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"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"

28 February - 24 March 2000

IN SITU *AND* EX SITU *APPROACHES TO THE CONSERVATION OF BIODIVERSITY*

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Outline for talks at ICTP's
Fifth Course on Mathematical Ecology
Trieste, 6-10 March, 2000

Three talks:

I) Monday, March 6, 1:30 pm: *Biodiversity status and trends. Why conserve biodiversity?*

II) Tuesday, March 7, 2:30 pm: *Principles of conservation biology.*

III) Wednesday, March 8, 10:30 am: In situ *and* ex situ *approaches to the conservation of biodiversity.*

I) Biodiversity status and trends. Why conserve biodiversity?

1) What is biodiversity?

Classic definition of biodiversity, following biological levels of organization: genes, individuals, populations, species, communities/ecosystems, biomes.

Begin with definition of species—basic unit of diversity measurement. Highlight that definition of species is not equally clear for all taxa.

Move up and down the hierarchy of the levels of organization to illustrate the other components of biodiversity: 1) from species "downward": populations, individuals and genes; 2) from species "upward": communities/ecosystems and biomes.

References:

Harper, J. L. and D. L. Hawksworth (1994) Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London B* **345**: 5-12.

Jenkins, M. (1992) Species diversity: an introduction. In: WCMC, Ed. *Global Biodiversity: Status of the Earth's Living Resources*, pp: 40-46. World Conservation Monitoring Centre (WCMC), Chapman and Hall.

2) Global biodiversity patterns

Maps of 1) latitudinal distribution of biodiversity and 2) megadiverse countries.

Origin of the term "hot spots". Megadiversity countries: seventeen of the world's counties (out of ~200) include between 60-70% of described species.

The paradox of biodiversity conservation: more resources where there are fewer species: 1) scientists per country (participants in UNEP's global biodiversity assessment), 2) per-capita GDP.

Discuss the idea that it is not only distribution abut also abundance that matters. Most species are rare. Seven forms of rarity.

References:

Adams, J. M. (1989) Species diversity and productivity of trees. *Plants Today* **2**: 183-187.

Myers, N. (1988) Threatened biotas: "hot spots" in tropical forests. *The Environmentalist* 8(3): 187-208.

Rabinowitz, D., S. Cairns and T. Dillon (1986) Seven forms of rarity and their frequency in the flora of the British isles. In: M. E. Soulé, Ed. *Conservation Biology: the Science of Scarcity and Diversity,* pp: 182-204. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

3) How many species are there?

Classic estimates and controversy by Erwin, May and others.

References:

May, R. M. (1990) How many species? *Philosophical Transactions of the Royal Society of London B* **330**: 293-304.

Pimm, S. L., G. J. Russell, J. L. Gittleman and T. M. Brooks (1995) The future of biodiversity. *Science* **269**: 347-350.

4) Extinction rates past and present

Background extinction rates. Evidence from the fossil record. Extinction is part of the Earth's evolutionary history, but rates have changes. Contrast with current extinction rates. Present range of estimates—including the most extreme ones.

Current rates associated to impact of human activities. Examples: 1) earth from space, 2) habitat destruction rates; photographs of mahogany harvesting, deforestation in Amazonia. Rates of habitat conversion.

References:

May, R. M., J. H. Lawton and N. E. Stork (1995) Assessing extinction rates. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 1-24. Oxford University Press.

Jablonski, D. (1995) Extinctions in the fossil record. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 25-44. Oxford University Press.

Bibby, C. J. (1994) Recent past and future extinctions in birds. *Philosophical Transactions of the Royal Society of London* ***B*** **344**: 35-40.

5) What are we loosing?

Direct (e.g. biotechnology) and indirect (e.g. ecosystem services, ecotourism) benefits from biodiversity. Biophilia. Aspirin example from Lovejoy in *Biodiversity II.*

Direct use of biodiversity: bioprospecting. International legal framework provided by the Convention of Biological Diversity. Property rights, benefit sharing and technology transfer.

The value of biodiversity in pharmaceutical research. Costs and benefits of drugs derived from natural products. The random sampling approach vs. the ethnobiological research approach. Case studies: Costa Rica's INBIO and Shaman Pharmaceuticals.

Bioprospecting in the Third World: making the First World healthier? Outline research agendas for major pharmaceutical companies. Turning bioprospecting into a truly equitable enterprise.

References:

Carlson, T. J., R. Cooper, S. R. King and E. J. Rozhon (1997) Modern science and traditional healing. *Royal Society of Chemistry* **Special Publication 200**: 84-95.

Carlson, T. J., M. M. Iwu, S. R. King, C. Obialor and A. Ozioko (1997) Medicinal plant research in Nigeria: an approach for compliance with the Convention on Biological Diversity. *Diversity* **13**(1): 29-33.

King, S. R., T. J. Carlson and K. Moran (1996) Biological diversity, indigenous knowledge, drug discovery, and intellectual property rights. In: S. Brush and D. Stabinsky, Eds., *Valuing Local Knowledge: Indigenous People and Intellectual Property Rights*, pp: 167-185. Island Press.

Simpson, R. D., R. A. Sedjo and J. W. Reid (1996) Valuing biodiversity for use in pharmaceutical research. *Journal of Political Economy* **104**(1): 163-185.

DiMasi, J. A., R. W. Hansen, H. G. Grabowsky and L. Lasagna (1991) Cost of innovation in the pharmaceutical industry. *Jorunal of Health Economics* **10**: 107-142.

II) Principles of conservation biology.

1) Definition of conservation biology

Conservation biology is one of the fastest-growing fields of modern scientific research. It is an applied discipline that integrates principles of natural and social sciences with the objective of achieving the long-term persistence of biodiversity on Earth. The current global biodiversity crisis is the driving force behind the discipline's rapid growth, but its origins and practice are older. Formal recognition of conservation biology as an academic field dates back to the 1960s; since then, it has gradually acquired a character of its own which differentiates it from the many other disciplines it continues to borrow from, including: ecology, genetics, population biology, sociology, economics, and policy.

2) Conservation biology as a crisis discipline

Because conservation biology has grown in response to the extinction crisis, much of the attention of conservation biologists has focussed on dealing with problems of small, threatened populations. Genetics and population ecology have played a prominent role. Outline Caughley's "small population" and "declining populations" paradigms..

Restoration ecology, the cost of putting it back together.

Preventative conservation: the wave of the future?

3) Using biogeographic and natural history data for planning wild species conservation

Conceptual framework for using quantitative methods of conservation biology for large-scale (e.g. sub-national, national, regional) species conservation planning exercises. Three fundamental, consecutive questions provide structure to the process: 1) What to conserve?, 2) Where to conserve?, and 3) How to conserve?

The first question is answered using biological indicators, which help define the target of conservation action; for example: identify centers of endemism or areas of high diversity, monitor changes in habitat quality, or locate foci of human disturbance.

Once the target is established, the second question is approached using gap analysis in conjunction with algorithms for the optimal selection of nature reserve networks. This approach is aimed at maximizing the number of species included in protected area systems, while minimizing the amount of land needed to do so. Reserve selection algorithms.

The third question refers to the design of management plans either for single (or groups of) protected areas or individual (or groups of) species. An integration of the techniques of population viability analysis with the principles of adaptive management of natural resources allows for contrasting different management options, by weighing their benefits (e.g. reduced risk of extinction) against their costs (e.g. resources required to implement each option) over time.

References:

Bioindicators:

Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution* **13**(7): 275-280.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss and M. A. Sanjayan (1993) Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7**(4): 796-808.

Pearson, D. L. and F. Cassola (1992) World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. *Conservation Biology* **6**(3): 376-391.

Rodríguez, J. P., D. L. Pearson and R. Barrera R. (1998) A test for the adequacy of bioindicator taxa: Are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? *Biological Conservation* **83**(1): 69-76.

Keystone and umbrella species:

Simberloff, D. (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biological Conservation* 83(3): 247-257.

PVA:

Possingham, H. P., D. B. Lindenmayer and T. W. Norton (1993) A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology* **1**: 39-45.

GAP analysis:

Scott, J. M. and B. Csuti (1997) Gap analysis for biodiversity survey and maintenance. In: M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson, Eds., *Biodiversity II: Understanding and Protecting our Natural Resources*, pp: 321-340. Joseph Henry Press, Washington, D.C., U.S.A.

Reserve selection algorithms:

Csuti, B., S. Polasky, P. H. Williams, R. L. Pressey, J. D. Camm, M. Kershaw, A. R. Kiester, B. Downs, R. Hamilton, M. Huso and K. Sahr (1997) A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biological Conservation* **80**: 83-97.

III) *In situ* and *ex situ* approaches to the conservation of biodiversity.

1) Major threats to biodiversity

A few famous cases of extinct species: 1) the dodo, 2) passenger pigeon. Large population sizes are not necessarily enough.

Threatened species of the world, by taxonomic group.

Species' threats are not uniformly distributed, maps of 1) extinct species of the world, 2) hotspots of endangered species in the US.

Evolving threats for endangered species. Most extinct species due to overexploitation; most threatened species due to habitat destruction (Endangered Species Handbook).

Example from Venezuela to illustrate evolving threats.

Causes of threat in the US.

References:

Dobson, A. P., J. P. Rodríguez, W. M. Roberts and D. S. Wilcove (1997) Geographical distribution of endangered species in the United States. *Science* **275**: 550-553.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos (1998) Quantifying threats to imperiled species in the United States. *BioScience* **48**(8): 607-615.

2) Classifying endangered species

History of Red Data Books and red Lists. Evolution of endangered species classification systems. The 1994 IUCN Red List Criteria—assessing extinction risk. The difference between risk assessment and priority setting: national/regional conservation planning.

References:

Mace, G. M. (1995) Classification of threatened species and its role in conservation planning. In: J. H. Lawton and R. M. May, Eds., *Extinction Rates*, pp: 197-213. Oxford University Press.

3) What are we doing to conserve biodiversity?

Present definition of *in situ* and *ex situ* approaches (based on glossary in UNEP's *Global Biodiversity Assessment*). Emphasize that habitat conservation is the ultimate purpose.

Conservation not only limited to wild species. Brief introduction to germoplasm banks and botanical gardens. Value of domestic animal breeds.

4) Nature reserve design and management

Theory of island biogeography. Single large or several small (SLOSS) debate. Pros and cons of ecological corridors.

Ecotourism and charges for ecosystem services as mechanisms for funding protected areas; achieving self-sufficiency.

Nature reserves alone are not enough. Most protected areas are too small for long-term survival of large carnivores (Newmark's analysis of parks in the US and Tanzania). many species require habitat in private lands. Need to think more broadly—integrated large-scale management. Habitat Conservation Planning in the US.

References:

Wilcox, B. A. (1980) Insular ecology and conservation. In: M. E. Soulé and B. A. Wilcox, Eds., *Conservation Biology: an Evolutionary-ecological Perspective*, pp: 95-118. Sinauer Associates, Inc., Sunderland, Massachusetts, U.S.A.

Margules, C., A. J. Higgs and R. W. Rafe (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation* **24**: 115-128.

Newmark, W. D. (1987) A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* **325**: 430-432.

Simberloff, D., J. A. Farr, J. Cox and D. W. Mehlman (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology* **6**(4): 493-504.

Aengst, P., J. Anderson, J. Chamberlin, C. Grunewald, S. Loucks, E. Wheatley and S. Yaffee (1997) Introduction to habitat conservation planning. *Endangered Species UPDATE* 14(7&8): 5-9.

5) Captive breeding for endangered species

Zoos and botanical gardens as a conservation tool. The evolution of zoos from collections of animals to conservation centers. Examples of species who have been saved by captive breeding. Problems with captive breeding: genetic, behavioral/social (e.g. adaptation to captivity), cost, lack of insterinstitutional continuity and coordination. The value of captive breeding as an educational tool and for fundraising for wild population conservation.

References:

Mench, J. A. and M. D. Kreger (1996) Ethical and welfare issues associated with keeping wild mammals in captivity. In: D. G. Kleiman, M. E. Allen, K. V. Thomnpson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 5-15. University of Chicago Press, Chicago, USA.

Wiese, R. J. and M. Hutchins (1994) The role of zoos and aquariums in amphibian and reptilian conservation. In: J. B. Murphy, K. Adler and J. T. Collins, Eds., *Captive Management and Conservation of Amphibians and Reptiles*, pp: 37-45. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA.

Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone and B. Miller (1996) Limitations of captive breeding in endangered species recovery. *Conservation Biology* **10**(2): 338-348.

6) Reintroductions and translocations

When are reintroductions appropriate? Reintroductions as the last front in conservation action. The Margarita parrot: an example of a successful reintroduction; cost of each parrot.

References:

Kleiman, D. G. (1996) Reintroduction Programs. In: D. G. Kleiman, M. E. Allen, K. V. Thomnpson, S. Lumpkin and H. Harris, Eds., *Wild Mammals in Captivity: Principles and Techniques*, pp: 297-305. University of Chicago Press, Chicago, USA.

Sanz, V. and A. Grajal (1998) Successful reintroduction of captive-raised yellow-shouldered amazon parrots on Margarita island, Venezuela. *Conservation Biology* **12**(2): 430-441.

Griffith, B., J. M. Scott, J. W. Carpenter and C. Reed (1989) Translocations as a species conservation tool: status and strategy. *Science* **245**: 477-480.

7) Additional bibliography

1) General reference

UNEP (1995) *Global Biodiversity Assessment*. United Nations Environment Programme, Cambridge University Press, Cambridge, UK.

WCMC (1992) *Global Biodiversity: Status of the Earth's Living Resources.* World Conservation Monitoring Centre, Chapman and Hall, London, UK.

Worldwatch Institute's *State of the World* annual reports

World Resources Institute's *World Resources* annual reports

2) Some recent textbooks

Caughley, G. and A. Gunn (1996) *Conservation Biology in Theory and Practice.* Blackwell Science, Cambridge, Massachusetts, USA.

Dobson, A. P. (1996) *Conservation and Biodiversity.* Scientific American Library, New York, USA.

Hunter, M. L. (1996) *Fundamentals of conservation biology.* Blackwell Science, Cambridge, Massachusetts, USA.

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Primack, R. B. (1995) *A Primer of Conservation Biology.* Sinauer Associates Inc., Sunderland, Massachusetts, U.S.A.

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at sufficient density on the surface of tumor vascular endothelium but absent from normal vascular endothelium (*15*). Promising candidate molecules for humans include endoglin (*16*), endosialin (*17*), an endoglin-like molecule (*18*), a fibronectin isoform (*19*), an osteosarcoma-related antigen (*20*), CD34 (*21*), collagen type VIII (*22*), the vascular endothelial cell growth factor (VEGF) receptors (*23*), and VEGF itself (*24*). The induction of tumor infarction by targeting a thrombogen to these or other tumor endothelial cell markers represents an intriguing approach to the eradication of primary solid tumors and vascularized metastases.

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2. R. K. Jain, *Sci. Am.* **271**, 58 (July 1994).
3. E. W. Davie, K. Fujikawa, W. Kisiel, *Biochemistry* **30**, 10363 (1991).
4. Human tTF (residues 1 to 219) was prepared as described [M. J. Stone, W. Ruf, D. J. Miles, T. S. Edgington, P. E. Wright, *Biochem. J.* **310**, 605 (1995)].
5. W. Ruf, A. Rehemtulla, T. S. Edgington, *J. Biol. Chem.* **266**, 2158 (1991).
6. L. R. Paborsky, I. W. Caras, K. L. Fisher, C. M. Gorman, *ibid.*, p. 21911; R. Bach, R. Gentry, Y. Nemerson, *Biochemistry* **25**, 4007 (1986); S. Krishnaswamy, K. A. Field, T. S. Edgington, *J. Biol. Chem.* **267**, 26110 (1992).
7. The C1300(Muγ) tumor model (*14*) was modified as follows: (i) we used antibody B21-2 to target I-A^d; (ii) we used C1300(Muγ) tumor cells, a subline of C1300(Muγ)12 tumor cells, that grew continuously in BALB/c *nu/nu* mice; and (iii) we did not add tetracycline to the mice's drinking water to prevent gut bacteria from inducing I-A^d on the gastrointestinal epithelium. Unlike immunotoxins, coaguligands do not damage I-A^d–expressing intestinal epithelium.
8. The B21-2 (TIB-229) hybridoma, secreting a rat immunoglobulin G2b (IgG2b) antibody to the I-A^d antigen, was purchased from the American Type Culture Collection. The CAMPATH-2 antibody is a rat IgG2b antibody to human CD7. The TF9-10H10 antibody (herein referred to as 10H10) is a mouse IgG1 nonneutralizing antibody to human TF [J. H. Morrissey, D. S. Fair, T. S. Edgington, *Thromb. Res.* **52**, 247 (1988)]. The MRC OX7 hybridoma (herein referred to as OX7) secretes a mouse IgG1 antibody that recognizes the Thy 1.1 antigen. The bispecific antibodies B21-2/10H10, CAMPATH-2/10H10, OX7/10H10, and B21-2/OX7 were synthesized as described [M. Brennan, P. F. Davison, H. Paulus, *Science* **229**, 81 (1985)].
9. To establish solid tumors, we injected 1.5 × 10^7 C1300(Muγ) cells subcutaneously into the right anterior flank of BALB/c *nu/nu* mice (Charles River Labs, Wilmington, MA). When the tumors had grown to ~0.8 cm in diameter, mice were randomly assigned to different experimental groups, each containing four to nine mice. Coaguligands were prepared by mixing bispecific antibodies (150 μg) and tTF (125 μg) in a total volume of 2.5 ml of 0.9% NaCl and incubating at 4°C for 1 hour. Mice received intravenous injections of 0.25 ml of this mixture per 25 g of body weight (that is, 0.6 mg/kg of bispecific antibody plus 0.5 mg/kg of tTF). Other mice received equivalent doses of bispecific antibodies or tTF alone. The injections were performed over ~45 s into one of the tail veins, followed by 200 μl of saline. In the tumor growth-inhibition experiments, the infusions were repeated 6 days later. Perpendicular tumor diameters were measured at regular intervals and tumor volumes were calculated. Differences in tumor volume were tested for statistical significance with the Mann-Whitney rank sum test for two independent samples. For histopathologic analyses, mice were anesthetized with metophane at various intervals after treatment and were exsanguinated by perfusion with heparinized saline. Tumors and normal tissues were excised and immediately fixed in 3% (v/v) formalin. Paraffin sections were cut and stained with hematoxylin and eosin or with Martius Scarlet Blue trichrome for the detection of fibrin. Animal care in all experiments was in accordance with institutional guidelines.
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11. At the treatment dose of 0.6 mg/kg B21-2/10H10 plus 0.5 mg/kg tTF, toxicity was observed in only 2 of 40 mice (thrombosis of the tail vein). The tTF itself was not toxic at 1.28 mg/kg when given intravenously.
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26. We thank G. Hale for CAMPATH-2, A. F. Williams for the OX7 hybridoma, A. Gilman for comments on the manuscript and for support, E. Derbyshire and C. Gottstein for discussions, J. Overholser for technical assistance, W. Ruf for tTF, and K. Schiller for help in manuscript preparation. Supported in part by grants from the Pardee Foundation and NIH (RO1-CA59569, RO1-CA54168, and PO1-HL16411).

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Geographic Distribution of Endangered Species in the United States

A. P. Dobson,* J. P. Rodriguez, W. M. Roberts, D. S. Wilcove

Geographic distribution data for endangered species in the United States were used to locate "hot spots" of threatened biodiversity. The hot spots for different species groups rarely overlap, except where anthropogenic activities reduce natural habitat in centers of endemism. Conserving endangered plant species maximizes the incidental protection of all other species groups. The presence of endangered birds and herptiles, however, provides a more sensitive indication of overall endangered biodiversity within any region. The amount of land that needs to be managed to protect currently endangered and threatened species in the United States is a relatively small proportion of the land mass.

Previous studies have shown that, on a continental scale, the distributions of well-studied taxa can act as surrogates or indicators for the distribution of poorly studied taxa (*1–4*). In contrast, studies of the distribution of "hot spots" of diversity for various taxa within the British Isles suggest that there is very little correlation between the distributions of different taxonomic groups (*5, 6*). To date, however, no such analysis has been done on a continental or national scale for those species most likely to vanish in the foreseeable future, that is, endangered species. If significant correlations occur in the geographic distributions of different groups of endangered species, it may be possible to use a few well-studied groups as indicators for the purposes of delineating protected areas for other poorly known taxa. The extent to which endangered species are concentrated in hot spots of potential extinctions and the extent to which hot spots for different groups overlap will influence the strategies we adopt to avert species extinctions and the impact of those strategies on other human activities (*7, 8*). If endangered species are highly concentrated, then fewer areas are likely to experience conflicts between species protection and other activities.

In this study, we used a database of threatened and endangered species in the United States to examine patterns in the geographic distribution of imperiled species (*9*). The database lists the counties of occurrence of all plants and animals protected under the federal Endangered Species Act in the 50 states, plus all species, subspecies, and populations proposed for protection under that statute as of August 1995 (a total of 924 species in 2858 counties). We grouped the species by state, county, and species group (amphibians, arachnids, birds, clams, crustacea, fish, insects, mammals, plants, reptiles, and snails) and then generated dis-

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*To whom correspondence should be addressed. E-mail: andy@eno.princeton.edu tribution maps using a geographic information system (*10*). These maps were designed to identify areas with unusually large numbers of endangered species.

