# Economic Associations among Causes of Species Endangerment in the United States

BRIAN CZECH, PAUL R. KRAUSMAN, AND PATRICK K. DEVERS

ASSOCIATIONS AMONG CAUSES OF SPECIES ENDANGERMENT IN THE UNITED STATES REFLECT THE INTEGRATION OF ECONOMIC SECTORS, SUPPORTING THE THEORY AND EVIDENCE THAT ECONOMIC GROWTH PROCEEDS AT THE COMPETITIVE EXCLUSION OF NONHUMAN SPECIES IN THE AGGREGATE

**Scientific assessment of the causes of species** endangerment is essential for formulating and implementing sound conservation policy. Under the Endangered Species Act (ESA), a species is listed as threatened or endangered only upon federal examination of its status, including the reasons for its demise (Rohlf 1989). Beyond the listing process, critical habitat designation and recovery planning require federal knowledge of endangerment causes. As a result of these requirements, information on species endangerment has consistently appeared in the *Federal Register* since the ESA was passed in 1973. Researchers rely on that body of information to assess patterns of species endangerment in the United States, yet surprisingly few studies have addressed the causes of species endangerment.

For example, Dobson et al. (1997) analyzed the geographical distribution of endangered species in the United States, but the causes of endangerment were not categorized in that work. Czech and Krausman (1997), cautioning that a strictly geographic analysis might result in a focus on "hotspots" and thus lead to imprudent policy decisions, provided a preliminary quantification of the causes of species endangerment in the United States. Wilcove et al. (1998) conducted a more thorough assessment, which included 700 "imperiled" species that were not federally listed. Easter-Pilcher (1996), Foin et al. (1998), and Flather et al. (1998) assessed to various degrees the causes of species endangerment in the course of investigating related topics. Other researchers have looked at the causes of species endangerment for smaller areas or for specific taxa. Collectively, the studies have shown that habitat loss is the most prevalent cause of species endangerment, with non-native species ranking second.

Several aspects of these studies suggest areas for further investigation. First, the studies have generally considered historical as well as current threats. Although the knowledge of historical threats is useful, ascertaining current policy implications depends on the analysis of current threats. Second, none of the studies examined the association of one cause of endangerment with another (or others). These associations among causes of endangerment carry implications for public land managers and policymakers. For example, if outdoor recreation and vandalism are strongly associated as endangerment causes, environmental assessments for recreational developments should address this association. (If, say, an environmental assessment takes into account only the impact of recreational facility construction or that of the recreational activity itself—neglecting the association between the recreational activity and vandalism—the magnitude of the effect on the species will be underestimated.) Finally, none of the studies investigated the implications of the causes of species endangerment for the American economy. As pointed out in the April 2000 special issue of *BioScience* on

---

Brian Czech (e-mail: Brian_Czech@fws.gov) is a conservation biologist in the Division of Refuges, US Fish and Wildlife Service, Arlington, VA 22203. His primary professional interests are conservation biology and ecological economics. Paul R. Krausman is a professor and research scientist in the School of Renewable Natural Resources, Biological Sciences East, University of Arizona, Tucson, AZ 85721, whose primary research interests are mammalian ecology and conservation. Patrick K. Devers is a graduate research assistant in the Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0321. His primary research interest is human dimensions of wildlife conservation.

*Table 1. Causes of endangerment for American species classified as threatened or endangered by the US Fish and Wildlife Service.*

| **Cause** | **Number of species endangered by cause, as indicated by Lowe et al. (1990), Moseley (1992), and Beacham (1994)** | **Estimated number of species endangered by cause, derived by extrapolation of 5% sample from *Federal Register*** |
|---|---|---|
| Interactions with non-native species | 305 | 340 |
| Urbanization | 275 | 340 |
| Agriculture | 224 | 260 |
| Outdoor recreation and tourism development | 186 | 200 |
| Domestic livestock and ranching activities | 182 | 140 |
| Reservoirs and other running water diversions | 161 | 240 |
| Modified fire regimes and silviculture | 144 | 80 |
| Pollution of water, air, or soil | 144 | 140 |
| Mineral, gas, oil, and geothermal extraction or exploration | 140 | 140 |
| Industrial, institutional, and military activities | 131 | 220 |
| Harvest, intentional and incidental | 120 | 220 |
| Logging | 109 | 80 |
| Road presence, construction, and maintenance | 94 | 100 |
| Loss of genetic variability, inbreeding depression, or hybridization | 92 | 240 |
| Aquifer depletion, wetland draining or filling | 77 | 40 |
| Native species interactions, plant succession | 77 | 160 |
| Disease | 19 | 20 |
| Vandalism (destruction without harvest) | 12 | 0 |

integrating ecology and economics, communicating the economic implications of ecological investigations is crucial for biodiversity conservation.

In this study, we provide a taxonomically comprehensive account of current causes of species endangerment in the United States and Puerto Rico. By subcategorizing habitat loss into components that correspond to various economic sectors, we hope to foster a better understanding of what government agencies—and the nation as a whole—need to do to conserve species. We also investigate some of the more consequential associations among causes that may have policy implications for public land managers or for economic sectors and explore some of the geographical characteristics of the causes of species endangerment.

