersen, pp. 23-33. Berlin: Springer-Verlag
 85. Karl SA, Bowen BW, Avise JC. 1995. Hybridization among the ancient mariners: characterization of marine turtle hybrids with molecular genetic assays. *J. Hered.* 86:262-68
 86. Kim JH, Yang SY. 1993. Systematic studies of the genus *Cobitis* (Pisces: Cobitidae) in Korea. IV. Introgressive hybridization between two spined loach subspecies of the genus *Cobitis*. *Korean J. Zool.* 36:535-44
 87. Knopf FL. 1986. Changing landscapes and the cosmopolitanism of the eastern Colorado avifauna. *Wildl. Soc. Bull.* 14:132-42
 88. Lamb T, Avise JC. 1986. Directional introgression of mitochondrial DNA in a hybrid population of tree frogs: the influence of mating behavior. *Proc. Natl. Acad. Sci. USA* 83:2526-30
 89. Lariviere S, Crete M. 1993. The size of eastern coyotes (*Canis latrans*): a comment. *J. Mammal.* 74:1072-74
 90. Leary RF, Allendorf FW, Forbes SH. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. *Conserv. Biol.* 7:856-65
 91. Lester LJ. 1992. Marine species introductions and native species vitality: genetic consequences of marine introductions. In *Introductions and Transfers of Marine Species*, ed. MR DeVoe, pp. 79-89. Charleston, SC: S Carolina Sea Grant Consortium
 92. Lever C. 1987. *Naturalized Birds of the World*. Harlow, Essex: Longman Sci. Tech.
 93. Lewontin RC, Birch LC. 1966. Hybridization as a source of variation for adaptation to new environments. *Evolution* 20:315-36
 94. Lynch JM. 1995. Conservation implications of hybridisation between mustelids and their domesticated counterparts: the example of polecats and feral ferrets in Britain. *Small Carnivore Conserv.* 13:17-18
 95. Macdonald IAW, Kruger FJ, Ferrar AA, eds. 1986. *The Ecology and Management of Biological Invasions in Southern Africa*. Cape Town: Oxford Univ. Press
 - 95a. Macdonald IAW, Loope LL, Usher MB, Hamann O. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. In *Biological Invasions: A Global Perspective*, ed. JA Drake, HA Mooney, F Di-castri, RH Groves, FJ Kruger, et al, pp. 215-55. Chichester UK: Wiley
 96. Maehr DS, Caddick GB. 1995. Demographics and genetic introgression in the Florida panther. *Conserv. Biol.* 9:1295-98
 97. Masterson J. 1994. Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* 264:421-24
 98. Mazourek JC, Gray PN. 1994. The Florida duck or the mallard. *Florida Wildl.* 48(3):29-31
 99. McMillan M, Wilcove D. 1994. Gone but not forgotten: Why have species protected by the Endangered Species Act become extinct? *Endangered Species Update* 11(11):5-6
 100. Meffe GK, Carroll CR. 1994. *Principles of Conservation Biology*. Sunderland, MA: Sinauer

101. Middleton S, Liittschwager D. 1994. *Witness. Endangered Species in North America*. San Francisco: Chronicle Books
102. Moore WS, Keening WD. 1986. Comparative reproductive success of yellow-shafted, red-shafted, hybrid flickers across a hybrid zone. *Auk* 103:42–51
103. National Research Council, Committee on Scientific Issues in the Endangered Species Act. 1995. *Science and the Endangered Species Act*. Washington: Natl. Acad. Press
104. Nigh TA, Pflieger WL, Redfearn PL Jr, Schroeder WA, Templeton AR, Thompson FR III. 1992. *The Biodiversity of Missouri. Definition, Status, Recommendations for Its Conservation*. Jefferson City, MO: Missouri Dep. Conserv.