A sorting algorithm based on the principle of complementary subsets was used to evaluate the extent to which endangered species are clustered into hot spots (*11–13*). The algorithm first selected the county with the greatest number of listed species; all species found in that county were then excluded from further consideration while the algorithm searched for the county with the greatest number of species that were not already selected. Ties for number of species were broken by assignment of top rank to the county with the smallest area (or secondarily, the county with the smallest human population). This process was continued iteratively until all listed species were included. The algorithm maximizes the number of species sampled while minimizing the area required to do so. It is clearly erroneous to assume, however, that because a particular species occurs in a county, a viable population can be maintained in that county. In this respect, our analysis underestimates the amount of land necessary to preserve species with large area requirements (such as grizzly bears, *Ursus arctos horribilis*). On the other hand, it is equally inaccurate to assume that the entire land area of a county is occupied by its endangered species. Thus, our analysis should not be taken as a measurement of how much land must be protected to conserve endangered species but rather as an approximate indication of the extent to which endangered species are concentrated geographically. We then subdivided the data and repeated the analysis for each species group to determine whether any particular group could be used as an overall indicator for others.

The greatest numbers of endangered species occur in Hawaii, southern California, the southeastern coastal states, and southern Appalachia (Fig. 1). When counties are selected on the basis of complementarity, the algorithm first selects counties in these regions (Fig. 2). The complementary ordering of counties generates accumulation curves that can be used to examine the extent to which endangered species are clustered in hot spots. The accumulation curves represent the total area required to sample all the endangered species in each taxonomic group when the counties are ranked from those with the most endangered species to those with the least (Fig. 3, A and B). For each group, more than 50% of endangered species are represented within 0.14 to 2.04% of the land area (*14*). For endangered birds, reptiles, and mammals, the sequential selection of counties on the basis of the unique species they contain leads to a steady increase in the number of populations of each endangered species already included in the counties sampled (Fig. 3C). The number of populations of most endangered plant and invertebrate species does not increase because many of these species are restricted to single counties. The data show that 48% of plants and 40% of arthropods are restricted to single counties. The average number of counties in which a listed plant or arthropod species is found is 3.9 and 4.4 counties, respectively. In contrast, only 36% of listed bird species are confined to single counties, whereas the average number of counties in which a listed bird is found is 62.7 (*15*). Comparable figures on the percentage of single-county species within other groups and the average number of counties in which a listed species is found are as follows: mammals, 26%, 32.9 counties per species; fish, 31%, 8.0 counties

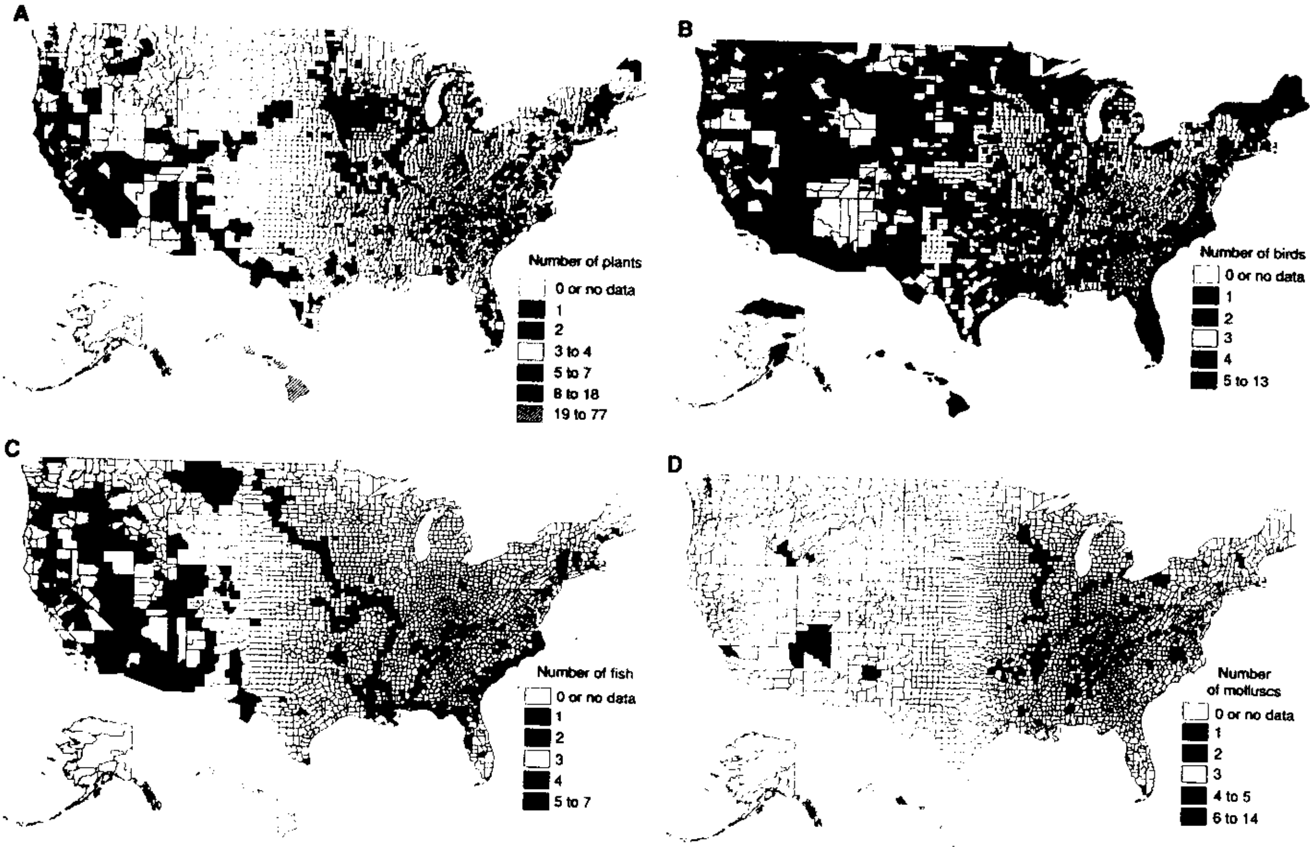

Fig. 1. The geographic distribution of four groups of endangered species in the United States. (**A**) Plants, (**B**) birds, (**C**) fish, and (**D**) molluscs. The maps illustrate the number of listed species in each county. Alaska and Hawaii are shown in the bottom left-hand corner of the maps (not to scale).

per species; herptiles (reptiles and amphibians), 14%, 18.8 counties per species; snails, 57%, 2.1 counties per species; and clams, 3%, 12.1 counties per species.

The utility of using any one group of endangered species as an indicator for other groups can be quantified by calculating the proportion of each other group that occurs in the subsets of counties that contain all the species in any individual group (Table 1). An initial examination of this table suggests that the counties that contain a complete set of endangered plant species will contain the greatest numbers of other endangered species. However, more counties are required to adequately sample endangered plants than are required for any other taxa, so we would expect this larger area to contain more species from other taxa. An area-independent index of predictive power may be obtained by comparing the number of species contained in the complementary counties for each group with the number of species that would occur if a set of counties of about the same total area were selected at random. The ratio of these two values provides an indication of how accurately the presence of endangered species in one group indicates the presence of endangered species in other groups. This index suggests that birds and then herptiles provide the best indicators for any particular area. In contrast, the presence of endangered fish or plant species provides only a weak indication that other endangered species are present in a given county.

We also examined the associations between the density of endangered species in each state, the intensity of human economic and agricultural activities, and the climate, topology, and vegetative cover of the state. We collated data on a variety of economic and topographic indicators using the annual statistical survey of the United States (*16*). Although there are complex and subtle associations between the variables included in this analysis, our initial stepwise multiple-linear regression analysis reveals that the overall density of endangered species is correlated with one anthropogenic and one climatic variable (correlation coefficient $r^2 = 0.80$, $P < 0.01$): the value of agricultural output and either average temperature or rainfall (*17*). When the analysis was repeated for each major taxonomic group, slightly different results were obtained. In particular, agricultural activity is the key variable for plants ($r^2 = 0.61$, $P < 0.01$), mammals ($r^2 = 0.68$, $P < 0.01$), birds ($r^2 = 0.64$, $P < 0.01$), and reptiles ($r^2 = 0.46$, $P < 0.05$). Water use and human population density are also significant predictors of the density of endangered reptiles ($r^2 = 0.42$, $P < 0.01$). As did previous studies of patterns of overall species richness (*18–20*), we found that geographic variables significantly influence the distribution of endangered species. For example, the diversity of endangered fish increases with the mean temperature and elevation of the state ($r^2 = 0.27$, $P < 0.01$). Climatic variables, such as mean temperature and rainfall, are the second or third most important independent variables

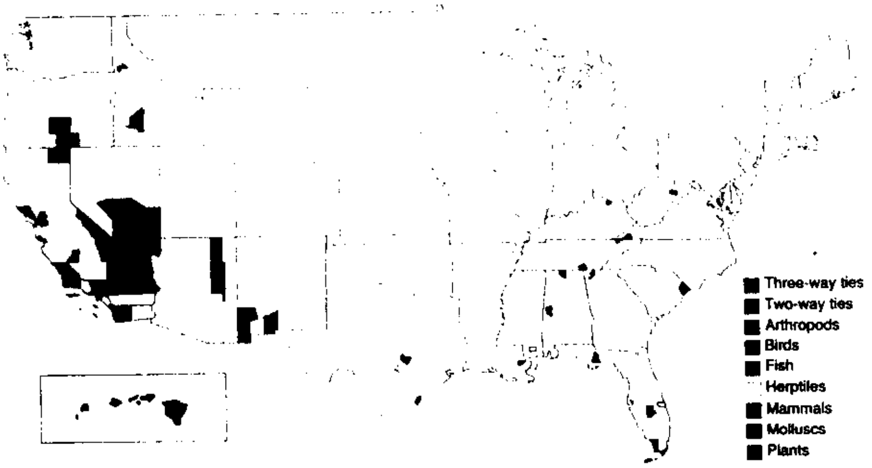

Fig. 2. Complementary set of counties that contains 50% of the listed species for each taxonomic group. The analysis identified two counties that contain large numbers of endangered species from three groups and nine counties that contain large numbers of species from two groups (Hawaii not to scale).

Table 1. Proportion of endangered species in other groups that are included in complementary county sets containing all the species in a given group. The second row gives the number of counties in the complementary set for each group; the third row gives the total area of these counties as a percentage of the U.S. land mass. The next eight rows give the total proportion of all other endangered species contained in the complementary set for any given group (columns). Power is an index of how well each species group indicates endangered species diversity in other groups; it is calculated by dividing the number of endangered species from other groups in this complementary county set by the number of such species in an equivalent area of randomly selected counties. A bootstrapping algorithm accumulated counties at random until their total area matched or just exceeded that of the complementary county set. For power$_a$, the algorithm selected from all U.S. counties. For power$_b$, the algorithm selected only from counties listed as containing endangered species. Because the area encompassed by the random county sets typically was greater than that of the complementary county sets, power underestimates the efficiency of each species group as an indicator for other groups. Power values are means (± SE) of 200 runs of the bootstrapping algorithm.

	Plants	Molluscs	Arthropods	Fish	Herptiles	Birds	Mammals
Species (*n*)	503	84	57	107	43	72	58
Counties (*n*)	136	38	37	57	28	19	29
Area (%)	9.61	1.15	2.38	4.76	0.97	1.59	2.08
Plants	1.00	0.16	0.22	0.15	0.14	0.38	0.27
Molluscs	0.39	1.00	0.29	0.44	0.01	0.02	0.06
Arthropods	0.54	0.14	1.00	0.16	0.44	0.12	0.19
Fish	0.55	0.15	0.21	1.00	0.09	0.13	0.21
Herptiles	0.74	0.21	0.49	0.35	1.00	0.35	0.42
Birds	0.94	0.43	0.47	0.38	0.42	1.00	0.53
Mammals	0.76	0.38	0.43	0.40	0.33	0.38	1.00
All others	0.73	0.21	0.31	0.18	0.25	0.31	0.28
Power$_a$	1.63 (0.02)	2.92 (0.08)	2.44 (0.11)	1.24 (0.04)	3.26 (0.17)	4.00 (0.16)	2.61 (0.08)
Power$_b$	1.46 (0.01)	2.67 (0.06)	2.66 (0.59)	1.10 (0.02)	2.67 (0.06)	3.29 (0.09)	2.40 (0.08)

for endangered plants, reptiles, and clams.

Virtually all taxa are characterized by aggregated geographic distributions of endangered species (*21*). These hot spots are probably the product of two interacting factors: centers of endemism [for example, clams in southwest Appalachia (*22*) and plants in Florida (*20*)] and anthropogenic activities (for example, urbanization and agricultural development). Consequently, in a few areas of the United States, the centers of endangered richness for different groups overlap. Two counties are hot spots for three groups: San Diego, California (fish, mammals, and plants), and Santa Cruz, California (arthropods, herptiles, and plants). Nine counties are hot spots for two groups: Hawaii, Honolulu, Kauai, and Maui, Hawaii (all birds and plants); Los Angeles, California (arthropods and birds); San Francisco, California (arthropods and plants); Highlands, Florida (herptiles and plants); Monroe, Florida (birds and mammals); and Whitfield, Georgia (fish and molluscs). Aside from these locations, the key areas for most groups overlap only weakly, which suggests that the endangered species hot spots for one group do not necessarily correspond with those for other groups. Nevertheless, the analysis confirms previous studies that suggest birds (*2*, *23*), and perhaps arthropods (*1*), act as important indicators for the presence of other endangered species. Unfortunately, the data available for endangered plants and arthropods are considerably less complete than those for other taxa (*24*, *25*). Increasing efforts to obtain information on these taxa is crucial to obtain a more complete picture of the geographic distribution of endangered species in the United States.

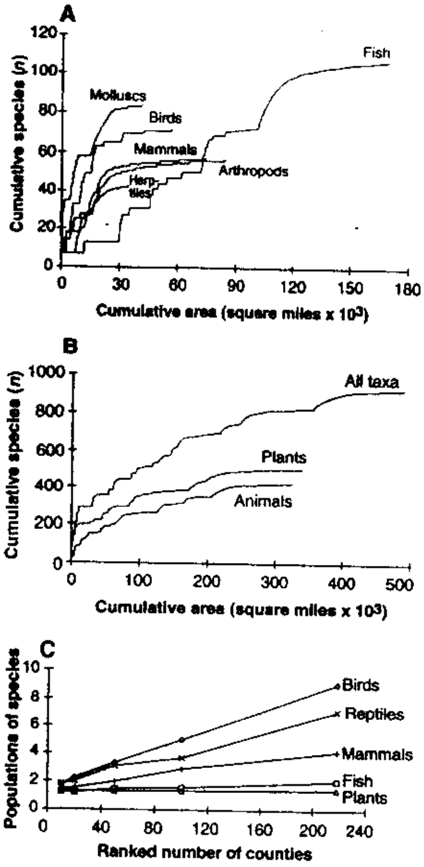

Fig. 3. (**A** and **B**) The relation between the cumulative area of land sampled and the cumulative number of listed species that are included. The sudden increases in the slopes of the curves occur when the algorithm switches to adding the next lowest integer number of species to the pool of species sampled—counties are added by picking the smallest counties that add this number of new species to the pool. (**C**) The average number of populations of each species in the sequentially selected counties.

Although there are no consistent correlations in the distributions of endangered species from different taxa, the existence of hot spots for most groups indicates that a large proportion of endangered species can be protected on a small proportion of land (*26*). If conservation efforts and funds can be expanded in a few key areas, it should be possible to conserve endangered species with great efficiency.

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14. Half of the currently listed plant species are found in the 13 highest ranked counties in their complementary county subset; the total area of these counties is 1.33% of the U.S. land mass. The equivalent figures for the other groups are as follows: molluscs, 6 counties (0.14%); arthropods, 9 counties (0.46%); fish, 14 counties (2.04%); herptiles, 7 counties (0.34%); birds, 4 counties (0.28%); and mammals, 7 counties (0.40%).
15. Mean values for birds are inflated by the occurrence of peregrine falcons (*Falco peregrinus*) and bald eagles (*Haliaeetus leucocephalus*) in a large number of counties throughout the United States. If data for these two species are excluded, the mean number of counties that each endangered bird species was located in would drop to 31.7, with 37% of endangered birds restricted to a single county.
16. U. S. Bureau of the Census, *Statistical Abstract of the United States: 1991* (U.S. Government Printing Office, Washington, DC, 1991).
17. The stepwise multiple regression analysis was performed on the entire data set and then on each major taxonomic division. Because complete sets of economic and geographic data are only available at the state level, the analysis was performed at this coarser geographic scale. The density of endangered species was expressed as the total number of endangered species recorded in the state, divided by total area of the state for all terrestrial species. In the case of predominantly aquatic species (fish and clams), only the area of each state classified as water or wetland was used to calculate density. The variables included in the analysis were the annual value of farm products produced in the state, the year in which the state was incorporated into the United States, water use in the state, manufacturing exports, percent of the net state area that is forested, percent of the state that is urban, percent of the state classified as wetlands, percent of the state classified as agricultural land, human population density in the state, percent of the human population living in urban areas, highest point in the state, average annual temperature in the state, and average annual rainfall in the state. The analysis was undertaken twice—once including Hawaii and once for just the mainland states. In both cases there was no substantial difference in the analyses, except for birds, plants, and all species combined. A large proportion of the endangered birds and plants occur only in Hawaii. When Hawaii is included in the analysis, its high density of endangered species and extreme values for several independent variables (such as extreme topography and tropical climate) combine to yield trends that are unrepresentative of the continental United States. For this reason, we have only provided results for the 49 continental states in the main text.
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26. Bringing these species to the point of recovery (by increasing their populations) would involve a greater amount of land than they currently occupy. However, as the geographic distributions of many endangered species do not overlap more than a single county, this is likely to be less of a problem for species groups with restricted ranges (such as plants and arthropods) than it is for birds and mammals.
27. We thank L. Turner and M. Hood at the Environmental Protection Agency for comments on the manuscript and for providing us with the raw data for this analysis; user support services at Golden Software, CO, for providing help in producing the maps in Figs. 1 and 2; and M. Scott, M. Bean, and three anonymous referees for comments on the manuscript. The work was made possible by a grant to the Environmental Defense Fund from the Charles Stewart Mott Foundation.

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Quantifying Threats to Imperiled Species in the United States

Assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease

David S. Wilcove, David Rothstein, Jason Dubow, Ali Phillips, and Elizabeth Losos

Biologists are nearly unanimous in their belief that humanity is in the process of extirpating a significant portion of the earth's species. The ways in which we are doing so reflect the magnitude and scale of human enterprise. Everything from highway construction to cattle ranching to leaky bait buckets has been implicated in the demise or endangerment of particular species. According to Wilson (1992), most of these activities fall into four major categories, which he terms "the mindless horsemen of the environmental apocalypse": overexploitation, habitat destruction, the introduction of non-native (alien) species, and the spread of diseases carried by alien species. To these categories may be added a fifth, pollution, although it can also be considered a form of habitat destruction.

Surprisingly, there have been relatively few analyses of the extent to which each of these factors—much less the more specific deeds encompassed by them—is responsible for endangering species. In general, scientists agree that habitat destruction is currently the primary lethal agent (Ehrlich 1988, Wilson 1992), followed by the spread of alien species (Wilson 1992). However, apart from several notable exceptions—including studies of North American fishes by Williams et al. (1989), endangered plants and animals in the United States by Flather et al. (1994, 1998), aquatic organisms by Richter et al. (1997), and imperiled birds by Collar et al. (1994)—few quantitative studies of threats to species have been conducted. More such studies are needed to provide conservationists, land stewards, and decision makers with a better understanding of the relationships between specific human activities and the loss of biodiversity.

In this article, we quantify the extent to which various human activities are imperiling plant and animal species in the United States. Our analysis has two parts: a coarse-scale examination of the numbers and types of US species imperiled by the major categories of threats, and a fine-scale analysis of the types of habitat destruction affecting US plants and animals protected under the federal Endangered Species Act (ESA). We also speculate on how these threats have changed over time and are likely to change in the future. We conclude with a brief discussion of the implications of our findings for the long-term protection of imperiled species in the United States.

Habitat loss is the single greatest threat to biodiversity, followed by the spread of alien species

An overview of the threats

To obtain an overview of the threats to biodiversity in the United States, we tabulated the number of species threatened by five categories of threats: habitat destruction, the spread of alien species, overharvest, pollution (including siltation), and disease (caused by either alien or native pathogens). We restricted this coarse-scale analysis to imperiled plants and animals occurring within the 50 states and falling into any of four categories: all full species of mammals, birds, reptiles, amphibians, and fish with status ranks of "possibly extinct," "critically imperiled," or "imperiled," as determined by The Nature Conservancy (TNC) in association with the Network of Natural Heritage Programs and Conservation Data Centers (Master 1991); all full species of freshwater mussels, butterflies and skippers, tiger beetles, and dragonflies and damselflies with status ranks of possibly extinct, critically imperiled, or imperiled, as determined by TNC; all full species of vascular plants with status ranks of possibly extinct or

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Table 1. Taxonomic breakdown of species used in the coarse-scale analysis. Included are species classified as imperiled by The Nature Conservancy and all species, subspecies, and populations that, as of January 1996, are listed as endangered or threatened under the Endangered Species Act or have been formally proposed for listing.