## Data considered

A World Wildlife Fund compendium by Lowe et al. (1990), Moseley (1992), and Beacham (1994) contains accounts of the 877 US (including Puerto Rican) species that were listed as threatened or endangered through August 1994. It is the only contiguous source that describes the threats to listed species and provides an efficient vehicle from which to assess the causes of species endangerment. It illustrates the many ways in which species become endangered, but the causes may be grouped into 18 categories based on similarities of economic activity or biological phenomena involved. For example, the category of agriculture encompasses the economic activities of clearing land for crop production, tilling soil, planting seed, growing crops, and harvesting. The category of genetic problems encompasses the biological phenomena of inbreeding depression, loss of genetic variability through drift, and hybridization.

To find out whether the material in the compendium, much of which derives from information in the *Federal Register*, faithfully reflects the causes of endangerment listed in the *Federal Register*, we drew a 5% ($n = 44$) sample of the 877 study species and ascertained the endangerment causes listed for those species in the *Federal Register*. We extrapolated these results and used Pearson's chi-square statistic to test the corroboration of the compendium data and the extrapolated *Federal Register* data. There is not a significant difference in the distributions of frequencies across the categories of endangerment as compiled from the compendium and extrapolated from the *Federal Register* sample ($\chi^2 = 22.08$, $P = 0.18$, 17 df). Of course, this lack of difference cannot validate the accuracy of either source in representing the causes of species endangerment, but it does suggest that the compendium is an unbiased representation of *Federal Register* data. Both sources indicate that, when the broad category of habitat loss is subcategorized, interactions with non-native species, urbanization, and agriculture are the three leading causes of endangerment (Table 1).

Species are rarely endangered by only one of the 18 causes, however. For most species, it is easier to determine multiple causes of endangerment than it is to determine the relative importance of each cause. However, by the time a species is endangered, any loss of individuals is important, rendering the relevance of "relative importance" questionable in many cases.

We classified causes as associated in cases where multiple causes endangered the same species. Association of endangerment causes can be supportive, effective, or incidental. Supportive association occurs when one cause of endangerment depends on another. For example, logging a particular area may depend on road construction, and both activities may endanger the same species. Effective association occurs when a species is endangered by independent causes that produce the same effect. For example, aquatic species can be endangered by farming, mining, logging, and other erosive practices that cause siltation. Incidental association occurs when a species is endangered by independent causes that produce different effects. For example, agriculture may endanger a species in one portion of its range by destroying habitat, whereas disease endangers the species in another portion of its range.

To detect regional trends of endangerment, we assigned each endangered species to a state, based on the distribution maps used in the compendium. Species existing in more than one state were assigned to the state in which the species remains most numerous. If that information was unavailable, then the species was assigned to the state encompassing the estimated geographic mean of the species' distribution. Most endangered species, however, exist in only one state, and many exist in only one county (Dobson et al. 1997).

## Associations of species endangerment

For each species, every pairing of one cause of endangerment with another constitutes an instance of association. For each endangerment cause, the sum of these instances of association may be called "total association." Of the 18 categories of endangerment causes, urbanization ranks highest in total association. It endangers 275 species, which are endangered also by the other 17 causes in 836 instances (Table 2). For example, urbanization endangers the Florida snail kite (*Rostrhamus sociabilis plumbeus*), but the kite is endangered also by non-native species, agriculture, groundwater depletion, and pollution (Lowe et al. 1990).

For some purposes, the proportion of associations to the number of species endangered, or the "proportional association," is a more relevant parameter than total association. Roads—their construction, presence, and maintenance—are the endangerment cause with the greatest proportional association (Table 2). The 94 species endangered by roads are also endangered by other activities in 408 instances; the proportional association is 408/94 = 4.3. The cause with the least proportional association is disease. The 19 species endangered by disease are also endangered by other activities in only 38 instances; the proportional association is 38/19 = 2.0.

Urbanization and agriculture are associated in more cases ($n$ = 124) of endangerment than any other pair of

***Table 2. Associations among species endangerment causes. Each cell indicates the percentage of species endangered by the cause specific to the column that is simultaneously endangered by the cause specific to the row. For example, 19% of the species endangered by cause 2 (urbanization) are simultaneously endangered by cause 1 (non-native species), while 17% of the species endangered by cause 1 (non-native species) are simultaneously endangered by cause 2 (urbanization). To find the cause most frequently associated with recreation, for example, look for the highest figure in column 4, not in row 4. (The cause most frequently associated with recreation is urbanization.)***