105. Nowak RM. 1991. *Walker's Mammals of the World*. Vol. 2. Baltimore: Johns Hopkins Univ. Press. 5th ed.
106. Nowak RM. 1992. The red wolf is not a hybrid. *Conserv. Biol.* 6:593–95
107. O'Brien SJ. 1994. When endangered species hybridize: the U.S. hybrid policy. See Ref. 100, 69–70
108. O'Brien SJ, Roelke ME, Yuhki N, Richards KW, Johnson WE, et al. 1990. Genetic introgression within the Florida panther *Felis concolor coryi*. *Natl. Geogr. Res.* 6:485–94
109. Owen M, Atkinson-Willes GL, Salmon DG. 1986. *Wildfowl in Great Britain*. Cambridge: Cambridge Univ. Press. 2nd ed.
110. Phillips JC. 1915. Experimental studies of hybridization among ducks and pheasants. *J. Exp. Zool.* 18:69–144
111. Phillips MK, Henry VG. 1992. Comments on red wolf taxonomy. *Conserv. Biol.* 6:596–99
112. Posschl S. 1994. Rare Przewalski's horse returns to the harsh Mongolian steppe. *New York Times*, Oct. 4, p. B9
113. Reed CEM, Murray DP, Butler DJ. 1993. Black stilt recovery plan *Himantopus novaezealandiae*. *Threatened Species Recovery Plan No. 4*. Wellington, NZ: Dep. Conserv.
114. Rhymer JM. 1994. Reticulate evolution in Hawaiian island ducks. In *Proc. XXI Int. Ornithol. Congr.*, August 20–25, Vienna, Austria
115. Rhymer JM, Williams MJ, Braun MJ. 1994. Mitochondrial analysis of gene flow between New Zealand mallards (*Anas platyrhynchos*) and grey ducks (*A. superciliosa*). *Auk* 111:970–78
116. Rieseberg LH. 1991. Hybridization in rare plants: insights from case studies in *Cercocarpus* and *Helianthus*. In *Genetics and Conservation of Rare Plants*, ed. DA Falk, KE Holsinger, pp. 171–81. New York: Oxford Univ. Press
117. Rieseberg LH, Gerber D. 1995. Hybridization in the Catalina Island mountain mahogany (*Cercocarpus traskiae*): RAPD evidence. *Conserv. Biol.* 9:199–203
118. Rieseberg LH, Wendel JF. 1993. Introgression and its consequences in plants. See Ref. 72a, 70–109
119. Robinson TJ, Elder FFB. 1993. Cytogenetics: its role in wildlife management and the genetic conservation of mammals. *Biol. Conserv.* 63:47–51
120. Robinson TJ, Morris DJ. 1991. Interspecific hybridization in the Bovidae: Sterility of *Alcelaphus buselaphus* x *Damaliscus dorcas* F1 progeny. *Biol. Conserv.* 58:345–56
121. Rogers CE, Thompson TE, Seiler GJ. 1982. *Sunflower Species of the United States*. Bismarck, ND: Natl. Sunflower Assoc.
122. Roy MS, Geffen E, Smith D, Ostrander EA, Wayne RK. 1994. Patterns of differentiation and hybridization in North American wolflike canids, revealed by analysis of microsatellite loci. *Mol. Biol. Evol.* 11:553–70
123. Rozhnov VV. 1993. Extinction of the European mink: ecological catastrophe or a natural process? *Lutreola* 1:10–16
124. Samson F, Knopf F. 1994. Prairie conservation in North America. *BioScience* 44:418–21
125. Schlefer EK, Romano MA, Guttman SI, Ruth SB. 1986. Effects of twenty years of hybridization in a disturbed habitat on *Hyla cinerea* and *Hyla gratiosa*. *J. Herpetol.* 20:210–21
126. Schonewald-Cox CM, Chambers SM, MacBryde B, Thomas L, eds. 1983. *Genetics and Conservation*. Menlo Park, CA: Benjamin/Cummings
127. Searle JB. 1993. Chromosomal hybrid zones in eutherian mammals. See Ref. 72a, pp. 309–53
128. Short LL. 1969. Taxonomic aspects of avian hybridization. *Auk* 86:84–105
129. Shrader-Frechette KS, McCoy ED. 1993. *Method in Ecology. Strategies for Conservation*. Cambridge: Cambridge Univ. Press
130. Simberloff D. 1988. The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* 19:473–511
131. Simberloff D. 1995. Why do introduced species appear to devastate islands more