	Number of imperiled species	Number of imperiled species with threats data	Percentage of imperiled species with threats data
Vertebrates	541	494	91
Mammals	88	85	97
Birds	101	98	97
Reptiles	40	38	95
Amphibians	69	60	87
Fishes	243	213	88
Invertebrates	471	331	70
Dragonflies and damselflies	33	18	54
Freshwater mussels	150	102	68
Crayfish	110	67	61
Tiger beetles	8	6	75
Butterflies and skippers	46	33	72
Other invertebrates	124	104	84
Plants	1478	1055	71
Total	2490	1880	75

critically imperiled, as determined by TNC; and all species, subspecies, or vertebrate populations listed by the US Fish and Wildlife Service (USFWS) or the National Marine Fisheries Service as threatened or endangered or officially proposed for listing under the ESA as of 1 January 1996. (The ESA permits the listing of species and subspecies of plants and animals as well as "distinct population segments" of vertebrates.) A total of 2490 imperiled species, subspecies, and populations fit these criteria.

Information on the threats to each of these species, subspecies, and populations was obtained from a number of sources, including the *Federal Register* (i.e., the listing notices published for all species designated as threatened or endangered under the ESA), a survey of biologists conducted by Richter et al. (1997) for aquatic species, the Natural Heritage Central Databases managed by TNC, and interviews with specialists in particular species groups and geographical regions. We included only known threats and excluded potential or hypothetical ones. We did not attempt to distinguish between ongoing and historical threats, partly because such information is usually lacking and partly because the distinction itself is problematic in the case of habitat destruction. Nor did we try to distinguish between major and minor threats to each species because such information was not consistently available. In a few cases, it was impossible to assign a particular human activity to one of the major threat categories; we excluded these activities from our coarse-scale analysis.

We were able to obtain information on threats for 1880 (75%) of the 2490 imperiled species, subspecies, and populations that met our criteria for inclusion in this study (Table 1). (For 52 of the species, we could not identify any anthropogenic threats.) We used the resulting database to determine the relative significance of the major threats categories and to investigate differences between species groups in their vulnerability to particular threats. We compared the distribution of threats among plants and animals, among vertebrate and invertebrate animals, and within vertebrate classes. We also compared the distribution of threats among terrestrial and aquatic species, Hawaiian and mainland vascular plants, and Hawaiian and mainland birds. For all comparisons, statistical significance was assessed using the chi-squared contingency test (two-tailed).

We emphasize at the outset that there are some important limitations to the data we used. The attribution of a specific threat to a species is usually based on the judgment of an expert source, such as a USFWS employee who prepares a listing notice or a state Fish and Game employee who monitors endangered species in a given region. Their evaluation of the threats facing that species may not be based on experimental evidence or even on quantitative data. Indeed, such data often do not exist. With respect to species listed under the ESA, Easter-Pilcher (1996) has shown that many listing notices lack important biological information,

Table 2. Percentages of species in different groups that are imperiled by habitat degradation and loss, alien species, pollution, overexploitation, and disease. Categories are nonexclusive and therefore do not sum to 100.

Cause	All species (n = 1880)	Vertebrates (n = 494)	Invertebrates (n = 331)	Plants (n = 1055)	Mammals (n = 85)	Birds (n = 98)	Reptiles (n = 38)	Amphibians (n = 60)	Fishes (n = 213)	Freshwater mussels (n = 102)	Crayfish (n = 67)	Tiger beetles (n = 6)	Butterflies and skippers (n = 33)	Other invertebrates (n = 104)
Habitat degradation/loss	85	92	87	81	89	90	97	87	94	97	52	100	97	94
Alien species	49	47	27	57	27	69	37	27	53	17	4	0	36	52
Pollution	24	46	45	7	19	22	53	45	66	90	28	0	24	19
Overexploitation	17	27	23	10	45	33	66	17	13	15	0	33	30	46
Disease	3	11	0	1	8	37	8	5	1	0	0	0	0	0

including data on past and possible future impacts of habitat destruction, pesticides, and alien species. Depending on the species in question, the absence of information may reflect a lack of data, an oversight, or a determination by USFWS that a particular threat is not harming the species. The extent to which such limitations on the data influence our results is unknown.

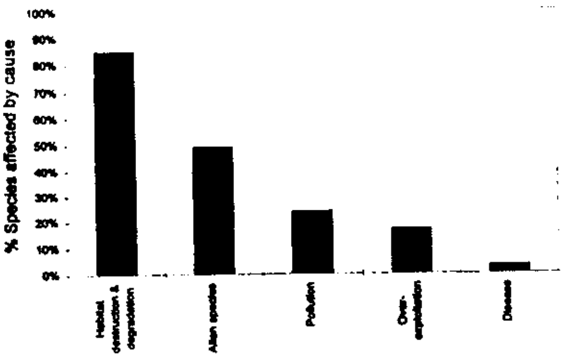

Figure 1. The major threats to biodiversity. Data refer to species classified as imperiled by The Nature Conservancy and to all endangered, threatened, and proposed species, subspecies, and populations protected under the Endangered Species Act. See also Table 2.

Ranking the threats

Table 2 presents a summary of the percentages of species that are imperiled by habitat loss, alien species, pollution, overexploitation, and disease. Not surprisingly, habitat destruction and degradation emerged as the most pervasive threat to biodiversity, contributing to the endangerment of 85% of the species we analyzed (Figure 1). Indeed, habitat loss is the top-ranked threat (in terms of the number of species it affects) for all species groups. Competition with or predation by alien species is the second-ranked threat in the overall analysis, affecting 49% of imperiled species.

Alien species affect a higher proportion of imperiled plants (57%) than animals (39%); this difference is statistically significant (chi square = 60.23, d.f. = 1, $P<<0.001$). However, certain groups of animals (most notably birds and fish) appear to be as broadly affected as plants by alien species. There is also an unsurprising biogeographic component to the alien species problem: Higher proportions of Hawaiian birds and plants than continental birds and plants are threatened by alien species (Table 3, Figure 2). Similarly, a much higher proportion of Hawaiian birds is threatened by disease than is the case for continental birds. By contrast, nearly the same proportion of Hawaiian plants and continental plants are affected by disease (Table 3, Figure 3).

For all aquatic animal groups (amphibians, fish, dragonflies and damselflies, freshwater mussels, and crayfish), pollution is second only to habitat loss as a cause of endangerment. Our finding that a large number of aquatic species are threatened by pollution may reflect the fact that our definition of pollution includes siltation, which is one of the leading threats to aquatic biodiversity in North America (Richter et al. 1997).

A closer look at habitat destruction

Given the primacy of habitat destruction as a threat to biodiversity, we examined its causes in greater detail. For this fine-scale analysis, we focused exclusively on US species, subspecies, and populations that have been added to the federal endangered species list or have been formally proposed for such listing by USFWS as of 1 January 1996. We focused on listed species because more information is usually available for them than for imperiled but unlisted species. We also included species that are federally listed or proposed for listing from Puerto Rico, the US Virgin Islands, and the Pacific Trust Territories. A total of 1207 species, subspecies, and populations was included in this phase of the analysis (Figure 4). (USFWS has listed as endangered all Hawaiian snails of the genus *Achatinella*. Approximately 41 species in that genus have been described to date, of which at least 18 are thought still to survive. However, USFWS did not treat these species individually in its formal listing notice in the *Federal Register*. For the purposes of this part of our analysis, we have therefore counted the entire genus as one "species.")

Categorizing habitat destruction. For the fine-scale analysis, we divided habitat destruction and degradation into 11 major categories (see box page 611). As in the coarse-scale analysis, we did not distinguish between current and historical threats or between major and minor threats. In many instances, the apparent threat to a species was actually spawned by another threat. Wherever possible, we attributed threats to their ultimate cause, based on the information in the *Federal Register*. For example, logging operations near a stream can lead to siltation, which is harmful to certain rare fishes and mussels. Thus, logging rather than siltation would have been scored as the threat to those fishes and mussels. For all comparisons of the prevalence of specific threats in different species groups, statistical significance was assessed using the chi-squared contingency test (two-tailed).

Again, we note some caveats with

Table 3. Percentages of imperiled birds and plants in Hawaii and in the continental United States that are threatened by habitat degradation and loss, alien species, pollution, overexploitation, and disease. Categories are nonexclusive and therefore do not sum to 100.

Cause	Continental US birds (n = 56)	Hawaiian birds (n = 42)	Continental US plants (n = 641)	Hawaiian plants (n = 414)
Habitat degradation/loss	88	93	90	66
Alien species	48	98	30	99
Pollution	38	2	12	0
Overexploitation	39	24	13	6
Disease	4	81	1	0

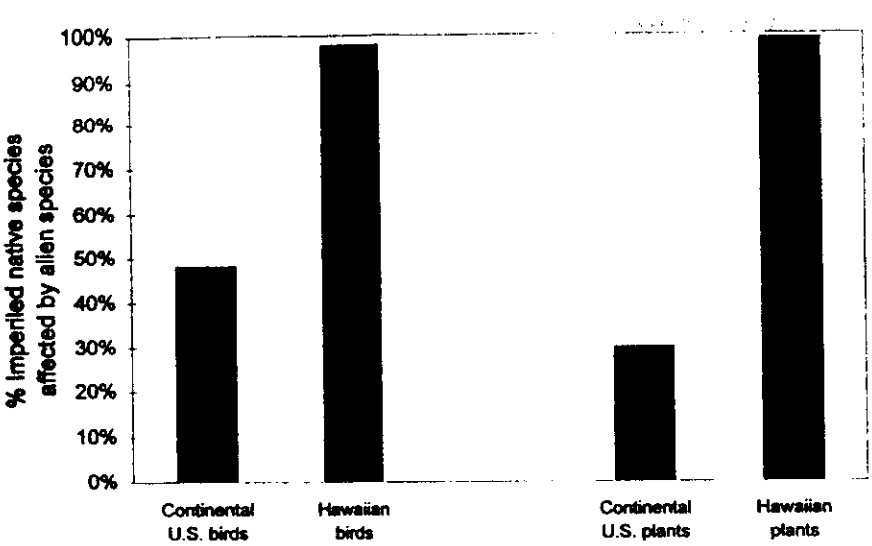

Figure 2. A comparison of the impacts of alien species on imperiled birds and plants in Hawaii and in the continental United States. A much higher proportion of Hawaiian birds and plants than continental birds and plants is threatened by alien species (chi-square = 27.60, d.f. = 1, $P << 0.001$ for birds; chi-square = 484.28, d.f. = 1, $P << 0.001$ for plants). Data are taken from Table 3.

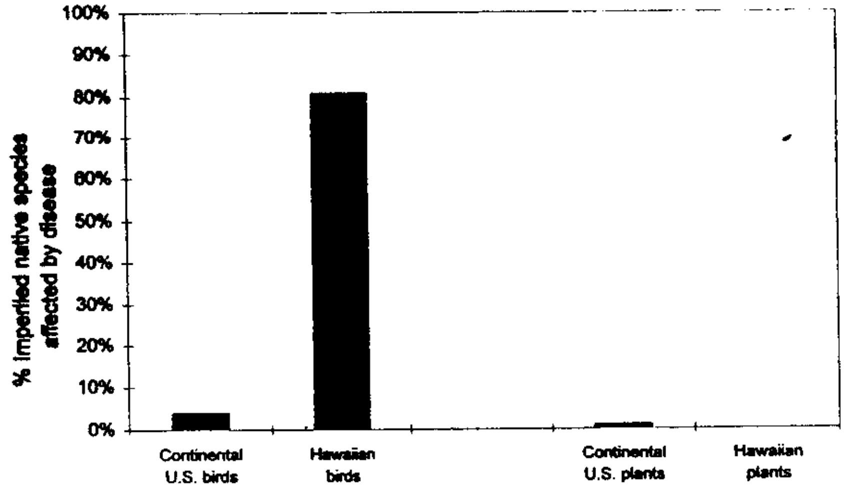

Figure 3. A comparison of the impacts of disease on imperiled birds and plants in Hawaii and in the continental United States. A much higher proportion of Hawaiian birds than continental birds is threatened by disease (chi-square = 62.03, d.f. = 1, $P << 0.001$). By contrast, similar proportions of Hawaiian and continental plants are affected by disease (although the difference is statistically significant: chi-square = 4.02, d.f. = 1, $P = .045$).

respect to the data in this phase of the analysis. Species added to the endangered list prior to 1980 (238 species) tended to have fewer threats delineated in the listing notices than species listed in later years. Although there may be a biological basis for this difference, we strongly suspect that it reflects the less controversial nature of endangered species protection at that time. Before 1980, USFWS probably was under less pressure to produce detailed justifications for its listing decisions. We do not know how this pattern may have influenced our results. Also, as noted in our coarse-scale analysis, assessments of the threats to individual species are often based on the subjective opinions of knowledgeable individuals, rather than experimental evidence or quantitative data.

Ranking the causes of habitat destruction. The most overt and widespread forms of habitat alteration were, as might be expected, the leading threats to species that are either listed or proposed for listing (hereafter referred to collectively as "endangered" species), as measured by the number of species they affect (Table 4). These forms include agriculture (affecting 38% of endangered species), commercial development (35%), water development (30% when agricultural diversion is included; 17% for just dams, impoundments, and other barriers), and infrastructure development (17%). Not surprisingly, the impacts of water development are felt most acutely by aquatic species. Ninety-one percent of endangered fish and 99% of endangered mussels are affected by water development, in contrast to 10% of mammals and 22% of birds. Within the category of infrastructure development, roads affect a wide array of species (15% of all endangered species), confirming their reputation as "a leading threat to biodiversity" (Noss and Cooperrider 1994).

Outdoor recreation also harms a large number of endangered species (27%). It affects a significantly higher proportion of plants than animals (33% vs. 17%; chi square = 39.03, d.f. = 1, $P << 0.001$). Within the category of outdoor recreation, the use of off-road vehicles is implicated in the demise of approximately 13% of endangered species.

Among extractive land uses, logging, mining, and grazing have contributed to the demise of 12%, 11%, and 22%, respectively, of the endangered species we analyzed. Both logging and mining are especially serious threats to freshwater mussels, probably because they result in increased amounts of silt, in the cases of both logging and mining, and of toxic pollutants, in the case of mining. Livestock grazing, on the other hand, is particularly harmful to plants, affecting 33% of endangered plant species compared to 14% of endangered animals; the difference is highly significant (chi square = 51.95, d.f. = 1, $P << 0.001$).

Finally, 168 species (14%) are threatened by disruption of fire regimes in the ecosystems in which they live. Of these, 85 (7%) are threatened by fire suppression and 83 (7%) are threatened by controlled or uncontrolled fires.

Comparisons with other studies

Flather et al. (1994, 1998) catalogued the threats to US endangered species based on information from the *Federal Register*, the USFWS *Endangered Species Technical Bulletin*, recovery plans for individual species, federal agency reports, and consultations with USFWS biologists and state Natural Heritage Program scientists. Their analysis covered 667 species, subspecies, and populations protected by the ESA as of August 1992; it did not include species proposed for listing.

Although the way in which Flather et al. categorized threats was not identical to our approach, the major findings from the two studies can still be compared. These authors also identified habitat loss and alien species as the two most widespread threats to endangered species, affecting more than 95% and 35% of listed species, respectively. (Comparable figures from our study are 85% for habitat destruction and 49% for alien species.) The smaller percentage of species affected by exotics in Flather et al.'s study probably reflects the large number of Hawaiian species that were included in our study but were not on the endangered species list at the time Flather et al. conducted theirs. Flather et al. (1998) also point out that the relative frequency of particular threats to species varies geographically.

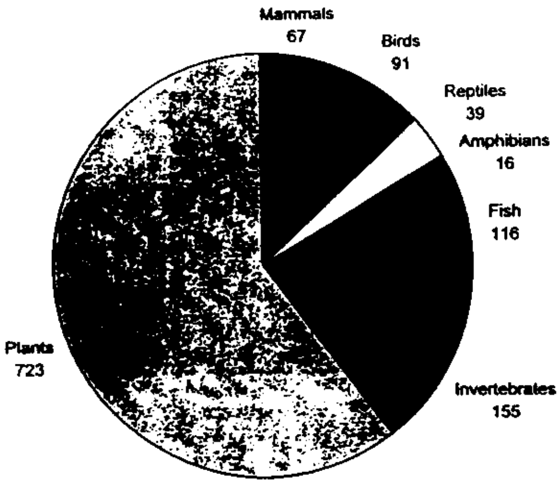

Figure 4. Taxonomic breakdown of the species, subspecies, and populations used in the fine-scale analysis. The 1207 species, subspecies, and populations include those that are listed as endangered or threatened under the Endangered Species Act or are proposed for listing.

Two previous studies have focused on threats to aquatic species. Williams et al. (1989) catalogued threats to 364 species and subspecies of imperiled fish from Canada, the United States, and Mexico; Richter et al. (1997) surveyed aquatic biologists to identify the threats to 135 imperiled freshwater fishes, crayfishes, dragonflies and damselflies, mussels, and amphibians in the United States. Narrowing the scope of Williams et al. to imperiled US and Canadian fishes (254 species), we can compare their results with ours. The findings of the two studies are similar: Williams et al. identified habitat destruction and degradation as the most widespread threat to imperiled fishes, affecting 96% of the species (versus 94% in our study; Table 2). Next in significance was an amalgamated category of hybridization, alien species, predation, and competition, which affected 39% of the fish species (versus our tally of 53% for alien species, which probably covers most of the same threats). Finally, Williams et al. found that overharvest and disease affected 4% and 2%, respectively, of the fishes (versus 13% and 1% in our study).

Richter et al. (1997) concluded that the three leading threats to aquatic species nationwide were agricultural nonpoint pollution (e.g., siltation and nutrient inputs), alien species, and altered hydrologic regimes due to dams and impoundments. This conclusion is consistent with our findings from the fine-scale analysis, which identified pollution and impoundments (including dams) as significant threats to fish and mus-

The major categories of habitat destruction used in this analysis

- Agriculture (including agricultural practices, land conversion and water diversion for agriculture, pesticides and fertilizers; excluding livestock grazing)
- Livestock grazing (including range management activities)
- Mining, oil and gas, and geothermal exploration and development (including roads constructed for and pollutants generated by these activities)
- Logging (including impacts of logging roads and forest management practices)
- Infrastructure development (including bridges, dredging for navigation, and road construction and maintenance)
- Road construction and maintenance specifically (including logging and mining roads)
- Military activities
- Outdoor recreation (including swimming, hiking, skiing, camping, and off-road vehicles)
- Off-road vehicles specifically
- Water development (including diversion for agriculture, livestock, residential use, industry, and irrigation; dams, reservoirs, impoundments, and other barriers to water flow; flood control; drainage projects; aquaculture; navigational access and maintenance)
- Dams, impoundments, and other barriers to water flow specifically
- Pollutants (including siltation and mining pollutants)
- Land conversion for urban and commercial development
- Disruption of fire ecology (including fire suppression)

sels (Table 4). Our coarse-scale analysis, which included a larger pool of imperiled species than the fine-scale analysis, also highlighted the importance of alien species as a threat to US fish.

Richter et al. (1997) point out that there are important geographic differences in the nature of the threats facing aquatic species. Aquatic species in the eastern United States are experiencing particular harm from agricultural nonpoint pollution; in the West, the dominant threat is alien species, followed by habitat degradation and altered hydrologic regimes. Richter et al. attribute these differences to differences in both land use patterns in the East versus the West and in the ecological sensitivities of eastern versus western species.

Using information from USFWS recovery plans, Schemske et al. (1994) identified the primary cause of endangerment for each of 98 US plant species protected under the ESA. These authors did not distinguish between historical and contemporary threats, and they listed only one (i.e., the primary) threat per species, although they acknowledged that most species experience more than one threat. The top six threats in their study (in terms of frequency of appearance) were development (affecting 20.4% of the species); grazing (10.2%); collecting (10.2%); water control (8.2%); oil, gas, and mining (8.2%); and trampling (8.2%). By contrast, our coarse-scale analysis identified habitat destruction and alien species as the two most widespread threats to imperiled plants, affecting 81% and 57% of species, respectively. Moreover, in our fine-scale analysis of habitat destruction, the top five threats to imperiled plants protected under the ESA were land conversion (i.e., development; 36%), agriculture (33%), grazing (33%), outdoor recreation (33%), and disruption of fire ecology (20%).

The consistently higher percentages for all threats in our study compared to that of Schemske et al. (1994) undoubtedly stem from our practice of tallying multiple threats per species. Perhaps the most noticeable difference between the two studies lies in their assessments of the importance of alien species as a threat to rare plants. Schemske et al. (1994) considered alien species the primary threat to only 6.1% of the plants they studied, whereas we found that 57% of endangered plants were affected by alien species. Their lower percentage stems in part from the small number of Hawaiian plants that had been listed as endangered or threatened at the time of their study. Our results do indicate that alien species are a frequent threat to continental plants as well (Table 3), but they are not necessarily the primary threat, which may account for the remainder of the difference.