| Cause | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | Total[a] | Proportional[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Non-native spp. | | 19 | 20 | 25 | 40 | 30 | ***47***[c] | 19 | 13 | ***50*** | 10 | 18 | 17 | ***71*** | 31 | 25 | ***58*** | 33 | 769 | 2.52 |
| 2. Urbanization | 17 | | ***55*** | 39 | 37 | 28 | 41 | 34 | 40 | ***50*** | 33 | 37 | ***55*** | 12 | 36 | 35 | 16 | 25 | 836 | 3.04 |
| 3. Agriculture | 14 | ***45*** | | 22 | 37 | ***50*** | 31 | ***53*** | 43 | 41 | 18 | 43 | ***49*** | 11 | ***45*** | 18 | 5 | 25 | 809 | 3.61 |
| 4. Recreation | 15 | 26 | 15 | | 32 | 6 | 24 | 10 | 27 | 29 | 26 | 19 | 31 | 13 | 9 | 23 | 5 | 5 | 533 | 2.87 |
| 5. Livestock | 24 | 24 | 30 | 32 | | 24 | 40 | 26 | 31 | 43 | 18 | 28 | 34 | 24 | 12 | 22 | 11 | 25 | 699 | 3.84 |
| 6. Reservoirs | 16 | 16 | 36 | 6 | 21 | | 12 | ***59*** | 35 | 24 | 3 | 30 | 31 | 11 | 29 | 12 | 0 | 17 | 539 | 3.35 |
| 7. Modified fire | 22 | 21 | 20 | 18 | 31 | 11 | | 13 | 16 | ***44*** | 10 | 26 | 27 | 24 | 4 | 12 | 0 | 0 | 538 | 3.74 |
| 8. Pollution | 9 | 18 | 34 | 8 | 20 | ***53*** | 13 | | 37 | 29 | 9 | 33 | 29 | 10 | 23 | 16 | 0 | 8 | 540 | 3.75 |
| 9. Mining | 6 | 20 | 27 | 20 | 24 | 30 | 16 | 36 | | 23 | 18 | 39 | 37 | 8 | 6 | 12 | 0 | 0 | 509 | 3.64 |
| 10. Industry | 22 | 24 | 24 | 20 | 31 | 20 | 40 | 26 | 21 | | 6 | 19 | 30 | 14 | 10 | 3 | 0 | 17 | 563 | 4.30 |
| 11. Harvest | 4 | 15 | 9 | 17 | 12 | 2 | 8 | 8 | 15 | 5 | | 12 | 11 | 15 | 8 | 3 | 16 | 42 | 273 | 2.28 |
| 12. Logging | 7 | 15 | 21 | 11 | 16 | 20 | 19 | 25 | 30 | 16 | 11 | | 37 | 7 | 3 | 6 | 32 | 8 | 406 | 3.72 |
| 13. Roads | 5 | 19 | 21 | 16 | 18 | 18 | 17 | 19 | 25 | 21 | 8 | 32 | | 5 | 13 | 16 | 5 | 25 | 408 | 4.34 |
| 14. Genetics | 21 | 4 | 4 | 6 | 12 | 6 | 16 | 6 | 5 | 10 | 12 | 6 | 5 | | 17 | 1 | 5 | 8 | 295 | 3.21 |
| 15. Aquifers | 8 | 10 | 16 | 4 | 5 | 14 | 2 | 13 | 4 | 6 | 5 | 2 | 11 | 14 | | 6 | 0 | 8 | 211 | 2.74 |
| 16. Native species | 6 | 10 | 6 | 10 | 9 | 6 | 6 | 8 | 6 | 5 | 6 | 5 | 13 | 1 | 6 | | 16 | 33 | 198 | 2.57 |
| 17. Disease | 4 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 6 | 1 | 1 | 0 | 4 | | 8 | 38 | 2.00 |
| 18. Vandalism | 1 | 1 | 1 | 3 | 2 | 1 | 0 | 1 | 0 | 2 | 4 | 1 | 3 | 1 | 1 | 5 | 5 | | 41 | 3.42 |

[a] This column provides the total number of associations exhibited by the cause.

[b] This column provides proportional associations; total associations divided by the number of species endangered.

[c] Pairwise proportional associations comprising the upper five percentile are in bold and italics.

***Everglades snail kite* (Rostrhamus sociabilis plumbeus). *The Florida snail kite is endangered by multiple causes. Photo: US Fish and Wildlife Service.***

causes. The species simultaneously endangered by both causes include 45% of the species endangered by urbanization and 55% of the species endangered by agriculture. This strong association—most likely a product of the drastic modification of habitat at the urban–rural interface—is supportive, in that agricultural areas tend to support urbanization for the sake of market efficiency (Cramer and Jensen 1994).

The greatest proportional pairwise association involves species endangered by genetics problems, 71% of which are endangered also by interactions with non-native species. This strong association may reflect the preponderance of Hawaiian species that are threatened by non-native species; island species may be predisposed to low heterozygosity because of the relative frequency with which island populations are exposed to population bottleneck events (MacArthur and Wilson 1967). It may also reflect the rapid development of genetics expertise and the resulting attention granted to genetic phenomena in recent years; Hawaiian species have generally been listed more recently than other species.

To further explain and explore the causes of species endangerment, to reveal other noteworthy associations of causes, and to describe prevalent geographic patterns, we discuss each of the 18 causes in decreasing order of endangerment frequency. Implications for policy and research follow.

***Interactions with non-native species.*** When a species suddenly appears in an ecosystem (e.g., when it is introduced by humans), it can cause the rapid extinction of native species. Non-native species are typically exotics from other countries, but they include North American species that have become established in ecosystems outside the limits of their natural range or those that have rapidly become prominent in areas where they were historically rare and relatively unimportant. We did not include domesticated crops and animals in this category, but we did include feral livestock and pets.