- than mainland areas? *Pac. Science* 49:87–97
132. Spence JR, Gooding RH, eds. 1990. Evolutionary significance of hybridization and introgression in insects. *Can. J. Zool.* 68:1699–1805
 133. Spongberg SA. 1990. *A Reunion of Trees*. Cambridge, MA: Harvard Univ. Press
 134. Stuart C, Stuart T. 1991. The feral cat problem in southern Africa. *Afr. Wildl.* 45:13–15
 135. Svärdsön G. 1970. Significance of introgression in coregonid evolution. In *Biology of Coregonid Fishes*, ed. CC Lindsey, CS Woods, pp. 33–59. Winnipeg: Univ. Manitoba Press
 136. Templeton AR. 1986. Coadaptation and outbreeding depression. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. ME Soulé, pp. 105–16. Sunderland, MA: Sinauer
 137. Templeton AR. 1994. Coadaptation, local adaptation, outbreeding depression. See Ref. 100, pp. 152–53
 138. Thomas JW, Forsman ED, Lint JB, Meslow EC, Noon BR, Verner J. 1990. *A Conservation Strategy for the Northern Spotted Owl*. Washington, DC: USGPO
 139. Towns DR, Daugherty CH, Cromarty PL. 1990. Protocols for translocation of organisms to islands. In *Ecological Restoration of New Zealand Islands*, ed. DR Towns, CH Daugherty, IAE Atkinson, pp. 240–54. Wellington: NZ Dep. Conserv.
 140. United States Congress. Office of Technology Assessment. 1993. *Harmful Non-Indigenous Species in the United States*. Washington, DC: USGPO
 141. United States Fish and Wildlife Service. 1988. *Endangered Species Act of 1973. As Amended Through the 100th Congress*. Washington, DC: Dep. Interior
 142. Verspoor E, Hammar J. 1991. Introgressive hybridization in fishes: the biochemical evidence. *J. Fish Biol.* 39 (Suppl. A):309–34
 143. Vrijenhoek RC. 1989. Population genetics and conservation. See Ref. 150, pp. 89–98
 144. Waddington CH. 1956. Genetic assimilation of the *bithorax* phenotype. *Evolution* 10:1–13
 145. Waite TL. 1993. Relative puts rare European duck at extinction's door. *New York Times*, April 13, p. B-8
 146. Waples RS. 1991. Pacific salmon, *Oncorhynchus* spp., the definition of "species" under the Endangered Species Act. *Mar. Fisheries Rev.* 53:11–22
 147. Warren RJ. 1994. An emerging management tool: large mammal predator reintroductions. See Ref. 100, pp. 346–47
 148. Wayne RK. 1992. On the use of morphologic and molecular genetic characters to investigate species status. *Conserv. Biol.* 6:590–92
 149. Wayne RK, SM Jenks. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature* 351:565–68
 150. Wear KS. 1995. Hybrid lupine (*Lupinus arboreus* x *L. littoralis*) on the Samoa Peninsula, Humboldt County, CA. Arcata, CA: Nature Conservancy
 151. Western D, Pearl M. 1989. *Conservation for the Twenty-First Century*. New York: Oxford Univ. Press
 152. Whitmore DH. 1983. Introgressive hybridization of smallmouth bass (*Micropterus dolomieu*) and Guadalupe bass (*M. treculi*). *Copeia* 1983:672–79
 153. Wiegand KM. 1935. A taxonomist's experience with hybrids in the wild. *Science* 81:161–66
 154. Williams MJ, Roderick C. 1973. Breeding performance of grey duck (*Anas superciliosa*), mallard (*Anas platyrhynchos*) and their hybrids in captivity. *Int. Zoo Yearbk.* 13:62–69
 155. Wilson CC, Hebert PDN. 1993. Natural hybridization between Arctic char (*Salvelinus alpinus*) and lake trout (*S. namaycush*) in the Canadian Arctic. *Can. J. Fish. Aquatic Sci.* 50:2652–58
 156. Wilson EO, Brown WL. 1953. The subspecies concept and its taxonomic application. *Syst. Zool.* 2:97–111
 157. Witkowski A. 1989. Fishes introduced to Polish waters and their effect on environment. *Przegląd Zoologiczny* 33:583–98