Collar et al. (1994) identified the primary threat to each of 1111 bird species they regarded as imperiled. Because they evaluated endangered birds worldwide, focused on primary threats only, and categorized the

Table 4. Percentages of federal endangered, threatened, or proposed species, subspecies, or populations that are harmed by various types of habitat destruction and degradation. Categories are nonexclusive and therefore do not sum to 100.

Cause	Overall (n = 1207)	Vertebrates (n = 329)	Invertebrates (n = 155)	Plants (n = 723)	Mammals (n = 67)	Birds (n = 91)	Reptiles (n = 39)	Amphibians (n = 16)	Fish (n = 116)	Insects (n = 39)	Arachnids (n = 4)	Crustaceans (n = 20)	Mollusks (n = 23)	Mussels (n = 69)
Agriculture	38	40	57	33	25	42	33	63	45	56	75	55	35	64
Livestock grazing	22	17	10	33	19	20	8	19	16	15	0	30	9	1
Mining, oil and gas, geothermal	11	12	31	11	2	3	13	13	23	10	0	0	17	58
Logging	12	16	25	7	12	18	13	19	19	5	25	5	13	46
Infrastructure development (including roads)	17	16	12	20	9	8	28	38	17	23	25	10	9	6
Road construction and maintenance	15	15	10	17	8	8	23	38	16	18	25	5	9	6
Military activities	4	2	1	5	2	3	5	0	0	0	0	5	4	0
Outdoor recreation (including ORVs)	27	16	19	33	18	15	31	25	9	41	0	30	26	4
Off-road vehicles	13	6	12	16	6	7	13	13	1	31	0	25	4	0
Water development (including dams, etc.)	30	47	66	15	10	22	28	63	91	21	0	70	48	99
Dams, impoundments, and other barriers	17	28	54	5	3	9	15	13	64	15	0	15	35	96
Pollutants	20	27	66	7	5	10	21	25	55	26	75	55	48	97
Land conversion for commercial development	35	30	42	36	31	33	56	44	16	67	75	65	13	29
Disruption of fire ecology	14	5	6	20	7	8	5	6	0	18	25	0	4	0

threats differently than we did, their results are not directly comparable to ours. Nonetheless, it is worth noting that both studies identified habitat loss as the most widespread threat. In Collar et al.'s study, the next most important threats, in order of decreasing frequency, were small range or population, overhunting, and alien species. In our study, the next most important threats, also in order of decreasing frequency, were alien species, disease, overhunting, and pollution. The higher rankings accorded alien species and diseases in our analysis are probably due to the Hawaiian avifauna, which constitutes a large fraction of endangered birds in the United States and is profoundly affected by these threats. In our study, we did not classify small range per se as a threat.

Changes in threats over time

As human activities and customs change over time, one would expect to see corresponding changes in the threats to biodiversity. Because our study does not distinguish between historical and contemporary threats, it is not well suited to test this hypothesis. For example, the relatively large percentage of species affected by overexploitation (17%) includes a variety of animals that were once hunted but are now reasonably well protected from this threat (e.g., the whooping crane [*Grus americana*] and the California condor [*Gymnogyps californianus*]). Similarly, pesticide pollution is listed as the primary threat to the bald eagle (*Haliaeetus leucocephalus*) and to North American populations of the peregrine falcon (*Falco peregrinus*), but the primary pollutant harming both species—DDT—has been banned in the United States since 1972 (although it continues to be used in other countries where peregrines spend the winter). Thus, our study may overestimate the number of animals that are currently harmed by overexploitation and pollutants.

There are no accurate figures on the total number of alien species now established in the United States, although the Office of Technology Assessment [OTA] (1993) has estimated that there are at least 4500 (a number that OTA acknowledges is probably an underestimate). What is indisputably clear, however, is that the cumulative number of alien species in the United States has skyrocketed since the late 18th century (Sailer 1978, OTA 1993); this pattern holds for all types of species, from plants, to insects, to vertebrates. Given that the cumulative number of alien species is increasing over time, one may confidently predict that alien species will pose an ever-increasing threat to native flora and fauna.

A somewhat more complicated question is whether the *rate* of alien introductions has increased over time, which would indicate a rapidly worsening situation for imperiled species. The data from published studies are ambiguous on this point. Reviewing the numbers of alien terrestrial vertebrates, fishes, mollusks, and plant pathogens added to the United States per decade over the past 50 years, OTA (1993) found no consistent increase for any of the groups. The greatest numbers of terrestrial vertebrates and fishes were added during the 1950s and 1960s, whereas the 1970s saw the greatest increase in the numbers of mollusks and plant pathogens. On the other hand, a detailed study of alien species in the San Francisco Estuary shows that there have been more introductions in recent years than in earlier years (Cohen and Carlton 1995).

Many factors influence the rate at which alien species are introduced into the United States, so the lack of a consistent increase in that rate over time should not be surprising. Species can be brought into the country and released intentionally, or their release can occur as an unintentional byproduct of cultivation, commerce, tourism, or travel. Each new development in the field of transportation creates new opportunities for the transport of alien species, from the first sailing ships to reach US shores, to the building of the nation's road and highway system, to the advent of jet airplanes. As transporation technology changes, so do the opportunities for alien stowaways. Empty cargo ships arriving in the United States, for example, used to carry dry ballast in the form of rocks and soil, which was then off-loaded around wharves to provide cargo space. Numerous insects and plants were accidentally introduced into the United States in this dry ballast, including fire ants (*Solenopsis invicta* and *Solenopsis richteri*) and purple loosestrife (*Lythrum salicaria*). Today, ships use water for ballast instead of dry material, thus ending the spread of alien species via dry ballast. However, the release of ballast water into US waterways has been implicated in the introduction of at least eight alien species since 1980, including the zebra mussel, *Dreissena polymorpha* (OTA 1993). Finally, the public's growing infatuation with ornamental plants, tropical fish, and tropical birds has led to numerous unintentional releases of alien species, including over 300 plants in California alone (McClintock 1985).

Looking ahead, as the human population of the United States continues to grow, one might predict an increase in the frequency of biodiversity threats associated with urbanization, such as infrastructure development, water development, and land conversion. Comparable increases in the proportion of species affected by agriculture are also a possibility. There is, in fact, good reason to suspect that a growing human population in the United States will disproportionately affect this nation's imperiled species. Dobson et al. (1997) have shown that most endangered species in the United States are clustered in a relatively small number of areas, particularly in Hawaii, Southern California, and Florida. The human populations in all three states are projected to increase at rates well beyond the national average. Thus, whereas the population of the United States as a whole is expected to grow by 14% between 1995 and 2010, the populations of Hawaii, California, and Florida are projected to increase by 27%, 27%, and 22%, respectively (US Bureau of the Census 1995).

Although climate change was not listed as a current threat to any species in our databases, it is almost certain to become one in the foreseeable future due to increasing concentrations of greenhouse gases from fossil-fuel use, land-use changes, and agriculture. Climate models developed by the Intergovernmental Panel on Climate Change predict a 0.9–

3.5 °C increase in global mean temperature over the course of the next century (Houghton et al. 1995). That increase will cause a rise in sea levels of 15–95 cm and significant changes in the frequencies of severe floods and droughts.

These changes are likely to affect a broad array of imperiled species. For example, Morse et al. (1993) estimate that 7–11% of North America's vascular plant species would no longer encounter a suitable climatic regime ("climate envelope") within their present ranges in the event of a 3 °C increase in temperature. Due to their small ranges and weak dispersal abilities, imperiled plants would be disproportionately affected. Morse et al. (1993) also estimate that 10–18% of North America's rare plants could be excluded from their climate envelope due to climate change.

In another well-publicized study, Britten et al. (1994) noted that relictual populations of the critically endangered Uncompahgre fritillary butterfly (*Boloria acrocnema*) living atop a few peaks in the San Juan Mountains of southwestern Colorado were extremely vulnerable to unusual weather events. They further hypothesized that a regional warming trend (as might occur due to global climate change) could eliminate all of the butterfly's habitat, essentially pushing it off of the mountains and into extinction. Indirect support for this hypothesis comes from a recent study of another butterfly. Parmesan (1996) censused populations of the Edith's checkerspot (*Euphydryas editha*) throughout its known range (Baja California, the western United States, and western Canada) and found significant latitudinal and altitudinal differences in the proportion of populations (in suitable habitat) that had become extinct. Populations in Mexico were four times more likely to have vanished than those in Canada, a North–South gradient in survival that is consistent with the predicted impacts of global warming on species' ranges.

Conservation implications

The major findings of this study confirm what most conservation biologists have long suspected: Habitat loss is the single greatest threat to biodiversity, followed by the spread of alien species. However, the discovery that nearly half of the imperiled species in the United States are threatened by alien species—combined with the growing numbers of alien species—suggests that this particular threat may be far more serious than many people have heretofore believed. The impact of alien species is most acute in the Hawaiian Islands, as demonstrated by the fact that nearly 100% of the archipelago's imperiled plants and birds are threatened by alien species, compared with 30% and 48%, respectively, for mainland plants and birds (Table 3). This finding is also consistent with numerous other studies that have highlighted the unique vulnerability of island communities to alien species (Culliney 1988, Simberloff 1995).

Pollution (including siltation) ranks well below alien species as a threat to imperiled species in general, but it exceeds alien species as a threat to aquatic taxa. As Richter et al. (1997) point out, the pollutants affecting the largest number of aquatic species are agricultural pollutants, such as silt and nutrients, that enter lakes and rivers as runoff from farming operations. These nonpoint source pollutants have proved to be exceedingly difficult to regulate and control (Young and Congdon 1994).

Finally, this study and one by Wilcove and Chen (in press) raise troubling questions about the future of imperiled species in the United States. Both studies found that a high proportion of imperiled species is threatened by either fire suppression within their fire-maintained habitats or alien species. Both types of threats must be addressed through active, "hands-on" management of the habitat, such as pulling up alien plants and trapping alien animals or using prescribed fire to regenerate early successional habitats. Although the ESA prohibits actions that directly harm listed animals and, to a lesser extent, listed plants, it does not require landowners to take affirmative actions to maintain or restore habitats for listed species. Thus, a landowner is under no obligation to control exotic weeds, undertake a program of prescribed burning, or do any of the other things that may be absolutely necessary for the long-term survival of many imperiled species. In fact, it may be possible for a landowner to rid himself of an endangered species "problem" by literally doing nothing and waiting until the habitat is no longer suitable for the species in question. Even those landowners who care deeply about endangered species and wish to protect them face a daunting burden: The costs of undertaking these management actions can be considerable and, at present, are usually not tax deductible.

With a growing list of species in need of attention and less money to spend per species (Wilcove et al. 1996), the USFWS cannot hope to cover the necessary management costs for most of the plants and animals it aspires to protect. Nor can it count on the goodwill of landowners to contribute their own money or labor for actions they are not obligated to perform and that ultimately may result in restrictions on the use of their property. As a nation, therefore, we are incurring a growing "management debt" associated with efforts to protect imperiled species. To address this problem, it will be necessary to supplement the regulatory controls of the ESA and other wildlife protection laws with a wide array of incentives to reward landowners who wish to manage their property to benefit endangered species (Wilcove et al. 1996). Without such incentives, the United States stands to lose a large proportion of its imperiled plants and animals.

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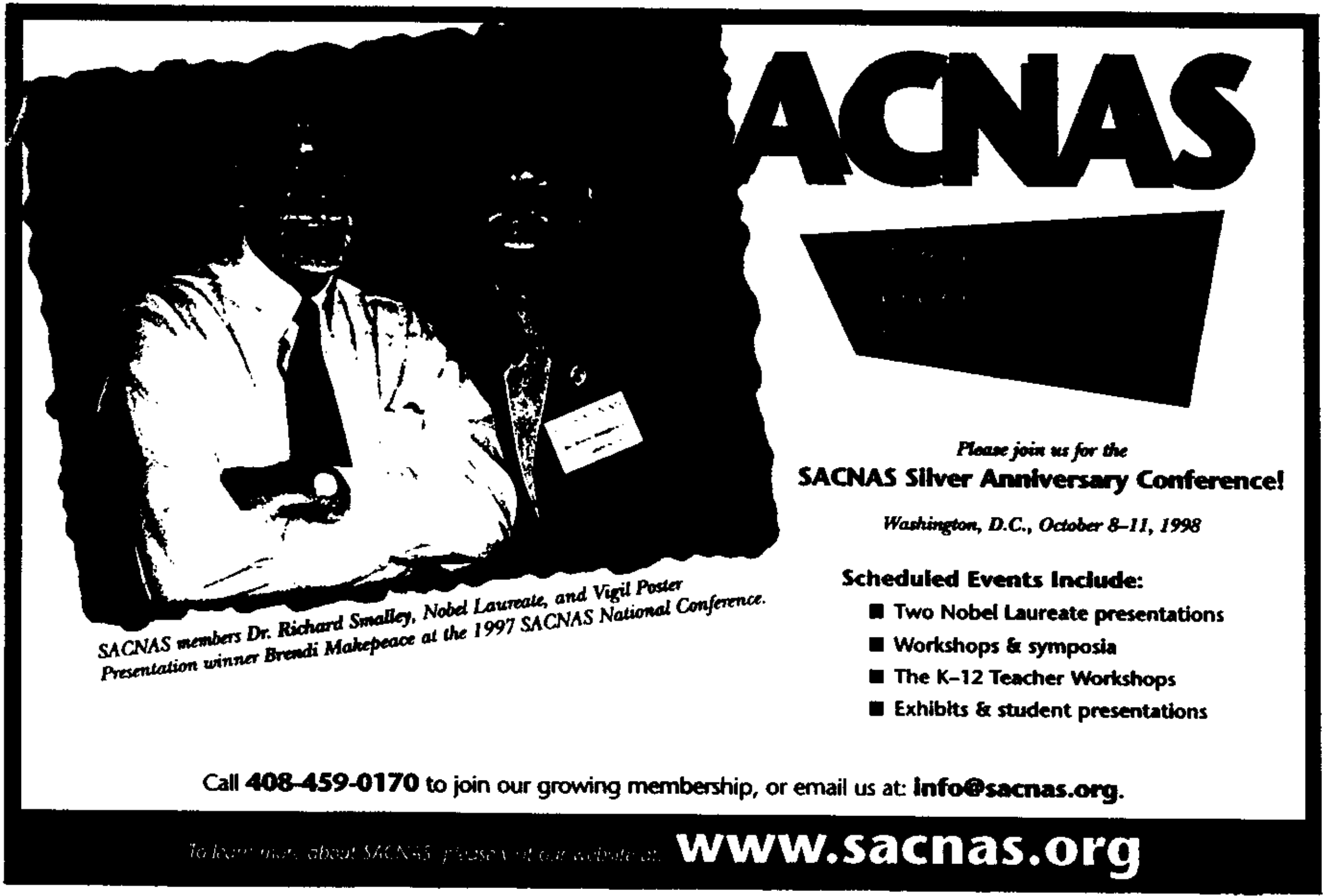

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13

Classification of threatened species and its role in conservation planning

Georgina M. Mace

13.1 Introduction

Over the next several decades, actions will need to be taken towards preserving the many species now facing extinction. Unfortunately, this will be done in the context of enormous ignorance about most of those species, with limited resources, and with continuing developments that contribute to species' extinction. In this chapter, I review the role that categorizing species according to their perceived risk of extinction can play, and outline some of the practical advantages and disadvantages of this approach. In particular, I shall focus on the fact that categorizing risk levels is only a first step. Deciding what to do next and developing rational methods for setting priorities will be just as important, and presents additional challenges.

13.2 The role of threatened species lists

Threatened species lists are produced most commonly in the Red Lists and Red Data Books of IUCN—the World Conservation Union. These were formally established in the early 1960s (Scott *et al.* 1987*b*) and although their size, format, and style has evolved since that time, the basic concept of providing readily assimilated information to focus attention on the plight of endangered species remains. The Red Data Book concept has been very successful, and there are now many regional, national, and taxonomic lists based on it (Burton 1984; R. Fitter and M. Fitter 1987; Thomas and Morris, Chapter 8).

Early on it was clear that general awareness-raising was most important, and species were selected partly on the basis of their appeal (Talbot 1959). However, by the mid-1960s there was a more serious attempt to make the lists comprehensive, although it soon became clear that this was going to be impossible for many plants and invertebrates (Scott *et al.* 1987*b*).

Increasingly, the lists have been used for more than just raising awareness and have been applied to setting priorities for species conservation. In this context it is important that the process for categorizing species is objective, standardized, and equally applicable across broad taxonomic groups whose basic biology and life histories differ fundamentally. The current categorization system is perceived to have problems in this regard, and recently, steps have been taken towards revising methods used to categorize species. (R. Fitter and M. Fitter 1987; Mace and Lande 1991; Master 1991; Mace *et al.* 1992).

13.3 Problems with threatened species categories

Apart from these difficulties over methodology, there are other general criticisms of threatened species lists, which also need to be taken into account in reviewing their role. First is the concern that a focus on species alone will be insufficient to meet the general needs of biodiversity conservation (Scott *et al.* 1987*a*). There has recently been much progress in the development of analytical methods to set priorities among areas for conservation on the basis of some measure of their species complement (Forey *et al.* in press). However, species are the units of extinction considered here, and an understanding of their dynamics is crucial to a consideration of community and ecosystem processes, and to the development of effective conservation strategies for all of these (Pimm 1992). Recent empirical studies have shown that where species data are poor, area-based methods that select for diversity can be effective if a sufficient number of sites can be selected, but incorporation of species information provides a much better selection (Thomas and Mallorie 1985). In addition, where species play a 'flagship' role, they can provide an effective method for ecosystem preservation (Dietz *et al.* 1994; Losos 1993). Species-based approaches should be a component of area-based methods, and the two should be used in conjunction and not as alternatives.

A second problem is that published lists of threatened species inevitably focus on well-known forms. Two large sets of species, the undescribed and the unstudied are, to their detriment, under-represented (Diamond 1989). Effective species conservation involves at least three different activities: describing species, researching their status, and protecting them. Threatened species classifications only fulfil a part of this process and should not eclipse the others. The system should not prejudice the poorly known species, but equally should be rigorous in the analysis of any existing species data (see below). This is one of the most challenging areas in developing systems for categorizing threat.

A major problem with existing Red Lists is that, for the most part, they have not been comprehensive in their review of species in particular taxonomic groups or geographic regions. Species are generally listed when a biologist becomes aware that a species has a problem; they do not often result from any systematic review (Diamond 1989). As WCMC (1992) note, among the higher taxa in the IUCN (1990) Red List, only the birds had been fully considered. About 50% of mammal species, and probably less than 20% of reptiles, 10% of amphibians, 5% of fish, and a much smaller proportion of invertebrates had been reviewed. Therefore, non-inclusion in a Red List can mean either that a species has been reviewed and its status considered sufficiently secure, or that the species, for whatever reason (usually lack of information), was not considered. Clearly, these two need to be distinguished explicitly. One solution is to regard all species as endangered until proven otherwise—the so-called Green List (Imboden 1987; Diamond 1987). While this suggestion has a certain logic and attraction, it is probably unworkable and might detract attention away from the task of collecting information about the poorly known species.

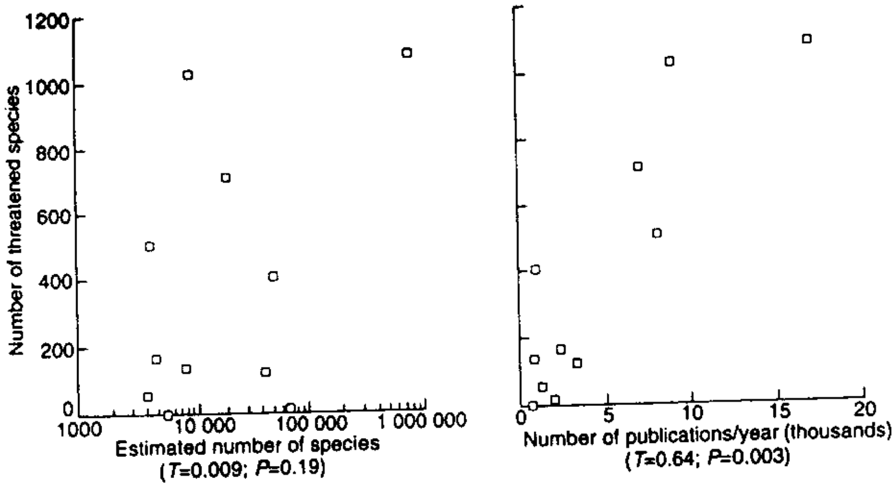

Fig. 13.1 The relationship between the number of species listed as threatened among major taxa (mostly phyla) (WCMC 1992) and the estimated total species number (left-hand graph), and the number of papers published on the same groups (from May 1988) (right-hand graph). The taxa are mammals, birds, reptiles, amphibians, fish, molluscs, annelids, insects, arachnids, crustaceans, and echinoderms.