The non-native species category is the eighth most important cause of endangerment on the mainland, where urbanization endangers over twice as many species ($n$ = 247) as do non-native species ($n$ = 115). However, non-native species endanger 182 species in Hawaii, almost all of which are plants ($n$ = 156) and birds ($n$ = 25). Most of the problem with exotic species in Hawaii involves grazing by feral pigs, goats, sheep, and cattle that originate from nearby farms and ranches, helping to explain why the association with domestic livestock grazing is stronger than any other association involving non-native species (Table 2). Other notorious exotics include rats (*Rattus* spp.), mongooses (*Herpestes* spp.), feral house cats, axis deer (*Axis axis*), mynas (*Gracula* spp.), mosquitoes (*Culex* spp.), phibiscus snow scale (*Pinnaspis strachani*), water hyacinth (*Eichhornia crassipes*), strawberry guava (*Psidium cattleyanum*), and various hymenopterids (mainly parasitic wasps and predaceous ants; Lowe et al. 1990, Moseley 1992, Beacham 1994).

***Urbanization.*** When a minimum of 1000 people per 1.6 km$^2$ reside in a contiguous area with at least 50,000 people, the area is classified by the US Bureau of the Census as urban (Edmondson 1991). Urbanization endangers species by replacing habitat directly and by depleting resources needed to support urban economies. The diversity of effects on species is reflected in the aforementioned preponderance of associations with other endangerment causes. Next to agriculture, urbanization is the most ubiquitous threat, endangering 275 species in 31 states and Puerto Rico. Sixty-one species are endangered in California, 64 in Florida, and 26 in Texas—three of the most rapidly urbanizing states. In the combined area of Utah, Nevada, and Idaho, only two species are endangered by urbanization, at least in part because the majority of the Great Basin is owned by the public and unavailable for private development.

***Agriculture.*** The most obvious ecological effect of agriculture is habitat destruction. Some species coexist with farming to a degree, but soil erosion, siltation of nearby water bodies, and modification of species assemblages are processes that eventually take their toll on many species. Incidental take can also occur, as when a farmer plows through the shallow burrow of a kangaroo rat (*Dipodomys* spp.). Agriculture has more endangerment associations than any other cause except urbanization (Table 2).

Among the regions, the Southeast has the greatest number ($n$ = 98) of the 224 species endangered by agriculture;

among the states, California has 43, tying with Florida for having the greatest number of species endangered by agriculture. Agriculture is also the most ubiquitous of endangerment causes, endangering species in 35 states and Puerto Rico.

***Outdoor recreation and tourism development.*** This category includes disturbance created by hikers, hunters and fishermen, horseback riders, skiers, rock climbers, dirt bikers, 4-wheel drivers, tourists, and the construction of facilities for any of these. It represents a spectrum of human activity ranging from solitary wilderness pursuits to organized social pleasures, and it blends into the category of urbanization when the construction of tourist facilities endangers species in urbanizing areas. Also, the outskirts of urban areas tend to support high levels of recreation, and the strongest association of outdoor recreation is with urbanization (Table 2).

California hosts the greatest number ($n$ = 32) of species endangered by recreation, followed by Hawaii ($n$ = 26) and Florida ($n$ = 19). In terms of ecosystems, the Mojave Desert and the Great Basin are areas of high recreation impact. Twelve species in Utah and Nevada (and several from eastern California) are endangered by recreation.

***Domestic livestock and ranching activities.*** Livestock grazing and related ranching activities have been a cause of species endangerment since the 1800s (Carrier and Czech 1996). The strongest association of this category is with non-native species (Table 2). This association is supportive, in the sense that livestock grazing modifies plant and animal community composition. In another sense, however, this association is incidental, because many of the species endangered by grazing live in Hawaii, where non-native species are rampant for a variety of reasons unrelated to grazing.

***Reservoirs and other surface water diversions.*** The Southeast and Southwest have the most species endangered by water diversions. Species that are geographically limited to an inundated area may be obliterated. Reservoirs and dams block movements of species that need access to other portions of a river for part of their life cycle (e.g., spawning). Reservoirs modify water temperature, depth, and other in-stream characteristics, and they often host introduced predatory species (Minckley and Douglas 1991). In addition to their association with pollution in the Southeast, reservoirs have a supportive association with agriculture in the West (Table 2).

***Modified fire regimes and silvicultural practices.*** Modifications of fire regimes and silvicultural practices have been implicated in the endangerment of 144 species. Fire suppression is the problem in nearly all cases. A formidable array of ecological, social, and political factors have the cumulative effect of suppressing natural fire (Czech 1996). Nearly half of the species endangered by fire suppression are in Florida. Modification of a natural fire regime often changes the composition of biotic communities (Wright and Bailey 1982), suggesting that the strong association of this category with non-native species (Table 2) is largely supportive.

***Pollution of water, air, or soil.*** Of the 144 species endangered by pollution, 85 are found in the Southeast. All except 18 of these species are fish or mussels. Most of the rest are plants, snails, and other invertebrates of aquatic or mesic environments. Pollution is most strongly associated with reservoirs (Table 2), but this association is largely incidental and reflects the fact that pollution and reservoirs are especially problematic for riverine species and that pollutants tend to accumulate in reservoirs. Mining, logging, farming, ranching, and industry are supportively associated with pollution. Urban developments are supportively and effectively associated with pollution.