Nevertheless, it is clear that the highest proportion of threatened species are found among the well-known birds and mammals (WCMC 1992). Intensity of interest is hard to measure, but one available index is the number of papers published on different major taxa. In Fig. 13.1, the numbers of published papers cited in *Zoological Record* (from May 1988) is significantly and positively correlated with the number of species listed as threatened in the same groups in the IUCN 1990 Red List (from WCMC 1992). There is no relationship between the estimated number of described species and the number listed as threatened. There are, of course, other possible explanations for this pattern. In particular, large-bodied forms may be more extinction-prone than small ones (Diamond 1984; Belovsky 1987, but see Lawton, Chapter 10) and for practical reasons less attention may be focused on small-bodied species. However, this is unlikely to be a complete explanation (WCMC 1992, Smith *et al.* 1993*b*).

A final problem is that in both major systems used today, the IUCN (1990) definitions and the United States Endangered Species Act (see Rohlf 1989), the definitions for endangered status are merely stated in terms of '. . . in danger of extinction . . .'. Without any reference to a time-frame, or to the likelihood of extinction within this time-frame, the categories may be interpreted in different ways by different authorities. This can result in the same species being classified quite differently, or in different taxa or different regional floras and faunas being judged by quite different standards. If conservation action is to be based on them, threatened species categories will require an approach that is better validated. A more objective system that can be challenged and judged against an accepted set of rules is needed.

13.4 Systems for classifying species according to risk of extinction

With this background to the role of threatened species categories, a review of a range of recently published systems is presented in Table 13.1. It is not comprehensive; rather it aims to provide a representative sample of recent systems, and complements a full review by Munton (1987).

Most of these are based around existing IUCN definitions, usually with some amendments. Many regional threatened species lists in the United States use the Endangered Species Act definitions as a basis (see also Munton 1987). In addition, the classification of rarity by Rabinowitz (1981) has been used and two more recent proposals based on quantitative criteria (Mace and Lande 1991, Mace *et al.* 1992) have been adopted for some well-studied taxonomic groups. Others have been developed entirely independently (Table 13.1).

The main conclusion from the information presented in Table 13.1 is that threatened species listings measure a number of characteristics that are not directly related to the extinction risk. Sometimes this is done overtly by separating these into distinct categories. For example, 'out of danger' in the IUCN system does not qualify a species for threatened status. But many characteristics that could lead to listing in a threatened category do not necessarily reflect threat. For example, a restricted geographic distribution is sufficient to qualify a species for inclusion in the IUCN category 'rare', and the category 'insufficiently known' includes species that are 'suspected' to belong in one of the threatened categories, but about which there is little information. These categories are therefore measuring multiple characteristics of species, many of which may have a bearing on planning for their conservation, but not necessarily reflecting their risk of extinction.

All systems reviewed use small population size specifically in defining threatened status, though only a minority (5/19) present any quantitative guidelines. The effect of turning from qualitative to quantitative definitions may be significant. In less well-known groups it is likely that the number in the threatened category will decline, because of the difficulties of applying quantitative criteria to poorly known species. However, in general, the application of quantitative criteria to well-studied vertebrate groups has led to an increase in the number of species listed as threatened (Seal *et al.* 1993; Mace 1994). Some consequences are exemplified in the categorizations made by Green (1992) for waterfowl and Osborne (in press) for cycads. Both these groups had previously been classified by the IUCN criteria. In both cases there was an

Table 13.1 Characteristics used in definitions of threatened species categories

[1] Taxon	[2] Region	[3] Based on	[4] In danger of extinction	[5] Will become endangered	[6] Pop. size small	[7] Small range or no. of sites	[8] Commercial or specific threats	[9] Recovered from threat	[10] Protection status	[11] Declining	[12] Declined but not threatened	[13] Suspected threatened but no data	[14] Not threatened	[15] Endemic to region	[16] Ref. no
														–	1–4
Vertebrates	Global	IUCN	+	+	+	+		+				+	+	–	5
Primates	Africa	IUCN	+	+	+	+									
Lemurs	Madagas-														
	car &											+			6
	Comores	IUCN	+	+	+	+						+		–	7
Swallowtail	Global	IUCN	+	+	+	+		+							
butterflies															
Dolphins,															
porpoises,												+		–	8
& whales	Global	IUCN	+	+	N	+								–	9
Birds	Africa	IUCN	+	+	+	+		+		+	+				
Amphibia &												+		–	10
reptiles	Global	IUCN	+	+	+	+		+				+		–	11
Invertebrates	Global	IUCN	+	+	+	+	+							–	12
Waterfowl	Global	M – L			N		+			+			+	–	13
Cycads	Global	dIUCN			N					+				+	14
All	Thailand		+		+	+			+						
All	Virginia,														15
	USA	ESA	+	+	+	+	+				+	+			16
All	Baltic	IUCN	+	+	+	+									
Primates	Africa &												+		17, 18
	Asia		+	+	N	+							+		19
All	Americas	TNC	+		+	N						+			20
Plants	Australia		+	+	N	+			+						
Migrant															21
birds	Neotropics	Rab			+	+	(+)							+	22
Insects	Britain	IUCN			+	N		+		+					
Other												+		+	23
invertebrates	Britain	IUCN			+	N		+		+					

Column [3]: IUCN, IUCN criteria; M-L, Mace and Lande (1991); dIUCN, Mace *et al.* (1992); ESA, Endangered Species Act (Rohlf 1989); Rab., Rabinowitz *et al.* 1986, TNC, Master (1991)

Columns [4]–[15]: +, characteristic scored in threatened species categorization system; N, numerical guidelines given; –, not relevant

Column [16]: 1, IUCN (1972); 2, IUCN (1978); 3, IUCN (1979); 4, IUCN (1975); 5, IUCN (1988); 6, IUCN (1990); 7, IUCN (1985); 8, IUCN (1991); 9, Collar and Stuart (1985); 10, IUCN (1982); 11, IUCN (1983); 12, Green (1992); 13, Osborne (submitted); 14, TISTR (1991); 15, Terwilliger (1990); 16, Ingelof *et al.* (1993); 17, Oates (1986); 18, Eudeu (1987); 19, Master (1991); 20, Briggs and Leigh (1988); 21, Reed (1992); 22, Shirt (1987); 23, Bratton (1991) increase in the number of taxa (species or subspecies) listed as threatened (61 to 74 for cycads; 36 to 52 for waterfowl). However, this was not simply due to a shifting of boundaries, there was quite a substantial change in the set of taxa listed as threatened. In the cycads, 15 taxa were threatened according to IUCN definitions but not threatened by the quantitative criteria, and 20 were threatened according to quantitative criteria but not threatened by IUCN definitions. The equivalent figures for waterfowl are 27 and 11 taxa, respectively.

Almost all the systems also use small range size or number of sites explicitly, usually in a definition for a category such as 'rare'. Rarity can take a variety of forms and the framework suggested by Rabinowitz (1981) and Rabinowitz *et al.* (1986) is useful for considering extinction risk in relation to different forms of rarity (Thomas and Mallorie 1985; Rabinowitz *et al.* 1986). Species with small population sizes, restricted ranges, and narrow habitat specializations are always considered especially vulnerable, and the classically 'common' species with abundant populations over large geographical ranges and broad habitat types are always considered 'safe'. However, there is little consensus about the relative risks faced by taxa belonging to the other 6 forms of rarity (see Reed 1992; Kattan 1992). There also two practical problems which limit the use of these classifications at a general level. One is that each of these three variables is actually a continuum, and some arbitrary decisions have to be made about where the cut-off points lie. Secondly, there are always difficulties and compromises in the measurement of habitat specificity.

Several criteria relate in some way to management or its consequences and this is a difficult area in the categorization of threat. On the one hand, there are demands to have species listed as threatened, even if past or current management has led to a stable or increasing population. This is especially the case where threatened species categories are translated directly into legislation or into species protection. A logical consequence is that dependence upon protection would need to be a criterion for endangered status, and no species under management would ever leave the threatened species lists. On the other hand, an aim of conservation action should be to reduce the number of species listed as threatened. It would seem to be more logical to differentiate between threatened forms (i.e., those that are thought to be currently at high risk of extinction) and species dependent upon continuing management. This is not quite the same as the intent of the IUCN category 'out of danger' (now rarely used) which is used for cases where a species was previously listed but has recovered, and is therefore an historical rather than a continuing status assessment.

It seems surprising that population declines have not more commonly played a role in the listing of species, yet only 5 out of the 19 systems incorporate this in their definitions. Fundamentally, an endangered species in one that is showing or is expected to show evidence of decline. Combined with small population size or small range sizes, population decline seems intuitively to be a more reliable indicator of risk than do either of these two characteristics alone.

The categorization of species that have shown marked reduction in numbers or range from recent or historical levels is a reflection of a widespread concern that

conservation should do more than prevent extinction. Functioning ecosystems should be maintained with their species complement at some level that may be well above that needed to prevent extinction. This view relies on the notion that there is some 'correct' or 'stable' level for each and every species, but it is very difficult to determine where this should be set. Historically and geologically, species numbers have always fluctuated and it is difficult to know how to implement this kind of approach practically. In any case, this would be an entirely different enterprise from the current one which is to limit the current extinction crisis.

In many published lists of threatened species a large number are classified as suspected of being threatened but with insufficient data to make a definite judgement. The category 'insufficiently known' in the IUCN definitions is specifically for this situation, and it has been widely applied. The classification is not useful for conservation planning since it is unclear where these species sit in relation to those that can be said definitively to have a high or moderate extinction risk, and it does not indicate anything about the kind of information that is required or that which is available. Conversely, taking species that are poorly known out of the threatened species lists altogether, may prejudice their survival simply on the basis that we know little about them. In addition, species may be classified as insufficiently known for a variety of reasons. They may be at risk because their only known habitat is being lost, but so little is known about their status that it is impossible to say whether they are 'endangered', 'vulnerable' or 'rare'. Alternatively, they may be known only from historical records from a remote site rarely visited by naturalists. Their actual status could be anything from extinct to common. Finally, Cooke (1991) gives a reasoned argument for a very broad application of the 'insufficiently known' category in the categorization of cetaceans. He argues that this category should be applied to species that are not definitely known *not* to satisfy the criteria for any of the other threatened categories, and that the only situation where this could be true would be where all or most populations are known *not* to be declining. This requires good information and among the cetaceans only one species (the grey whale) qualifies. Therefore, all others that are not classified in another threatened category are classified as insufficiently known. If this logic were applied to many groups the vast majority of species would be classified in this category.

Ideally, three things could help resolve the problem of how to treat poorly known species. First, the criteria for the categories could explicitly include risks derived from habitat change or loss affecting many species for which direct information on status is lacking. Second, classifications could be accompanied by some statement about the extent and reliability of information used to make the evaluation. Third, there could be a separate classification for species for which additional information is required before extinction risk can be evaluated. This would be distinct from the Red List and would more effectively highlight those species in need of survey or study, as opposed to those known to need protection. However, these measures alone do not solve the problem of how best to cope with the extent of our ignorance.

Few systems have explicitly included 'not threatened' in their categorization scheme, and as discussed earlier, this has led to uncertainty about the status of those species not listed. There seems to be no logical reason why this cannot be included, except for a reluctance be publish an assessment that could be so easily and disastrously proven wrong. If confidence can be placed in the criteria for threatened categories and a taxon can be shown to not qualify, then this should be stated. In fact, very often the information is so poor that the taxon cannot be shown *not* to qualify; which is a manifestation of the problem of how best deal with poorly known forms (see above). Undoubtedly, there should be a 'not threatened' or similarly named category, as there should be a category for taxa that have not even been evaluated against the definitions.

Finally, a number of regional studies have included categories that reflect the distribution of taxa inside and outside the region, especially to indicate those that are endemics, or whose major populations are found locally. This is generally more useful for conservation planning than assessing extinction risk (see below).

13.5 The proposed new IUCN criteria

The development of new IUCN categories is now well under way (Mace *et al.* 1992). These new definitions and criteria are still under active review and refinement, but an outline is presented here of version 2.1 (IUCN/SSC 1993).

The threatened species classification scheme falls within a larger scheme which will be applicable to all species and which will indicate whether a species has been assessed, whether there was sufficient information to categorize according to threat level and, if so, whether the species was felt to be threatened, not threatened or in need of continuing conservation management. The threat categories are defined only in terms of extinction risk, with decreasing threat levels over increasing time periods (Mace and Lande 1991). There are three threat categories ('critical', 'endangered', and 'vulnerable') which fall on a continuum, and a fourth category ('susceptible') which is reserved for taxa that do not qualify for any of the higher threat categories but which, as a consequence of restricted distributions are continually at risk of extinction. A series of quantitative criteria are provided for the categories of 'critical', 'endangered', and 'vulnerable', and to qualify for listing a species has to satisfy one of these. The five criteria are measures of: (1) observed, inferred or projected decline rates; (2) small populations that are either single or fragmented associated with an observed, inferred or projected decline; (3) small geographic range areas or extents associated with an observed, inferred or projected decline; (4) very small population sizes; and (5) a quantitative analysis predicting a given extinction risk within a specified time period (see Mace *et al.* 1992).

The system was designed to be appropriate for all macro fauna and flora, and although early drafts presented separate criteria for different major taxa, it became clear that with this approach species that had unusual life histories for their own major taxa might be judged by inappropriate criteria. It was therefore more conservative to consolidate criteria for diverse major lifestyles into a single set of criteria, and allow meeting any one to qualify the species for listing at that level. Depending on the perspective of the classifier, some of the criteria therefore may appear inappropriate or even absurd. However, under this system what matters is whether any of the criteria are met, not whether all are appropriate. The current review procedure has aimed to investigate whether application of the proposed criteria to diverse taxonomic groups indicates false listings and so far it has not appeared necessary to alter this structure, although there are concerns about some of the levels set.

13.6 Estimating extinction rates from threatened species lists

Because most lists are based on non-quantitative criteria and definitions, they cannot be used to make predictions about extinction rates. Smith *et al.* (1993*a*) have recently analysed the changes in species lists in IUCN Red Lists published between 1986 and 1990 to make some estimates of extinction risk. However, as they make clear, for most taxa these will be underestimates because of incomplete evaluations (see above). However, once the definitions for categories, and the criteria that determine listing under them, become quantitative, it will be possible to use these lists to make estimates of future extinction rates. A major caveat here is that listing of a taxon under a threat category does not necessarily constitute a prediction, because the very fact that it has been perceived to be in trouble, and placed on a Red List, should encourage effective conservation actions that reduce the extinction risk.

At this early stage in their development it is not appropriate to use the new draft IUCN criteria in this context. However, the quantitative definitions and criteria proposed by Mace and Lande (1991) have now been applied to a range of vertebrate taxa, mainly through activities of various IUCN Species Survival Commission Specialist Groups (Seal *et al.* 1993; Mace 1994). For a range of higher taxa, species and subspecies have been classified as 'critical' (50% risk of extinction in 5 years or 2 generations, whichever is longer), 'endangered' (20% risk of extinction in 20 years or 10 generations, whichever is longer), 'vulnerable' (10% risk of extinction in 100 years) or 'safe'. These assessments can be used to make some very rough estimates of future extinction rates, using a similar methodology to Smith *et al.* (1993*a*), except that here the analysis is based on evaluations of extinction risks across all extant members of certain higher taxa, instead of on recorded extinctions. The data presented in Table 13.2 are compilations from Mace (1994) and show the percentage of species in 10 vertebrate taxa placed in each of the threatened categories 'critical', 'endangered', and 'vulnerable'. Only species-level estimates are presented here, although in most taxa (not marsupials and canids) many classifications were made at subspecific level, and the species not then evaluated. The categories are defined by single risk and time points, but for the purpose of this analysis all were standardized to 100 years by fitting exponential extinction functions.

On this basis, no 'critical' taxa and only about 33% of 'endangered' taxa are expected to persist for 100 years. Applying these survival rates across threatened

Table 13.2 Extinction rates for vertebrate species calculated from threatened species categories

	'Critical' (%)	'Endangered' (%)	'Vulnerable' (%)	No.	Est. % extinct in 100 yr	Est. yr to 50% extinction
Reptilia						
Boidae	5.9	12	35	17	17	365
Varandidae	0	3.5	34	29	6	1168
Iguanidae	4.0	8.0	56	25	15	428
Birds						
Anseriformes	4.6	8.3	20	109	16	404
Gruidae	17	0	50	6	19	335
Psittaciformes	7.3	8.3	24	302	15	421
Bucerotidae	10	30	40	10	34	166
Mammals						
Marsupiala	3.4	11	34	179	14	453
Canidae	5.9	12	21	34	16	403
Cervidae	29	29	21	14	50	101

Data on threat levels categorizations from workshop documents reproduced in CBSG (1992)

classes gives the percentage of species in each group that are expected to be extinct in 100 years time (Table 13.2). These percentages range from 6% to 50%. The 50% figure for cervids may be rather inflated because most cervid taxa were evaluated at the subspecific level, where the proportion of threatened forms was lower (see Mace 1994). These values are similar to estimates of species extinction rates derived from species–area curves. Recent estimates for tropical forest species lie between 10% and 40% loss over 100 years (Reid 1992).

From these values, the characteristic extinction time, or estimated time to 50% extinction, can be calculated, and these values are shown in the final column of Table 13.2. They range from about 100 years to over 1000, but for most taxa are around 300–400 years. These time periods are much shorter than those calculated from recorded extinctions and at the very low end of estimates based on transitions of species through existing Red List categories (Smith *et al.* 1993*a*). Smith *et al.* (1993*a*) note that their estimates were likely to be low due to under-recording, and the results of this analysis, where recording is complete, bear this out.

There are, however, several reasons why these estimated times might be rather too short. First, the definitions for these categories are based on time periods measured in years or generations, and the generations measure will be used whenever species generation lengths exceed 2.5 years (for 'critical') or 2 years (for 'endangered'). Most of the taxa in Table 13.2 have generation lengths substantially longer than this. Second, there could be a bias from only using taxa that were not evaluated at subspecific level, since these might commonly be

Table 13.3 Vertebrate extinction rates at different taxonomic levels and adjusted for generation length

Level	'Critical' (%)	'Endangered' (%)	'Vulnerable' (%)	No.	Est. % extinct in 100 yr		Est. yr to 50% extinction	
					Low	High	Low	High
Species	5.9	9.7	28	725	15	11	433	613
Subspecies	8.3	16	28	554	22	14	281	447

restricted range forms or island endemics, which would then be expected to have a higher extinction risk. In Table 13.3 the average values across all species and subspecies in this data set are analysed, and the effects of increasing generation length to 6 years (a rough estimate of a median) is shown. In fact, on average, the subspecies data give higher extinction risks (22% expected extinct in 100 years compared to 16% for species), and have a characteristic extinction time of 281 instead of 433 years. Increasing generation length increases the characteristic extinction time for species from 433 years to 613, and for subspecies from 281 to 447.

These estimates are still very crude. The criteria used to classify taxa into the categories are only very approximate (Mace and Lande 1991) and have not been, and probably cannot be, generally validated. Further, the procedure used to standardize them all to a 100-year period is simplistic. Also, the taxa were assessed in workshop sessions, and are inevitably based on very little information. There is undoubtedly a strong inclination to be highly conservative in making estimates under these conditions, especially as in most cases there was no option to place taxa into an 'insufficiently known' category, although some remained unclassified (Seal *et al.* 1993). They may therefore represent worst-case assessments. Finally, the results should not be generalized across other vertebrate taxa since the groups so far analysed probably represent higher order taxa that most clearly contain large numbers of threatened forms. No such analysis has yet been performed on, for example, rodents or passerine birds, and the outcome might be quite different.

The results are, however, interesting since they generally corroborate analyses made on species extinction rates from entirely independent methods: from species–area curves (Reid 1992) and from analyses of rates of movement of species through categories in existing Red Lists (Smith *et al.* 1993*a*).

13.7 The application of threatened species categories in setting priorities for conservation action

Interesting as the analysis of extinction rates is, the compilation of threatened species lists should not necessarily be an end in itself. In terms of conservation action aimed at limiting the extinction rate, the categories can be used in systems for setting conservation priorities, and determining appropriate short- and longer-term activities. In this section I review these schemes and the factors they incorporate.

Table 13.4 lists a number of priority classification schemes incorporating threat categories at particular taxonomic and/or regional levels. The schemes are quite diverse. Some have been developed by national or regional conservation authorities, others are global priorities for taxonomic groups prepared by Specialist Groups of the IUCN Species Survival Commission, and others are for very specific purposes. Equally diverse is the number of different characteristics that have been used in the setting of priorities. Not included in Table 13.4 are the algorithms that have been used to develop priority rankings, most of which translate scores on each of the characteristics into a single rank. In most cases, the threat category is dominant in the final rank. For example, in some cases (e.g., Oates 1986; Wager and Jackson 1993) there are simply more ranks for the threat classification than for other variables so that high-risk species will tend score highly overall. In others (e.g., Garnett 1992) the first ranking is by threat category and other variables are only brought in later on.

In a few of these examples, the threat category is the only character used, and is directly translated into a priority. More commonly, other features are scored. The most commonly applied variable after threat category is the association of the evaluated species with other species. All other things being equal it is appropriate to focus attention on taxa whose protection will benefit a greater number of other species, and although most of the systems used here are relatively simple, there is no reason why the more sophisticated algorithms developed recently (Pressey *et al.* 1993; Forey *et al.* in press) should not be used in this context. This procedure could also incorporate another commonly used characteristic, reflecting the taxonomic or genetic uniqueness of the taxon. Simplistically, this characteristic will favour species that are taxonomically distinct (e.g. a monotypic genus) but various kinds of taxonomic weighting schemes could be used here (Williams and Humphries in press).

A number of variables associated with high extinction risk are also commonly scored, such as small population size, restricted range or number of sites, declines, and specialized habits or habitats. Generally, these contribute to the threat level estimation. Protection status is a variable that should much more obviously be used in setting priorities than in evaluation of threat. At a planning level, it will be important to know to what extent different species at the same level of risk are already receiving protection of some sort, and in many classifications this is further subdivided into considerations of how effective this protection is (e.g., Briggs and Leigh 1988). The same is true of evaluations of the status of the species outside the region. In many cases, species threatened in one particular political region are secure elsewhere, and may simply be at the edge of their range. These species should rank lower than equally threatened forms that are endemic to the region, or that are globally threatened.

Recovery potential is an interesting variable, and again one that might be more

Table 13.4 Characteristics used in systems for evaluating conservation priorities

[1] Taxon	[2] Region	[3] Threat level	[4] Pop. size	[5] Range size/site number	[6] Pop. decline	[7] Protection status	[8] Recovery potential	[9] Association with other species	[10] Social/ economic value	[11] Status out of rgion	[12] Ecological specialization	[13] Taxonomic or genetic value	[14] Poor data	[15] Ref. no.
Tortoises & freshwater turtles	Global	+				+								1
Old World fruit bats	Global	+												2
Canids	Global	+												3
Swallowtail butterflies	Global	+						+						4
Small carnivores	Global	+	+	+	+	+					+		+	5
Black rhino	Africa		+					+				+		6
Freshwater fish	Australia	+					+	+	+			+		7
Birds	Australia	+								+		+		8
Primates	Africa & Asia	+						+				+		9
All	Americas	+						+				+		10
Plants	Australia	+	+	+				+						11
Migratory birds	Neotropics		+	+							+			12
All	New Zealand	+	+	+	+	+			+		+			13
Birds	Americas	+	+	+		+							+	14
Vertebrates	Florida, USA	+	+	+	+	+	+			(+)	+		+	15

Columns [3]–[14]: +, characteristic scored in priority setting system

Column [15]: 1, Stubbs (1989); 2, Mickleburgh *et al.* (1992); 3, Ginsberg and Macdonald (1990); 4, New and Collins (1991); 5, Schreiber *et al.* (1989); 6, Cumming *et al.* (1990); 7, Wager and Jackson (1993); 8, Garnett (1992); 9, Oates (1986); 10, Master (1991); 11, Briggs and Leigh (1988); 12, Reed (1992); 13, Molloy and Davis (1992); 14, Collar *et al.* (1992); 15, Millsap *et al.* (1990)

frequently applied. However, its use poses some demanding analyses and raises some difficult questions to do with species triage. When should species with low recovery potential be given low priority on the basis that scant resources for conservation should be allocated to species that will respond, and should some 'hopeless cases' be written off altogether?

The analysis of species data for setting conservation priorities is an important developing area, and one that has so far received rather little attention. It is, however, one of the most significant applications of threatened species categories.

13.7 Conclusions

The development of more objective and systematic methods for evaluating the threat status of species will have many implications for conservation action. At one level, it will allow a better general evaluation of the extent of the current species extinction spasm, and what the regional and taxonomic biases are. At a practical level, however, it will permit the incorporation of threat levels into the rational planning of conservation actions.

Summary

Threatened species lists are widely consulted as sources of information on the status of species. However, their application to planning for conservation is limited because they have not been developed systematically, and because the criteria used to judge extinction risk are subjective. Recently, new proposals have been made which will increase the broader usefulness of these lists, and components of these proposals are reviewed here.

Apart from indicating the geographical and taxonomic groups containing most threatened species, these lists can provide other kinds of information. Some data from threatened species classifications using quantitative criteria provide a new method for estimating extinction rates in a variety of vertebrate taxa. This analysis suggests that over the next 100 years, the extinction rate could be as high as 15–20% in these groups. These values are comparable to those based up extrapolations from species–area curves.

However, allocating threatened species categories is only a first step towards developing rational systems for setting conservation priorities. These systems will need to consider a quite different set of variables, including those for incorporating species conservation priorities in area-based planning.

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CHAPTER 6

INSULAR ECOLOGY AND CONSERVATION

Bruce A. Wilcox

One of the most profound developments in the application of ecology to biological conservation has been the recognition that virtually all natural habitats or reserves are destined to resemble islands, in that they will eventually become small isolated fragments of formerly much larger continuous natural habitat. Hence, beginning with the seminal monographs by Preston (1962) and MacArthur and Wilson (1967), many ecologists and biogeographers have come to recognize the potential importance of studies of islands and other ecological isolates to conservation.

Typically, the term "isolate" has been used to connote any discrete ecological unit which is insulated from other similar units. In addition to a true island, an isolate can be a stand of trees or other distinct vegetation type, or even a pond or lake. On a smaller scale, an individual tree, shrub or portion thereof can be an "island" from the perspective of very small organisms. For these reasons, "isolate" as it is used here is an ecological community with more or less distinct boundaries. The study of isolate ecosystems, most commonly called "island biogeography," also implies a narrower scope than is actually encompassed. Because of its generality, the term "insular ecology" is preferred here to "island biogeography."

The attractiveness of insular ecology is due, in large part, to the quantitative manageability of discrete ecological entities which have definable physical and biological properties. In particular, because they have definite boundaries, isolates can be described by the amount of area encompassed, proximity to other habitats, as well as taxonomic composition, which is known to be largely related to the former two properties. These properties are those of primary interest to the conservation biologist since they are affected by habitat loss and insularization. Reduction in the total amount of area encompassed by natural habitat and fragmentation into disjunct insular parcels obviously have negative effects on natural ecosystems. So far, insular ecology has only begun to rigorously define the effects and only in a very general way. A much more thorough development of this field is necessary to implement long range conservation strategies. It is hoped this discussion will provide some additional stimuli in this direction. To this end, this chapter begins by reviewing insular ecological theory, then discusses its implications to conservation and considers differences among the major vertebrate taxa in the effects of habitat loss and insularization.

THE SPECIES-AREA RELATION

The study of insular ecology began with the species-area relation (Preston, 1962; MacArthur and Wilson, 1963; 1967). It has become axiomatic in ecology that if isolates or sample quadrats are censused, those of greater area will have more species. This relationship occurs, primarily, because larger areas have more habitat and greater habitat diversity (which includes numerous factors contributing to the stability of individual species populations). The quantitative relationship between species and area can be shown to follow from properties of ecological communities that have practical consequences to conservation.

A typical species-area relation is plotted in Figure 1. Assuming an adequate range of areas are used, species-area plots result in curves which approximate this form. That is, the addition of equal amounts of area contributes fewer species not yet observed. This relation is often expressed by $S = CA^z$, where S and A are the number of species and area, and C and z are dimensionless parameters whose values need to be fitted for each set of species-area data. C is not particularly meaningful here; z is of more interest and its interpretation will occupy much of this discussion.

Since the above expression for the species-area relation is a power function, logarithmic transformation of the variates, species and area, or the axes upon which they are plotted produces a linear relationship (Figure 2). This manipulation of the data allows the values of C and z to be readily calculated by applying linear regression analysis where $\log S = z \log A +$ constant; note that z is now the slope of the line.

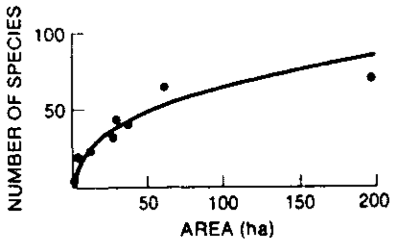

FIGURE 1. An example of a species-area relation: the number of breeding bird species in different size plots of North American deciduous forest. (Data from Preston, 1960)

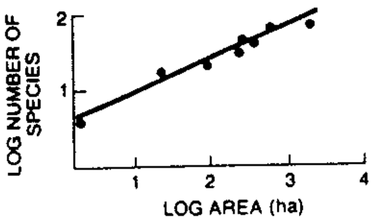

FIGURE 2. The species-area relation in Figure 1 plotted on logarithmic axes.

The power function can adequately describe many, but not all species-area relations (May, 1975; Diamond and Mayr, 1976; Schoener, 1976). When the power function is appropriate, that is when the log-log transformation produces an approximately linear relation, the resulting z-values (slopes) vary depending on whether the observations are isolates or samples—terms used to describe the nature of the entities being sampled (Preston, 1962). Isolate in this sense is analogous to "universe" in that it refers to the total collection of individuals comprising an ecological community. A sample, on the other hand, is some fraction of such a community. Thus a random transect or quadrat is a sample and successively larger samples together eventually become an isolate (a continent could be considered the largest possible isolate). Aside from the form of the species-area curve, a basic empirical rule is that z-values for samples are lower than those for isolates. Samples range between approximately 0.12 and 0.17 while isolates tend to vary between approximately 0.18 and 0.35 (Preston, 1962; MacArthur and Wilson, 1967), although some values may actually be more extreme than this (Diamond and May, 1976). To understand the reasons for this dichotomy it is important to consider the theoretical basis of the species-area relation as it has been recently clarified by May (1975).

The species-area relation and the apparently narrow range of observed z-values are the result of two underlying quantitative properties of ecological communities. The first is the approximately linear relationship between the number of individuals and area. The second is the relationship between the total number of individuals and the number of species, or the distribution of species abundance as it is often called. The form of this distribution is approximately lognormal for intact communities. As emphasized by May, the lognormal distribution is merely a statistical phenomenon of large, heterogeneous communities and probably has no other underlying biological significance. Also, the apparently narrow range encompassing observed z-values results from mathematical properties of the lognormal distribution.

The divergence of z-values for samples from those for isolates can be explained as a result of the failure of samples to represent a complete lognormal ensemble of species (Preston, 1962). That is, relative to an intact community, a sample is characterized by fewer total species and a higher species-individual ratio. In addition, some species are represented by only one to several individuals. The reason for this can be understood as follows. The smallest possible sample consists of one species represented by one individual. At first, successively larger samples will only contain individuals representing new species. This is because even the most abundant species has far fewer individuals than the rest of the species combined. However, as species accumulate, new species will be recorded less frequently and individuals will be added more frequently. As the size of the sample approaches that which encompasses the entire community, only the least abundant species in the community remain unrecorded. The higher species-individuals ratio of smaller samples inflates the species count. This does not occur in smaller isolates since the species-individual ratio should be more equitable regardless of size.

The key feature that differentiates a sample from an isolate is that the latter is a self-contained ecosystem insulated by barriers that tend to restrict normal movement or dispersal of organisms in or out. All of the immediate ecological requirements of a population are contained within an isolate. However, since vagility varies greatly among species, a habitat which produces isolates for some species may act as samples for others.

Isolates Which Behave As Samples

Depending on the degree of habitat insularity or the vagility of organisms, a system may behave either as a sample or an isolate. As an example, in their studies of bird faunas on the Solomon Archipelago, Diamond and Mayr (1976) calculated a z-value of 0.025 for the "highly vagile" species, conforming to that of extreme samples. However, the species with "low vagility" on the very same islands produced a z-value of 0.28, conforming to that of isolates. The same effect can be seen in another example as a result of distance to an archipelago from the source of colonizers. By assigning the archipelagos to "near" and "far" groups (Figure 3) it is seen that the "near" group behaves like samples and the "far" group like isolates. If z-values are calculated for individual archipelagos (within rather than among archipelagos), however, the opposite trend results: more distant archipelagos have lower z-values. This apparent anomaly is actually consistent with the above since distant archipelagos tend to be inhabited by a proportionately greater number of highly vagile species (Diamond and Mayr, 1976) or have a larger "effective" species pool (Schoener, 1976).

In summary, the loss and fragmentation of natural habitat will have different consequences depending on the vagility of organisms and the proximity of isolated fragments. Before discussing these consequences in more detail, let us first consider the most far-reaching theory in insular ecology.

THE EQUILIBRIUM THEORY

In addition to the foregoing explanation of the species-area relation, the autonomous nature of island ecosystems led Preston (1962) and MacArthur and Wilson (1963), independently, to postulate another. First,

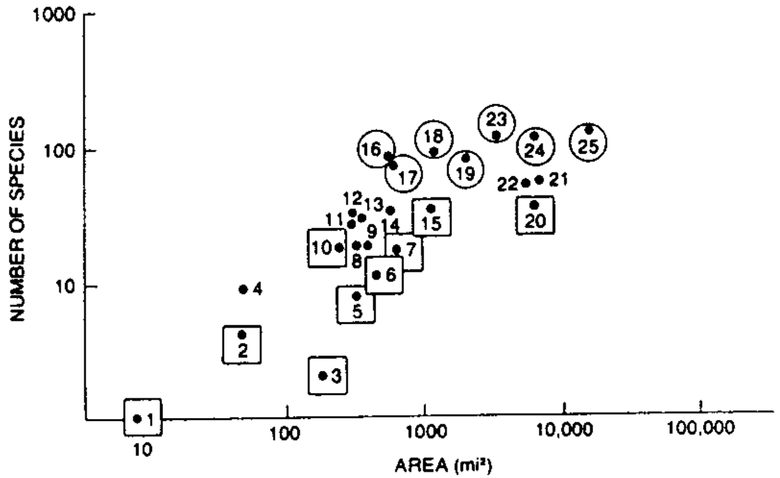

FIGURE 3. The number of land and freshwater bird species on various islands and archipelagos in the Pacific Ocean. "Near" islands (open circles) are those less than 500 miles from a colonization source (New Guinea). "Far" islands (squares) are those greater than 2,000 miles from a colonization source. Dots without circles or squares are islands of intermediate distance. (1) Wake, (2) Henderson, (3) Line, (4) Kusaie, (5) Tua Motu, (6) Marquesas, (7) Society, (8) Ponape, (9) Marianas, (10) Tonga, (11) Carolines, (12) Palau, (13) Santa Cruz, (14) Renell, (15) Samoa, (16) Kei, (17) Louisiade, (18) D'Entrecasteaux, (19) Tanimbar, (20) Hawaii, (21) Fiji, (22) New Hebrides, (23) Buru, (24) Ceram, (25) Solomons. (From MacArthur and Wilson, 1963)

consider that area sets an upper limit on the number of individuals. Second, that the probability of a species becoming extinct will increase with smaller population sizes. This is because small populations are more subject to demographic instability (Chapter 10), inbreeding depression (Chapters 8, 9 and 12) and inclement environmental conditions. Hence, it follows that area acts through extinction to limit the number of species, despite propagules from other islands or the mainland which provide a constant source of new species. This loss of species through extinction can be viewed as being balanced by the gain from colonization.* Thus, the outcome can be expressed as an equilibrium between colonization and extinction.

The equilibrium theory can explain the effects on species number due to variation in area and insularization independently of any assumptions about underlying species abundance distributions. This is demonstrated by the graphical analysis in Figure 4. The curves represent the rates of colonization and extinction for isolates differing in both their distance from a source of colonists and in size, as a function of the number of species present. The curves show that the rate of colonization is highest on "near" isolates and when there are fewer species. This is because the likelihood that a propagule will successfully reach an isolate is greater for shorter distances, and the likelihood that any such propagule will represent a species not yet present is greater when few species exist in an isolate. In a similar manner, the rate of extinction is highest in "small" isolates and when there are more species. This is because extinction probability is greater with less area (smaller population size) and when there are more species to go extinct. At the point of intersection of a colonization and extinction curve, the rates of both processes are equal and the equilibrium number of species, $\hat{S}$, is defined. Figure 4 shows how $\hat{S}$ varies with isolate size and distance; for example, "far" and "small" isolates equilibrate with the least number of species. It also shows (although the curves are purposely drawn in this manner) that the species-area relation can be affected by distance (colonization rates), since the disparity in $\hat{S}$ is greater between the two hypothetical "far" isolates than between the two "near" islands, which would result in a lower z-value for the latter. Figure 3 also illustrates the "distance" effect.

Species Turnover

The most striking feature of the equilibrium theory is its dynamic view of isolates. It proposes that species are constantly being lost and gained, one species being exchanged for another, such that turnover in

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*MacArthur and Wilson (1963, 1967) use "immigration" rather than "colonization" as the addition of new species. Both are to be distinguished from the arrival of new individuals representing species already present.

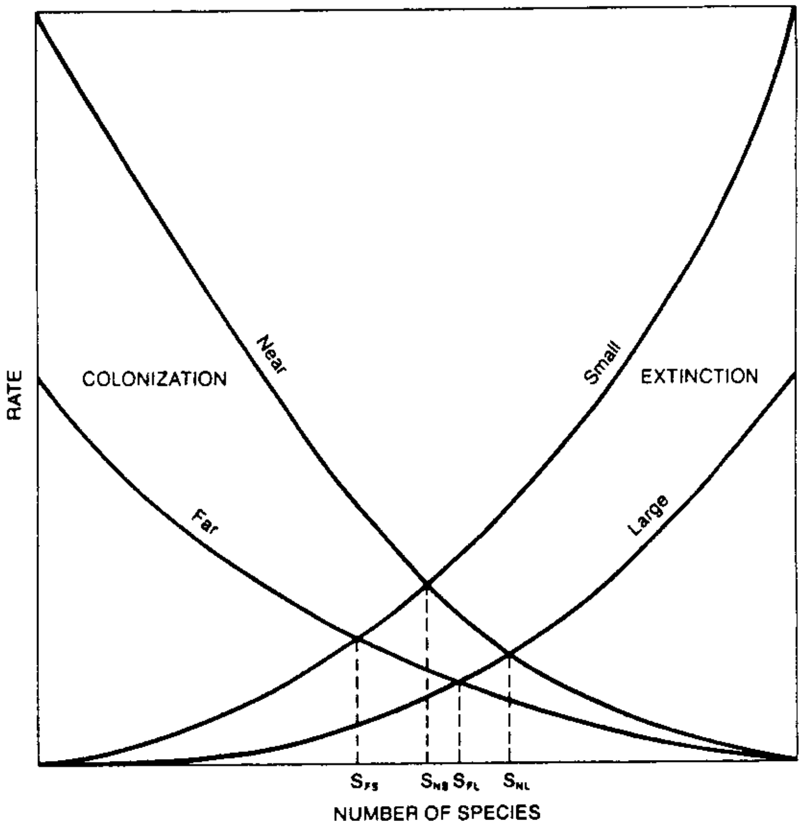

FIGURE 4. Graphic model of the equilibrium theory of island biogeography demonstates the effect of isolation and area on the number of species maintained at equilibrium. The colonization curves represent the rate of addition of new species to an isolate as a function of the number of species already present. This rate should be highest for "near" isolates since proximity to a source of colonists will increase the probability of receiving propagules. The extinction curves represent the rate of extinction as a function of the number of species on an isolate. This rate should be highest on small islands since population sizes are smallest. Concavity of the curves is predicted from heterogeneity in species colonization ability and negative species interactions with increasing species number. For any combination of colonization and extinction curves an equilibrium number of species, $\hat{S}$, is defined at their intersection. (For example, $\hat{S}_{FS}$ is the equilibrium number for an island that is both "far" and "small.")

species composition occurs. Until recently, evidence for turnover, though suggestive, was minimal and based primarily on island bird faunas where census intervals were too infrequent for accurate measurement (Diamond, 1969; 1971; Terborgh and Faaborg, 1973). These early estimates of average annual turnover rates ranged from 0.2 percent to 1.7 percent of the total bird fauna, although total compositional change over a 50 year period was as high as 44.0 percent (Diamond, 1969). Since longer census intervals tend to mask repetitive short-term turnover events, most of these estimates are being modified dramatically as data from short-term censuses become available. Average annual turnover rates for bird faunas are now ranging between 0.9 percent (Jones and Diamond, 1976) and 13.0 percent (Diamond and May, 1976) for islands. Estimates for bird species turnover in mainland habitats are showing similar values. Annual turnover rates of 13.6 percent were calculated for Illinois woods (Whitcomb et al., 1976) and 10.0 percent for a Finnish valley (Järvinen, in press). Where there are a sufficient number of estimates to make comparisons, the turnover rates for smaller islands are highest (Jones and Diamond, 1976). This accords with the prediction of the equilibrium theory for higher per species extinction rates on smaller islands.

These relative turnover rates should be distinguished from absolute turnover rates. According to theory, both vary inversely with area. Distance, however, may not detectably effect relative turnover because the absolute rate and number of species vary in the same direction (Williamson, 1978). Further, absolute turnover may not vary with distance as predicted by the equilibrium theory because of the rescue effect (Brown and Kodric-Brown, 1977).

So far, significant species turnover within the time span of modern biological exploration has not been recorded for vertebrates other than birds. This is not for a lack of data, however, since in theory the time scale of turnover for other groups should be much longer. For birds, at least, the evidence does suggest an important role for colonization-extinction equilibria, particularly in smaller isolates.