***Mineral, gas, oil, and geothermal extraction or exploration.*** Mining destroys habitats by removing vegetation and, in many cases, the soil beneath it. Moreover, every viable mine entails the exploration of nonviable areas. Of the 140 species threatened by mining, 134 exist on the mainland. There are more species endangered by mining in Tennessee, Georgia, Alabama, Arkansas, Louisiana, and Florida than in the rest of the United States combined, which is attributable to high levels of mining in areas with high levels of biodiversity and endemism (Lydeard and Mayden 1995).

Mining is most strongly associated with urbanization, agriculture, and pollution (Table 2). The association with pollution is supportive to the extent that mining produces pollution and results in heavy traffic in the vicinity of mines. The association with agriculture is largely effective, because the modified limnology of many southeastern rivers is a function of erosion and siltation caused by mining and agriculture. The association with urbanization is probably well represented by supportive, effective, and incidental factors.

***Industrial, institutional, and military activities.*** This category includes industrial development, military practices, and a few cases of government facility construction in rural areas. This category's strongest association is with urbanization (Table 2), and the association is clearly supportive. Industrialization is also supportively associated with pollution, which is a simultaneous source of endangerment for almost half ($n$ = 38) of the species endangered on the mainland under this category.

The strong association of this category with non-native species (Table 2) is largely incidental. Military activities endanger a variety of species on Hawaii (Lowe et al. 1990, Moseley 1992, Beacham 1994), where non-native species are most problematic.

**Harvest.** The harvest of wild species has little association with other endangerment causes; among all causes of species endangerment, only disease has lower proportional association. Harvesting threatens a disproportionate share of large, charismatic, or economically valuable species. It has long been a threat to raptors such as the bald eagle (Trefethen 1975) and remains an important factor of endangerment for the thick-billed parrot (*Rhynchopsitta pachyrhyncha*), Snake River chinook salmon (*Oncorhynchus tshawytscha*), and numerous sea turtle and whale species. Harvesting also threatens reintroduction efforts for the Rocky Mountain gray wolf (*Canis lupus*; Barker 1993).

**Logging.** Forests cover 32% of the land area in the United States (Cubbage et al. 1993), and the logging of forests endangers 109 species. The northern spotted owl (*Strix occidentalis caurina*) is the best known species endangered by logging, but similar situations exist outside the Pacific Northwest—in the Southwest, for example, the Mexican spotted owl (*Strix occidentalis lucida*) is endangered by logging, as is the red-cockaded woodpecker (*Picoides borealis*) in the Southeast.

Logging is supportively associated with pollution and roads and effectively associated with agriculture and mining (Table 2). Logging, agriculture, and mining contribute to siltation of streams in the Southeast, endangering a variety of mussel species. The main objective of most logging is timber extraction, although logging is frequently incidental to agricultural and industrial development.

**Road presence, construction, and maintenance.** Roads range from two-track jeep trails to eight-lane interstate highways and are known to endanger 94 species. Mammals such as the San Joaquin kit fox (*Vulpes macrotis mutica*), which hunt nocturnally along habitat edges, are run over by automobiles, as are reptiles that are attracted to warm roadbeds, such as the blunt-nosed leopard lizard (*Gambelia silus*). Roadside mowing destroys habitat for the elfin tree fern (*Cyathea dryopteroides*). The dwarf lake iris (*Iris lacustris*) is endangered by chemicals (including salt) used in road and roadside maintenance, while the building of roads in anakeesta shale results in sulfuric acid runoff that endangers the Smoky madtom (*Noturus baileyi*). Several sites of Minnesota trout-lily (*Erythronium propullans*) were simply obliterated by road construction, and road improvements were sufficient to destroy some patches of San Diego mesa mint (*Pogogyne abramsii*; Lowe et al 1990, Moseley 1992, Beacham 1994).

Roads are strongly associated in the supportive sense with urbanization, mining, agriculture, industrial activities, and logging (Table 2)—indeed, none of these activities is likely to intensify without concomitant road building, maintenance, or use.

**Genetic problems.** Inbreeding depression, loss of genetic variability through drift, and hybridization are known or suspected to endanger 92 species. Most of the genetic problems documented thus far affect fish and plant species. Genetic problems are particularly ominous because of their permanence. Whereas an aquifer can be recharged once water conservation is implemented, a depleted or hybridized genome may never regain its integrity. For species like the Florida panther (*Puma concolor coryi*), which numbered less than 50 in 1989 and exhibits signs of inbreeding (Roelke et al. 1993) and genetic invariability (Maehr and Caddick 1995), it is probably too late to salvage a vigorous genotype.

In a sense, any cause of a population decline is supportively associated with genetic problems because loss of genetic variability is a function of declining numbers (Li and Graur 1991). The strongest association of genetic problems is with non-native species (Table 2). Most of the species endangered by genetic problems are Hawaiian species that have reached extremely low numbers, often because non-native species have modified their habitats.

**Aquifer depletion and wetland drainage or filling.** Efforts to meet increased agricultural demands include irrigating drylands and draining wetlands to make them tillable. Wetlands are also filled for construction. These activities modify hydrological processes, and species composition changes accordingly. Of the 77 species endangered by aquifer depletion and wetland loss, 73 inhabit the mainland (especially Florida and coastal and central California, where wetland drainage and filling are rampant, and the arid Southwest, where groundwater pumping depletes aquifers).