NATURE RESERVES

The Sample Effect

Let us now consider insular ecology in terms of nature reserves. Most nature reserves, at the time they are designated as such, are effectively samples in that they represent only a portion of a much larger community. Thus, Serengeti National Park or Manu in the Amazon are samples of African savanna and Amazon rain forest, respectively. They contain fewer species, fewer individuals within each species and more species represented by only several individuals than would similar but larger reserves. A single reserve would have to include virtually the entire Amazon to contain all of its species (albeit a vast system of numerous small reserves could initially accomplish this). On the average though, extrapolating from observed z-values for samples, a reserve will initially exclude roughly 30 percent of the species of a community for each 10-fold decrement in area. For example, a reserve of 10 km^2 will be missing three out of every 10 species found in 100 km^2 of surrounding habitat. We will refer to this initial exclusion as the *sample effect.*

Short-term Insularization Effects

Typically then, a single area designated to preserve any community that does not take in the entire area of the community, will fail to include some of its species. This will occur because of a lack of appropriate habitat or due to species that are rare (Chapter 7) or patchily distributed in spite of habitat (Chapter 4). On the other hand, some species will be included even though their habitat requirements are not met. Under many circumstances, the boundaries of a reserve will not coincide with those of ecological systems, and the requirements for each species cannot be met within its confines. The migration of herds of wildebeest and elephant across the boundaries of large African national parks attest to this fact most dramatically. On any scale, however, the boundaries of a reserve will sever the resources of some species. As long as adjacent habitat remains, these species will be counted among those "protected" within the reserve. However, as the neighboring habitat is removed for agriculture and other forms of land use even more devastating, they will disappear unless intensively managed.

The above implies that dispersal across reserve boundaries as well as the availability of exogenous resources are required for the survival of some species in reserves. Two other conditions can be distinguished where dispersal is responsible for the occurrence of a species. Neighboring habitat may contribute species as non-breeding transients, which are nonetheless recorded as resident species (Simberloff, 1976). Alternatively, neighboring habitat may contribute recruits for minimally stable populations in suboptimal habitats. Since this amounts to preventing extinction in established but marginal populations, it has been dubbed the "rescue effect" (Brown and Kodric-Brown, 1977). The loss of species sustained directly by exogenous resources or dispersal will immediately follow the disappearance of adjacent habitat. These can be considered *short-term insularization effects.*

Long-term Insularization Effects

Colonization-extinction equilibria must, no doubt, play a role in the maintenance of species diversity in samples as well as isolates, although it is much less generally appreciated in habitats without well prescribed boundaries. Here we are simply extending the above notion that individuals dispersing from adjacent or contiguous habitat can shore up a faltering population. It is equally plausible that dispersing individuals may represent new colonists replacing populations which have failed altogether.

As a natural area becomes increasingly insular and colonization sources become increasingly fewer and more distant, colonization rates will, of course, diminish. Since, over the long-term, extinction events are inevitable in even the largest reserves, the reduced colonization rate will result in a net loss of species over time which will continue until the colonization and extinction rates are once again balanced. Of paramount interest, then, is the magnitude and time scale of this putative collapse to a new equilibrium.

Fortunately we need not depend entirely on theoretical conjecture to anticipate *long-term insularization effects*. For example, the frequently cited case of Barro Colorado Island provides a striking illustration (Chapters 2, 3, 4 and 7). Formed around 1914 with the flooding of the Panama Canal, Barro Colorado was designated a reserve soon thereafter. Since that time, however, many of its original species have become extinct, including 48 of its 208 breeding birds. About one-third of the extinctions appear to be the result of a colonization-extinction disequilibrium (Willis, 1974). Similar consequences of habitat fragmentation are documented in Chapter 7.

There is another matter of concern regarding the long-term effects of habitat insularization, particularly in nonflying taxa. These are the shifting climatic zones associated with glacial-interglacial cycles. The Pleistocene Epoch was marked by global temperature oscillations during which fairly extensive latitudinal (and altitudinal) shifts in climatic zones occurred. Normally, as climatic zones shift, so do the associated biotas. Insular regions, however, typically do not span a sufficient latitude to provide refugia for species ill-adapted to a novel climatic regime—and extinction results.

As an example, many species presently adapted to arid southwestern North America probably had the limits of their northernmost ranges pushed several hundred kilometers southward at the peak of the last glacial period. The adjacent islands apparently bear witness to this. Those of higher latitude have fewer nonflying vertebrate species than expected given the present mainland distributions of species. Notably, the arid-adapted reptile species are disproportionately under-represented on the more northern California islands, even on those with apparently suitable habitat (Wilcox, in press).

Barring catastrophic global temperate modification caused by man, the temperature oscillations of the past will be repeated. Therefore, unless long-term climatic shifts are taken into account, another factor can be added to the long-term effects of insularization.

FAUNAL COLLAPSE

Pleistocene Land-Bridge Islands

The combined short- and long-term insularization effects discussed above (even omitting climatic shifts) can potentially result in the eventual loss of most of the vertebrate species in even the largest reserves. This faunal collapse is documented by studies of land-bridge islands, whose mainland connections were severed hy the rising sea level around the close of the Pleistocene (Diamond, 1972*b*, 1973; Terborgh, 1974; Chapter 7). The last episode of rising sea level began around 18,000 years ago and ended some 6,500 years ago (Bloom, 1971). During this time the sea rose over 100 meters, inundating lowlands and leaving isolated fragments of such formerly vast continental regions as the Sunda Shelf in southern Asia (Figure 5). In this example, based on the present ocean depths of this region and the rate of sea level rise (Wilcox, 1978), the islands of Borneo, Sumatra and Java, and their fringing archipelagos were probably completely isolated by 10,000 years ago.

By estimating the number of species lost on these and other islands with a similar history, we can gain at least some idea of the fate of our reserves which are presently undergoing the insularization process. As shown in the following example, this is typically done by assuming that each island, before falling to its current level, originally had the same number of species that a mainland sample of the same size has at present.

The faunal composition and distribution of species on the Sunda Shelf prior to inundation cannot be known with certainty, though present faunal resemblance and fossil evidence strongly argues for its similarity to the Malay Peninsula. For example, the islands of Borneo, Sumatra and Java combined have virtually a complete Malaysian mainland mammal fauna though each is deficient in a number of species (Darlington, 1957; Terborgh, 1975). That is, a species missing on one island is often present on another (see Table I in Chapter 4). Evidence that these islands supported larger faunas at the close of the Pleistocene is also provided by fossil remains (Terborgh, 1975). Figure 6 shows the current level of diver-

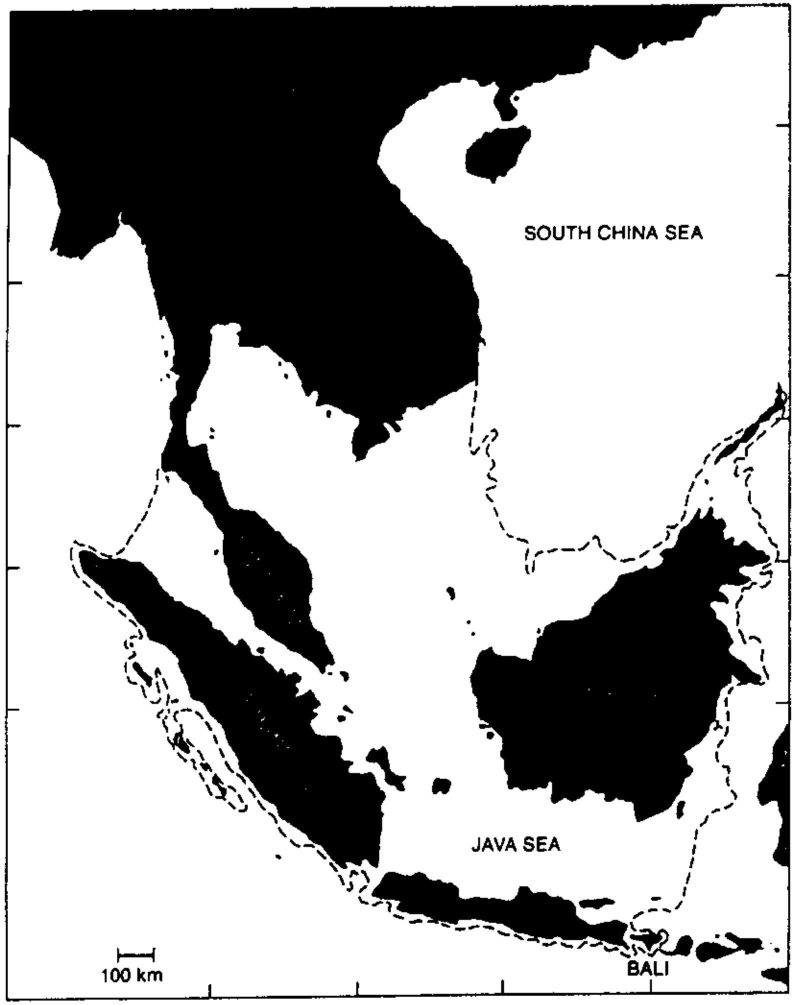

FIGURE 5. The Sunda Islands and the extent of the land surface of the Sunda Shelf during the last glacial period. The dashed line is the present 100 fathom contour and approximates the coastline of 18,000 years ago.

gence between the species area relation for the land mammal faunas of the Malaysian mainland and the Sunda Islands. Although the mainland curve is tenuously based on only two points, its z-value of 0.17 and that of the islands, 0.30, agree with theory and previous findings. Thus, the presumption is that island faunas all began near the upper curve and have since dropped to their present positions. The estimated species loss for each island can thus be calculated as the difference between the projected initial number of species, S_o, and the present number of species, S_p. Table I shows the results of such calculations for the Greater Sunda Islands.

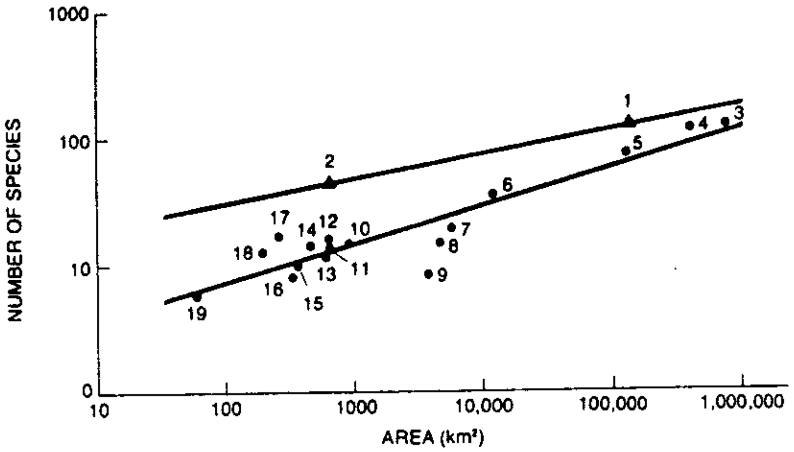

FIGURE 6. Species-area relations for the land mammals (excluding bats) of the Malaysian mainland (upper curve) and Sunda Islands (lower curve). The upper curve ($S = 15.4\ A^{.17}$) is presumed to approximate the species-area relation of the Sunda Shelf prior to fragmentation by the rising sea level at the close of the Pleistocene. The lower curve ($S = 1.8A^{.30}$ by linear regression) differs as a result of fragmentation and collapse of isolate faunas. (1) Malay Peninsula, (2) Krau Game Reserve, Pehang, Western Malaysia, (3) Borneo, (4) Sumatra, (5) Java, (6) Banka, (7) Bali, (8) Billiton, (9) Siberut, (10) S. Pagi, (11) N. Pagi, (12) Sipora, (13) Singapore, (14) Tanabala, (15) Tanamasa, (16) Pini, (17) Penang, (18) Tuangku, (19) Bangkaru. (Data from Medway and Wells, 1971; Chasen, 1940)

The species losses for these islands, the majority of which are species of large body size or high trophic level, are quite remarkable, especially because most of the islands are an order of magnitude larger than the largest existing nature reserves. Nevertheless, these figures alone probably provide only a crude view of the collapse process. If we could have directly monitored the loss of species from the time of initial isolation, we would, according to theory, observe that the rate of loss would have been highest at first, decreasing exponentially to approach asymptotically a new equilibrium.

The prevailing evidence suggests that the loss of species is approximated by an exponential function, such as $-kS^n$, where k is the relaxation

TABLE I. Estimated number of extinctions of land mammal species (excluding bats) since the formation of the Greater Sunda Islands.

Island	Area (km^2)	Initial number of species* (S_o)	Present number of species (S_p)	Extinctions** Number ($S-S_p$)	Percent $\left(\frac{S_o-S_p}{S_o}\right)$
Borneo	751,709	153	123	30	20
Sumatra	425,485	139	117	22	16
Java	126,806	113	74	39	35
Bali	5,443	66	19	47	71

* Initial number of species, S_0, are estimated from the species-area relation of mainland Malaysia.

** Total species loss is assumed to closely approximate or even underestimate extinctions. See text for more discussion.

parameter and n is an integer that might reasonably take on values from one to four, although two or three seems most probable on the basis of very limited data (Soulé et al., 1979). By using models of this general form, relaxation parameters or comparable measures of the magnitude of species loss with time have been estimated for a number of geographically and taxonomically divergent faunas (Diamond, 1972*b*; 1973; Terborgh, 1974*a*; 1974*b*; 1975; Case, 1975; Soulé et al., 1979). All of these findings show a tendency for smaller islands to have higher extinction rates. Also, the rate of species loss, as a proportion of the initial number of species and as a function of area and time, vary consistently in the manner predicted from intrinsic taxonomic differences. This will be discussed in more detail below.

Collapsing Reserves

The apparent universality in the general properties of the collapse process should allow extrapolation of these findings to nature reserves. One such attempt (Soulé et al., 1979) has been made using the large mammal species of the Sunda Islands as a model to predict the fate of similar species in East African reserves. Application of collapse theory to these reserves is particularly appropriate as insularization is nearly complete. In this study, relaxation parameters were calculated for several Sunda Island faunas to determine their relationship to island size. The size specific values were then applied to 19 East African national parks and game reserves to estimate species loss as a function of area and time. The results predict that the average reserve, which presently has 48 large mammal species and an area of about 4,000 km^2, will lose 11 percent of these in 50 years, 44 percent in 500 years and 77 percent in 5,000 years. Figure 7 shows the probable range of species loss trajectories for three of the national parks. This illustrates that as isolates, even the largest reserves in the world may be incapable of preserving most of their large mammal species without intensive management.

Extinction estimates have been calculated for other taxa in reserves using a similar approach. From his studies of bird faunas on tropical land-bridge islands Diamond (1972) predicted a loss of 51 percent for a hypothetical reserve of 7,800 km^2 in 10,000 years. This is smaller than predicted losses for the large mammals and probably results from smaller body size (allowing higher population densities) and higher colonization rates of birds, since collapse has both a colonization as well as an extinction component.

The theoretically predicted shapes of the colonization and extinction curves (Figure 4) as well as empirical evidence for their shapes approximated from actual data (Gilpin and Diamond, 1976) suggest a rather insignificant role for colonization (even where dispersal is possible) until species number nears equilibrium (Wilcox, 1978). For this reason, the net

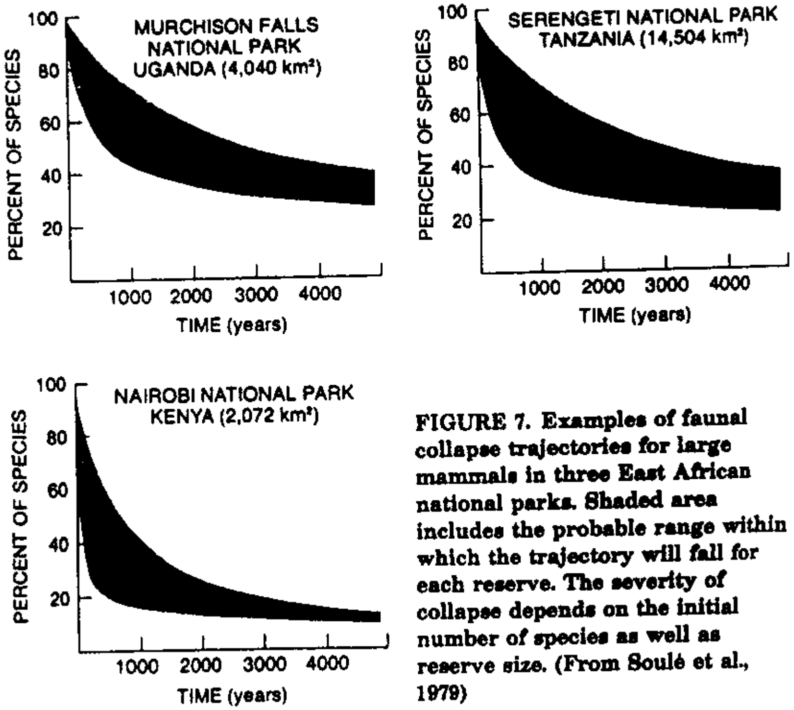

FIGURE 7. Examples of faunal collapse trajectories for large mammals in three East African national parks. Shaded area includes the probable range within which the trajectory will fall for each reserve. The severity of collapse depends on the initial number of species as well as reserve size. (From Soulé et al., 1979)

loss rates, particularly for the mammals shown above, approximate extinction rates. This theoretical detail may be largely irrelevant to collapsing reserves, however, since inter-reserve dispersal of many, if not most, vertebrates will be wholly curtailed. This will certainly be the case for the large mammals of East African reserves, unless heroic measures are taken.

TAXON-SPECIFIC CONSIDERATIONS

A misleading, but necessary, oversimplification of the MacArthur-Wilson equilibrium theory is the assumption of homogeneity in colonization and extinction rates among different species. This problem is partly ameliorated by confining biogeographical analyses to within taxa. However, even within a taxon such as birds, species exhibit a wide range of dispersal ability and extinction vulnerability (Diamond, 1972*b*; 1976; Jones and Diamond, 1976; Chapter 7).

Some generalizations can be made, however, that should bear on conservation decisions. Among the major vertebrate taxa there are two reasons why colonization and extinction rates are expected to differ. First, dispersal is greatly enhanced in the flying taxa (most birds and bats) over nonflying taxa (most mammals, reptiles and amphibians). It should be noted, however, that adaptations for passive dispersal as well as behavioral differences (willingness to cross inhospitable terrain) may vary independently of flight. Second, the lower metabolic rates of ectotherms (reptiles and amphibians) allows higher population densities, thus less vulnerability to extinction than in endotherms (mammals and birds). Among the endotherms, however, the generally larger body size of mammals (resulting in higher absolute metabolic demands and, thus, lower densities), should cause them to be more vulnerable to extinction than birds.

There are two major consequences of these generalizations. First, mammal faunas should collapse more rapidly than bird faunas, while reptile and amphibian faunas should be least prone to rapid collapse. In support of this, in addition to the evidence already cited above from the studies of Diamond (1972*b*) and Soulé et al. (1979), Case (1975) found that area dependent "relaxation times" were greater for lizard faunas than those calculated for bird and mammal faunas (Diamond, 1972*b*). Additional evidence was obtained by comparing relaxation parameters of these same temperate lizard faunas to those of tropical bird faunas on land-bridge islands (Wilcox, unpublished). The results shown in Figure 8 demonstrate an interesting concordance between the change in collapse rate with area, but an almost two orders of magnitude difference in the actual area associated with a given rate of collapse. This follows from the expectation that extinction rates are inversely proportional to isolate size in general, but that ectotherms have lower extinction rates per number of species on an isolate. More convincing, however, is a comparison of different faunas on the same islands in the Gulf of California (Wilcox, in preparation). Reptile faunas of the land-bridge islands appear extremely supersaturated compared to their deep-water counterparts (Soulé and Sloan, 1966; Case, 1975; Wilcox, 1978), while the mammal faunas also appear supersaturated, but less so. Finally, the bird faunas show no evidence of supersaturation, presumably having already collapsed to their equilibria in the 10,000 or so years since the islands were formed (M. Cody, personal communication).

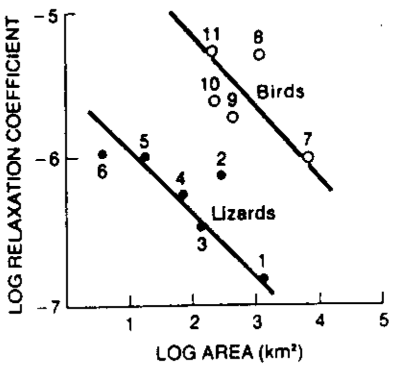

FIGURE 8. **Comparison of relaxation parameters as a function of island area for lizard and bird faunas. The curves demonstrate the dependence of extinction rates on area, also the relatively lower collapse rates for lizards. Relaxation parameters are calculated as in Terborgh (1974*a*), except isolation times that are estimated as in Wilcox (1978). Lizard faunas: (1) Tiburon, (2) Cedros, (3) San José, (4) Espiritu Santo, (5) San Marcos, (6) Coronados (data from Soulé and Sloan, 1966). Bird faunas: (7) Trinidad, (8) Margarita, (9) Coiba, (10) Tobago, (11) Rey (data from Terborgh, 1974*a*).**

A second major consequence of heterogeneity in colonization and extinction rates among the vertebrate taxa are differences in the relative number of species maintained at equilibrium. Because of a combination of low colonization and high extinction rates, nonflying mammals will be depauperate in relation to other vertebrates in isolates. Indeed, the absence or small numbers of mammal species on most islands without a history of recent land-bridge connections is well known. The great dispersal advantage held by the birds and bats, however, may more than compensate for their high extinction rates in comparison with the reptiles and amphibians, particularly where dispersal barriers are barely surmountable by non-flying organisms. At equilibrium, therefore, bird and bat faunas will be relatively richer than those of reptiles and amphibians in extreme isolates.