One species serves to illustrate the ends of the hydrological spectrum that are susceptible to alteration resulting in species endangerment. The Amargosa niterwort (*Nitrophila mohavensis*) is endangered because much of the wetlands it inhabits in Nevada were drained for peat mining. Since then, groundwater pumping for irrigation has reduced the spring flows that feed the remaining wetland. The niterwort now exists at only two sites and is vulnerable to demographic and genetic stochasticity (Lowe et al. 1990).

**Native species interactions.** We limited this category to species that lack native prey, species that are being preyed on by native species at unprecedented levels, or species that are missing part of a critical life cycle because of the absence of a native species. For example, the cave crayfish (*Cambarus aculabrum*) feeds on organic matter and detritus in the groundwaters of its cave system. Historically, much of the necessary organic matter was provided by gray bats (*Myotis grisescens*). With the drastic decline of the gray bat (another federally listed species; FWS 1982), the cave crayfish's existence was threatened. This category illustrates how endangerment may spread via food webs and other types of interspecific interactions. Such complexities may arise in any ecosystem, and there are no major geographic or thematic patterns associated with this cause.

***Disease.*** Disease is known to endanger 19 species. Although it is a natural occurrence in the evolutionary history of most species, disease is unnaturally endangering when it threatens the existence of a species that has been decimated by other unnatural causes. For example, canine distemper has been an important factor in driving the black-footed ferret (*Mustela nigripes*) nearly to extinction in the past two decades (Reading et al. 1996). Were ferrets not already limited in distribution by the decline of prairie dogs (*Cynomys* spp.), their primary prey, disease would not have been as threatening.

***Vandalism.*** The relatively small number ($n = 12$) of species endangered by vandalism reflects the pathological nature of such activity. However, the documented cases of vandalism may represent only a small fraction of actual occurrences. Species and their habitats are sometimes vandalized by landowners attempting to evade the provisions of the ESA's Section 9, which prohibits the taking of listed species by any party, public or private. Evasion of Section 9 may be the motive of, for example, vandals who have repeatedly destroyed Virginia round-leaf birch (*Betula uber*) trees and seedlings (Lowe et al. 1990).

## Species endangerment and economic growth

We have noted how the causes of species endangerment tend to correspond to various economic sectors, especially agriculture, mining, logging, ranching, outdoor recreation and tourism, and wild species harvest. We have also described some of the prominent geographical characteristics of species endangerment. Many of the species endangerment hotspots noted by ourselves and others (Dobson et al. 1997, Flather et al. 1998) are likewise hotspots of economic growth—most notably, southern Florida, southern California, and east–central Texas—where many or all economic sectors are active.

Although Table 1 is sufficient to identify various economic sectors as causes of species endangerment, Table 2 illustrates how species tend to be endangered by networks of associated causes, not by single causes that can be addressed via technical means. For example, the cause with the least proportional association is disease; therefore, research and management focusing on disease should be rendered inconsequential by other causes in relatively few cases. However, disease is the second least important of the endangerment causes (Table 1). Furthermore, although species endangered by disease are endangered by only two other causes on average, in no case is disease the only cause of endangerment. This fact supports our earlier proposition that most species do not become endangered by disease until they have been decimated by other causes, which are dominated by economic phenomena.

***Florida panther* (Puma concolor coryi). *The Florida panther is an example of species that are first endangered by economic activities and then by genetic problems stemming from low population size. Photo: US Fish and Wildlife Service.***

Table 2 also supports the assertion of ecological economists that the economy grows as an integrated whole (Boulding 1993). The causes of species endangerment that we identified represent not only sectors of the economy but infrastructure and activity designed to support or protect these sectors (roads, reservoirs, wetland drainage, fire suppression, and silvicultural activities) or byproducts of these sectors (pollution). Another cause—industrialization—encompasses a vast array of economic activities that depend on the basic sectors for raw materials and in turn produce goods used by those sectors, which explains the high proportional association exhibited by industrialization. Urbanization, the primary cause of species endangerment on the mainland United States, occurs because it offers economic advantages and represents an amalgamation of sectors or a process by which economic activities are concentrated geographically (Dunn 1983). The list of endangered species is growing because the scale of the integrated economy, and therefore the causal network of species endangerment, is increasing.

Table 2 is also consistent with the ecological principles of niche breadth and competitive exclusion. In the economy of nature, the success of one species comes at the expense of another, according to the principle of competitive exclusion (Pianka 1974). Because of the tremendous breadth of the human niche, the increasing scale of human economy amounts to the competitive exclusion of nonhumans in general (Czech 2000a).

These observations suggest that the implications of species endangerment assessments are primarily economic.

***Black-footed ferret* (Mustela nigripes). *Were ferrets not already limited in distribution by the decline of prairie dogs, their primary prey, diseases would not have been as threatening. The prairie dog decline is attributable largely to the livestock production sector. Photo: Larry Shanks, US Fish and Wildlife Service.***

Conservation policy, in other words, may amount to macroeconomic policy, and macroeconomic policy may largely define conservation policy. We therefore concur with Angermeier and Karr (1996), who stated that "conservation biologists should play a major role in articulating the value of biota [and] demonstrating links between biological integrity and economic stability" (p. 273).

## Policy implications

Neoclassical economists assert that economic carrying capacity perpetually increases via the principles of resource substitutability, increasing productive efficiency, and human capital (Solow 1988). However, the cumulative substitution may be of a diverse economic system for a diverse ecological system, and increasing productive efficiency may amount to a more efficient capability to extract the natural resources that comprise nonhuman species' habitats. The US economy is clearly becoming more diverse (Frank 1999) and its efficiency in extracting natural resources is clearly increasing (Simon 1996), all in concert with proliferating species endangerment (NRC 1995, Czech and Krausman in press).

Our results indicate that the use of increasing economic carrying capacity for the sole purpose of economic growth will result in a lengthier list of endangered and extinct species. However, if economic carrying capacity can grow without a concomitant increase in the scale of human economy, then species endangerment may subside. In other words, if substitutability and efficiency gains are employed as a buffer between the scale of human economy and economic carrying capacity, that buffer could constitute a growing source of nonhuman habitats. Similarly, profits resulting from advances in substitutability and efficiency could be invested in ecological restoration rather than manmade capital.

Some have asserted that the American economy has been undergoing a transformation from an industrial to an "information" economy—that is, an economy in which an increasing proportional expenditure is committed to information services and in which, theoretically, fewer natural resources are liquidated (Rothschild 1990). Based on the principles of trophic ecology, we do not believe that the transformation to an information economy will halt species endangerment. Information as a product is analogous to a high trophic level that appears only when the trophic pyramid achieves a certain volume. Alternatively, information services are analogous to a new niche that only appears when the ecosystem reaches an adequate complexity, which itself is a function of pyramid volume (Fortey 1998). In either case, the information economy requires a large base to commence and requires an expanding base to grow (Czech 2000b).

## Research implications

Identifying hotspots of species endangerment is not the same as identifying extraordinary opportunities for species conservation. In most cases, species conservation is a matter of real property acquisition, government regulation, cooperative management (often necessitated by regulation), or a combination thereof. As an area becomes a hotspot—economically and ecologically—acquisition becomes more costly and regulation more contested. The relationship between species endangerment prevalence and the value of species conservation efforts should be assessed across and within ecosystems.

We hypothesize that there is a cost per hectare that optimizes the number of species to be conserved, and that this cost per hectare would be intermediate. *Across* ecosystems, low cost per hectare would tend to be associated with areas that are low in economic and ecological diversity (e.g., playas in the desert Southwest). High cost per hectare would tend to be associated with areas of high economic diversity and high but already compromised ecological diversity (e.g., areas being subdivided in coastal and estuarine areas). In both cases, we hypothesize, species conservation effected per dollar invested would be low. *Within* ecosystems, it seems clear that the least expensive areas (i.e., those with little economic activity) would offer the greatest conservation value.

The most difficult aspect of investigating the relationship between species endangerment prevalence and the value of conservation efforts would be determining what constitutes conservation value. Is the conservation of a large, relatively natural area with no endangered species more valuable than the conservation of a small, relatively unnatural area with several endangered species? Species prioritization and risk assessment will play prominent roles in such investigations. For example, based on a synthesis of genetic, evolutionary, and ecological considerations, some would favor conserving the large area if the species to be conserved in the small area were primarily invertebrates (Czech and Krausman 1998). Others, basing their judgment largely on ethical concerns, would probably opt to conserve the small acreage no matter what species were involved (Windsor 1995).

Finally, there is an urgent need for ecologists and economists to collaborate on research designed to refine the relationship between economic scale and species conservation. This is the type of "consilient" research that Wilson (1998) promoted. With regard to species endangerment and ecological sustainability in general, Daly (1993, p. 29) posited that "the limits regarding what rates of depletion and pollution are tolerable must be supplied by ecology." Ecologists will certainly be helpful in ascertaining those limits, but their calculations will be of little utility unless economists concurrently and more precisely describe the relationship between economic scale and natural capital (and therefore nonhuman habitat) liquidation. Knowledge of that relationship is required to prescribe macroeconomic policies that are tantamount to conservation policies in the twenty-first century.

## Acknowledgments

The authors thank Bob Steidl, Mark Borgstrum, and Steven DeStephano for statistical and other advice. The late Eugene Maughan also provided assistance.

## References cited

Angermeier PL, Karr JR. 1996. Biological integrity versus biological diversity as policy directives: Protecting biotic resources. Pages 264–275 in Samson FB, Knopf FL, eds. Ecosystem Management: Selected Readings. New York: Springer-Verlag.

Barker R. 1993. Saving All the Parts: Reconciling Economics and the Endangered Species Act. Washington (DC): Island Press.

Beacham W. 1994. The Official World Wildlife Fund Guide to Endangered Species of North America, Vol. 4. Washington (DC): Walton Beacham.

Boulding KE. 1993. The Structure of a Modern Economy: The United States, 1929–89. Washington Square (NY): New York University Press.

Carrier WD, Czech B. 1996. Threatened and endangered wildlife and livestock interactions. Pages 39–50 in Krausman PR, ed. Rangeland Wildlife. Denver (CO): Society for Range Management.

Cramer GL, Jensen CW. 1994. Agricultural Economics and Agribusiness. 6th ed. New York: John Wiley & Sons.

Cubbage FW, O'Laughlin J, Bullock CS III. 1993. Forest Resource Policy. New York: John Wiley & Sons.

Czech B. 1996. Challenges to establishing and implementing sound natural fire policy. Renewable Resources Journal 14: 14–19.

______. 2000a. Economic growth as the limiting factor for wildlife conservation. Wildlife Society Bulletin 28 (1): 4–14.

______. 2000b. Shoveling Fuel for a Runaway Train: Errant Economists, Shameful Spenders, and a Plan to Stop Them All. Berkeley (CA): University of California Press, Berkeley.

Czech B, Krausman PR. 1997. Distribution and causation of species endangerment in the United States. Science 277: 1116–1117.

______. In press. The Endangered Species Act: History, Conservation Biology, and Public Policy. Baltimore (MD): Johns Hopkins University Press.

______. 1998. The species concept, species prioritization, and the technical legitimacy of the Endangered Species Act. North American Wildlife and Natural Resources Conference Transactions 62: 514–524.

Daly HE. 1993. Introduction to essays toward a steady-state economy. Pages 11–50 in Daly HE, Townsend KN, eds. Valuing the Earth: Economics, Ecology, Ethics. Cambridge (MA): MIT Press.

Dobson AP, Rodriquez JP, Roberts WM, Wilcove DS. 1997. Geographic distribution of endangered species in the United States. Science 275: 550–553.

Dunn ES Jr. 1983. The Development of the U.S. Urban System, Vol. II. Washington (DC): Resources for the Future.

Easter-Pilcher A. 1996. Implementing the Endangered Species Act. BioScience 46: 355–363.

Edmondson B. 1991. Census reveals 33 new urban markets. American Demographics 13: 8.

Endangered Species Act of 1973, as Amended. US Code. Vol. 16, secs. 1531–1544.

Flather CH, Knowles MS, Kendall IA. 1998. Threatened and endangered species geography. BioScience 48: 365–375.

Foin TC, Riley SPD, Pawley AL, Ayres DR, Carlsen TM, Hodum PJ, Switzer PV. 1998. Improving recovery planning for threatened and endangered species. BioScience 48: 177–184.

Fortey RA. 1998. Life: A Natural History of the First Four Billion Years of Life on Earth. New York: Alfred A. Knopf.

Frank RH. 1999. Luxury Fever: Why Money Fails to Satisfy in an Era of Excess. New York: Free Press.

Li WH, Graur D. 1991. Fundamentals of Molecular Evolution. Sunderland (MA): Sinauer Associates.

Lowe DW, Matthews JR, Moseley CJ. 1990. The Official World Wildlife Fund Guide to Endangered Species of North America, Vols. 1–2. Washington (DC): Walton Beacham.

Lydeard C, Mayden RL. 1995. A diverse and endangered aquatic ecosystem of the southeast United States. Conservation Biology 9: 800–805.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton (NJ): Princeton University Press.

Maehr DS, Caddick GB. 1995. Demographics and genetic introgression in the Florida panther. Conservation Biology 9: 1295–1298.

Minckley WL, Douglas ME. 1991. Discovery and extinction of western fishes: A blink of the eye in geologic time. Pages 7–17 in Minckley WL, Deacon JE, eds. Battle against Extinction: Native Fish Management in the American West. Tucson (AZ): University of Arizona Press.

Moseley CJ. 1992. The Official World Wildlife Fund Guide to Endangered Species of North America, Vol. 3. Washington (DC): Walton Beacham.

[NRC] National Research Council. 1995. Science and the Endangered Species Act. Washington (DC): National Academy Press.

Pianka ER. 1974. Evolutionary Ecology. New York: Harper and Row.

Reading RP, Clark TW, Vargas A, Hanebury LR, Miller BJ, Biggins D. 1996. Recent directions in black-footed ferret recovery. Endangered Species Update 13: 1–6.

Roelke ME, Martenson JS, O'Brien SJ. 1993. The consequences of demographic reduction and genetic depletion in the endangered Florida panther. Current Biology 3: 340–350.

Rohlf DJ. 1989. The Endangered Species Act. Stanford (CA): Stanford Environmental Law Society.

Rothschild M. 1990. Bionomics: Economy as Ecosystem. New York: Henry Holt.

Simon JL. 1996. The Ultimate Resource 2. Princeton (NJ): Princeton University Press.

Solow RM. 1988. Growth Theory: An Exposition. New York: Oxford University Press.

Trefethen JB. 1975. An American Crusade for Wildlife. New York: Winchester Press.

[FWS] US Fish and Wildlife Service. 1982. Gray Bat Recovery Plan. Denver (CO): Fish and Wildlife Reference Service.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E. 1998. Quantifying threats to imperiled species in the United States. BioScience 48: 607–615.

Wilson EO. 1998. Consilience: The Unity of Knowledge. New York: Vintage Books.

Windsor DA. 1995. Equal rights for parasites. Conservation Biology 9: 1–2.

Wright HA, Bailey AW. 1982. Fire Ecology, United States and Southern Canada. New York: John Wiley & Sons.