These predicted differences in the relative number of species maintained at equilibrium are reflected in species-area relations. For example, it was mentioned earlier that the more highly vagile species among birds produced lower *z*-values. A similar effect is seen by comparing the flying and nonflying vertebrate taxa of the West Indies. Figure 9 shows that the nonflying taxa are more severely affected by decreased area, that is, they have higher *z*-values. The birds and bats share the lowest *z*-value of 0.24, while the highest *z*-value, 0.48 for the nonflying mammals, follows from their double disadvantage of both poorer dispersal along with lower population densities. Brown (1971) also found a high *z*-value (0.43) for nonflying mammal faunas which he suggested resulted from a nonequilibrium condition where extinction but no colonization had occurred since the isolates formed. The reptiles and amphibians of the West Indies also produce a *z*-value (0.38) which is higher than expected for most isolates. This is more likely a consequence of a high rate of *in situ* speciation events on the larger islands, particularly Cuba and Hispaniola.

In general, nonflying mammals, because of poor dispersal, high metabolic rates and large body size are the most vulnerable to extinction due to habitat loss and insularization relative to other vertebrate taxa. Since extinction is the major component of species loss throughout most of the collapse process, reptiles and amphibians will, in time, fare best among the vertebrates—particularly under conditions of extreme habitat loss. Only those taxa that are capable dispersers, such as some birds and bats, will persist indefinitely without careful monitoring and intense management.

FUTURE RESEARCH AND APPLICATION

Applied insular ecology is still very much in its infancy. Although nearly two decades have past since Preston (1962) alluded to the conservation implications of island theory, its potential for application has only recently become generally known—and even then only among limited quarters. Research in this area, with few exceptions, has been basic, not problem-oriented or applied. However, future research must address specific practical problems if insular ecology is to contribute further to conservation.

From a practical viewpoint, there are two primary application approaches of insular ecology. The first involves insular dynamics within a reserve, or "patch dynamics." In a timely and provocative article, Pickett and Thompson (1978) have focused attention on the conservation implications of colonization-extinction dynamics internal to an isolate. They point out that since few external colonization sources are likely to exist for any future reserves, conservation biologists should consider colonization and extinction of species in habitat patches within reserves. With knowledge of species-specific colonization and extinction rates, in combination with information on the spatial and temporal distribution of habitat patches, "minimum dynamic areas" could be defined. This is the size of a reserve necessary to insure the occurrence of a sufficient number of habitat patches occupied by a species, such that the probability of simultaneous extinction of the species in all patches is diminishingly small.

This unquestionably should be the approach used where minimum dynamic areas will be of realistic dimensions, given inevitable conflicting land use options. For example, communities of small vertebrates or ar-

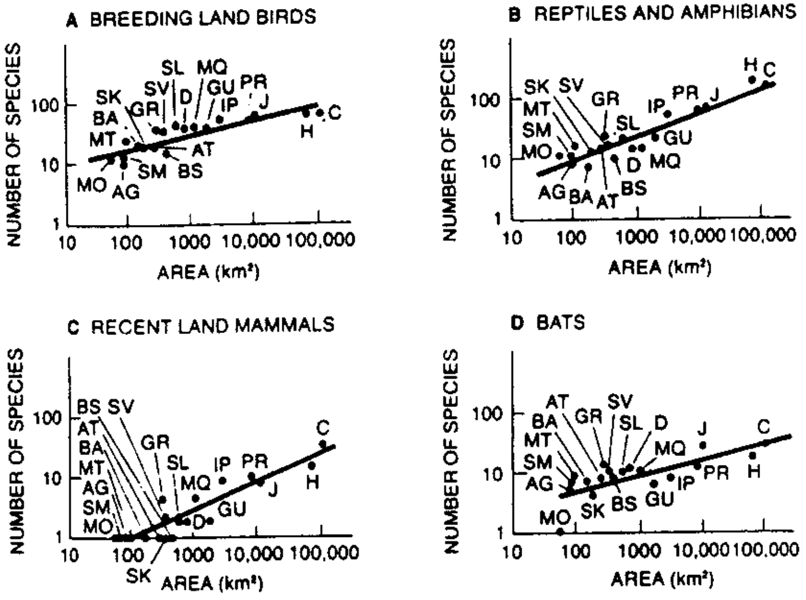

FIGURE 9. Species-area relations of four major vertebrate taxa on the same West Indian islands. The relative differences in the observed *z*-values follow from taxon-specific colonization and extinction rates. They suggest that consequences of habitat loss and insularization depend on metabolic rate, body size and dispersal ability. Species-area curves fitted by linear regression are as follows: (a) $S = 6.1A^{.24}$, (b) $S = 1.6A^{.38}$, (c) $S = 0.1A^{.48}$, (d) $S = 1.6A^{.24}$. (C) Cuba, (H) Hispaniola, (J) Jamaica, (PR) Puerto Rico, (IP) Isle of Pines, (GU) Guadeloupe, (MQ) Martinique, (D) Dominica, (SL) St. Lucia, (SV) St. Vincent, (BS) Barbados, (GR) Grenada, (AT) Antigua, (SK) St. Kitts, (BA) Barbuda, (MT) Montserrat, (AG) Anguilla, (SM) St. Martin, (MO) Mona. Recent Land Mammals include living and recently extinct native mammals. Many of the present mammal faunas include exotic species which have replaced native species. (Bird data from Bond, 1956, 1961 as compiled in Lack, 1976; reptile and amphibian data from Swartz and Thomas, 1975; mammal data from Varona, 1964)

thropods adapted to patches of successional habitat would probably require minimum areas no larger than moderate sized national parks. For many species, however, particularly the larger vertebrates, minimum dynamic areas will be considered excessive given the myopic economic demands of most societies. Under these circumstances, the second approach will be required. Multiple reserves or fragments of undisturbed habitat will have to be manipulated as "artificial archipelagos" in order to minimize the probability of simultaneous extinction in each isolate. The second approach will, of course, not be successful in preserving those species incapable of inter-isolate dispersal, or those that cannot be transported successfully or introduced by man. It should be considered a last resort.

Detailed autecological studies are required to determine minimum dynamic areas and optimal design of artificial archipelagos. Here, biogeography will be most useful. The geographical distribution of a species reveals much about its ecological requirements. Diamond's (1976*a*) "incidence functions" are an efficient biogeographic method of defining the survival requirements of species among isolates. The studies of Moore and Hooper (1975), Forman et al. (1976) and those described by Terborgh (Chapter 7) on bird species distributions among disjunct habitat fragments should serve as models for determining preservation requirements of specific insular communities.

Non-avian species have received far too little attention in insular ecology. Perhaps the ease of study and exuberance of ornithologists have contributed to a disproportionate share of attention being focused on birds. Nevertheless, studies of a wider range of taxa are needed, both to test current theory and provide a basis for intelligent conservation decisions.

Of all the biological approaches to conservation, insular ecology is probably of the most immediate importance. The extent to which its lessons are heeded and its successful applications developed in the next few years will play an important role in determining the ultimate fate of this planet's biological diversity.

SUMMARY

The relevance of insular ecology to conservation stems from the similarities between natural isolates, such as islands, and the disjunct fragments of natural habitat resulting from expanding human exploitation of the earth's land surface. Habitat fragmentation can be dissected into two components: habitat loss and insularization. Each contributes to a reduction in the number of species supported, although different mechanisms are involved.

Studies suggest that habitat loss contributes in two ways: first, by excluding a portion of a fauna, particularly the rare or patchily distributed species; second, by increasing the extinction rate of the remaining species as a result of lower population sizes. Habitat insularization also contributes in two ways: first, by extinguishing species "protected" within an area through the removal of required resources outside the area; second, by reducing accessibility for, and sources of, colonists necessary to offset extinction events.

If a reserve were observed from its inception, three classes of these effects could be discriminated on the basis of time-scale. First, the decision to set aside any single area for preservation immediately excludes a number of species characteristic of the greater region as a whole. The proportion excluded is described by the species-area relation for samples. This *sample effect* amounts to the exclusion of about 30 percent of the regional fauna for each 10-fold decrement in area. The sample effect can be minimized by a system of strategically placed smaller reserves. However, other consequences must be heeded.

Short-term insularization effects will closely track encroachment of habitat contiguous to reserves resulting in the loss of self-sufficiency for species dependent on resources outside a reserve. Such species that might be mistakenly thought to be protected by their mere presence in a reserve, include non-breeding transients and populations that are breeding but marginally sustained by dispersal (rescue effect).

Long-term insularization effects describe the consequences of colonization-extinction disequilibria and climatic changes. Extinction is inevitable for any population, though the probability rises sharply with decreasing population size, or reserve area. The decreased colonization rate imposed by artifical dispersal barriers and fewer, more distant colonization sources will add to the collapse towards a new equilibrium with fewer species. Shifting climatic zones associated with the glacial-interglacial cycle will contribute further to extinctions unless reserves are large enough to include refugia.

Using land-bridge islands as models of faunal collapse suggests that large mammal faunas even in reserves of several thousand km^2 will begin to lose a very measurable number of species almost immediately. These losses will amount to as much as half of the initial reserve census of species in several hundred years and three-quarters in several thousand years. Even these estimates may be optimistic since they assume that the reserves will be left to themselves and not subject to poaching and other types of incursion or encroachment.

The rate of faunal collapse and the eventual number of species maintained at equilibrium in a reserve will depend not only on size and insularity of reserves, but also on taxonomic differences. Among the vertebrates, for example, mammals (excluding bats) have combined poor dispersal and high metabolic requirements (lower population densities on average). As a result, they are most vulnerable to extinction, manifesting the highest rates of faunal collapse and fewest numbers of species at equilibrium. Birds and bats, however, because of lower metabolic requirements and superior dispersal ability, are slightly less vulnerable to extinction, manifesting lower collapse rates and greater numbers of species at equilibrium. Reptiles and amphibians generally have much lower metabolic requirements than birds and mammals. As a result, they are, by far, the least vulnerable to extinction, and manifest the lowest collapse rates. In some natural isolates, reptiles and amphibians may maintain equilibrium faunas with nearly as many species as birds or bats. Under the conditions of extreme insularity often produced when humans impose dispersal barriers, however, nonflying vertebrate faunas in general will ultimately be thoroughly extirpated (barring human intervention).

Two primary approaches in insular ecology are suggested for future research and application. First, "minimum dynamic areas" should be defined, whose colonization-extinction equilibria are maintained internally. Second, since such area requirements will be excessive for many vertebrate communities, multiple disjunct reserves should be set aside and maintained as artificial archipelagos. For both approaches more autecological studies in insular systems are needed, especially of non-avian species.

The manageability of future reserves as well as the ultimate fate of biological diversity will depend to no small degree on the extent to which insular ecology is successfully applied in the next few years.

SUGGESTED READINGS

Diamond, J.M., 1975, Assembly of species communities, in *Ecology and Evolution of Communities,* M.L. Cody and J.M. Diamond (eds.), Harvard University Press, Cambridge, Massachusetts, pp. 342–444. A unique and important study of island bird faunas of the Pacific that aims to elucidate the determinants of species' distributions and composition. Introduces "incidence functions" and is the first comprehensive theoretical treatment of an area which requires a thorough understanding for the formulation of sound conservation strategies, particularly concerning natural or artificial archipelagos.

Hooper, M.D., 1971, The size and surroundings of nature reserves, in *The Scientific Management of Animal and Plant Communities for Conservation,* E. Duffey and A.S. Watt (eds.), Blackwell Scientific Publications Ltd., London, pp. 555–561. An excellent, not excessively theoretical, discussion of some of the topics central to this chapter.

MacArthur, R.H. and E.O. Wilson, 1967, *The Theory of Island Biogeography,* Princeton University Press, Princeton, New Jersey. A pioneering study of the ecology and evolution of island communities that provides the theoretical framework for much of insular ecology.

May, R.M., 1975, Patterns of species abundance and diversity, in *Ecology and Evolution of Communities,* M.L. Cody and J.M. Diamond (eds.), Harvard University Press, Cambridge, Massachusetts, pp. 81–120. Discusses the theoretical basis of species abundance distributions and implications to the species-area relationship.

Moore, N.W. and M.D. Hooper, 1975, On the number of bird species in British woods, *Biol. Conserv.,* 8, 239–250. A good example of a biogeographic study of manmade isolates, with conservation implications.

Simberloff, D.S. and L.G. Abele, 1975, Island biogeography theory and conservation practice, *Science,* 191, 285–286. This paper and a series of rebuttals entitled "Island biogeography and conservation: strategy and limitations" (J.M. Diamond, *Science,* 193, 1027–1029; J.W. Terborgh, *Science,* 193, 1029–1030; R.F. Whitcomb et al., *Science,* 193, 1030–1032;-D.S. Simberloff and L.G. Abele, *Science,* 193, 1032) should be read together.

Soulé, M.E., B.A. Wilcox and C. Holtby, 1979, Benign neglect: a model of faunal collapse in the game reserves of East Africa, *Biol. Conserv.,* 15, 259–272. Describes, hypothetically, the fate of large mammal species where there is a lack of conservation strategy which considers insular theory.

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MODERN BIOGEOGRAPHIC THEORY: ARE THERE ANY LESSONS FOR NATURE RESERVE DESIGN?

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ABSTRACT

Several geometric design principles have been proposed by Diamond (1975) and Wilson & Willis (1975) for nature reserves, aimed at maximising species richness. Theoretical and empirical evidence is presented here both in favour of, and against, these designs. We conclude that they should be used with caution, if at all, since they are based on the unsubstantiated equilibrium theory of island biogeography and the equivocal species–area relationship.

INTRODUCTION

In recent years, species–area relations and the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) have been used to formulate a series of geometric design principles to maximise the number of species conserved in nature reserves (Diamond, 1975; Wilson & Willis, 1975; Diamond & May, 1976). These design strategies have received some criticism (e.g. Abele & Connor, 1979), which is especially valid where they have been quoted without any of the accompanying assumptions and restrictions, as in the recently published World Conservation Strategy (IUCN, 1980). In this paper we have tried to draw together evidence from recent reviews and theoretical papers, and to consider some implications from data on limestone pavements, both in favour of, and against, the use of these design principles.

Species–area relations and island biogeography

The species–area relationship is a formalisation of the observation that large areas of a given habitat usually contain more species than small areas of the same

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habitat. The number of species increases monotonically with area. Although there has been some debate over the best statistical model of this relationship (begun in 1921 and 1922 by Arrhenius and Gleason respectively), a power function model of the form

$$S = cA^z \qquad \text{or} \qquad \log S = \log c + z \log A,$$

where S is the number of species, A is area and c and z are fitted constants, has been shown to be the best simple model in most cases for the data available (e.g. Dony, undated; Connor & McCoy, 1979).

Preston (1962) was a strong advocate of the power function model and his support was based on the assumption of a dynamic equilibrium of species exchange between isolates. This idea was developed by MacArthur & Wilson (1967) in their equilibrium theory of island biogeography, which states that the number of species on islands of similar habitat in the same latitudes depends on the size and isolation of the islands, and is a balance between the rate of immigration and the rate of extinction. The immigration rate is supposed to decrease with increasing isolation and the extinction rate to increase with decreasing area. Thus, more distant and smaller islands are predicted to have a lower equilibrium number of species. The dynamic processes of immigration and extinction are proposed to lead to a turnover of species so that although the number of species should remain constant, the species composition should change over time.

One explanation of the species–area relationship is that large areas have larger populations so that species have less chance of becoming locally extinct, with the result that more species can exist together at any one time on a large area than on a small one. This is a prediction based on the equilibrium theory. Earlier explanations generally attributed the relation to increased environmental heterogeneity at larger areas. Both may well play a role in the observed species–area relations, but apportioning the roles is extremely difficult.

GENERAL CRITICISMS AND ASSUMPTIONS

Before discussing particular design strategies, there are four general points regarding assumptions underlying the designs which are worthy of discussion.

First, conservation implications drawn from species–area relations and the equilibrium theory of island biogeography are only concerned with the maximisation of species richness. Although this is clearly stated by both Diamond (1975) and Wilson & Willis (1975), it may not always be clear, especially when the so called 'optimal designs' are quoted or displayed out of the context of the discussion where they originally appeared: this has happened recently in the World Conservation Strategy (IUCN, 1980), where the designs appear in a chapter entitled 'Priority Requirements: genetic diversity'. The authors here implicitly equate genetic diversity and

species richness. These are related but different. More species certainly have a wider variety of genes than few species, but conserving only the most species-rich sites may mean the neglect of many species. There can be a variety of conservation aims, and these may not necessarily complement one another (Margules & Usher, 1981). If species richness is favoured and others such as rarity and representativeness given less importance, overall, many species and habitats may be lost and attainable maximum genetic diversity consequently lowered. In a study of the use of criteria for conservation evaluation in North Yorkshire, England, Margules (1981) found that criteria such as representativeness, naturalness, threat of human interference and rarity were used initially and diversity (taken as equivalent to species richness) was only important when comparing similar sites: there is little point in using species richness to compare the conservation value of, say, a calcareous grassland and an acid moorland. Even in what might be widely regarded as a uniform or homogeneous habitat, the relatively species-poor heather moorlands of North East Yorkshire, Margules (1979) identified 10 classes of vegetation community which had from 13 species in the most species-poor class, to 37 in the most species-rich.

This leads to our second point, the concept of habitat heterogeneity. Diamond (1975) states that he is concerned only with reserves in a homogeneous habitat; but at what level does a habitat become homogeneous? Biogeographic descriptions such as the land classifications from Australia published by CSIRO (Austin & Cocks, 1978; Laut *et al.*, 1978) describe successive levels of heterogeneity. At the lowest level, each site is unique. Therefore, when these are assigned on the basis of qualitative similarities into classes, a system of typological units is created (Isachenko, 1973) which have levels of heterogeneity. There is no such thing as a truly homogeneous habitat. In conservation practice habitats have mostly been represented by vegetation classes. It is now widely, but not universally, agreed that vegetation forms continua (Whittaker, 1967) and that classification is only a convenience for the purpose of description (Austin, 1978). Similar sites do form groups or classes but the degree of heterogeneity needs to be quantified to examine the relevance of ideas based on a concept of homogeneity.

Third, any conservation implications based on the equilibrium theory of island biogeography are doubtful because the theory itself is unsubstantiated. MacArthur & Wilson (1967), in the preface to their book, admit that general theories require a deal of faith and they did '. . . not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation.' In a recent comprehensive review of the empirical evidence for the theory, Gilbert (1980) severely criticises many studies purporting to demonstrate its truth. He cites 22 studies whose authors, he says, '. . . evidently believe that a demonstration of the species–area relationship proves the equilibrium theory to be true' (p. 214). He considers, however, that to demonstrate the applicability of the model in any given situation, it would be necessary to show that a close relationship exists between insular areas and the number of species they contain, that the number of species remains constant over time, and that an appreciable fraction of the species complement changes over time. Gilbert was unable to find any studies which fully satisfied these conditions. Williamson (1981) has no doubt that the major tenet of the theory—that there is a turnover producing an equilibrium between immigration and extinction—is correct, but points out that those involved seem always to be casual species. We have no knowledge of the time scales required, or of the population sizes necessary, for species to join communities. Each of these sources should be consulted for more details, but the clear message is that the equilibrium theory of island biogeography is insufficiently validated to support its application to conservation. Some specific points arising from this will be made in the discussion of the designs themselves.

Fourth, even if we were to accept the equilibrium theory as true, there is at least one major difference between real islands and habitat islands. Real islands are surrounded by an environment which is totally inhospitable to terrestrial species. In contrast, not only can many species found on most habitat islands (or patches) survive in the surrounding environment, but some may have major populations in neighbouring habitat types. For example, there are 311 species of higher plants found on limestone pavements in England, Scotland and Wales (Ward & Evans, 1975). Only the fern *Dryopteris villarii* could be said to be largely dependent on the pavement habitat and even so, 20% of its British population is found elsewhere (Gilbert, 1970). *Thelypteris robertiana*, *Ribes spicatum*, and *Actaea spicata* are other rare species often found on limestone pavements, but they are also woodland species. Any conservation strategy for these species based on a network of island reserves would need to include woodlands as well as limestone pavements.

THE SPECIFIC DESIGN STRATEGIES

The application of the equilibrium theory of island biogeography to conservation practice has mainly involved the possible consequences of the creation of so-called habitat 'islands' by a reduction in the area of habitat concerned and increased isolation of the remaining 'islands'. Assuming the equilibrium theory, a consequence of this fragmentation is supersaturation, i.e. a newly isolated fragment will hold more species at the time of isolation than is possible at equilibrium. Relaxation will ensue, with the rate of local extinction exceeding the rate of immigration, towards an equilibrium number of species. Conservation implications drawn from this theory and the species–area relation are primarily concerned with maximising the number of species contained in a system of reserves at equilibrium, and minimising local extinction rates from newly isolated reserves.

The design strategies for which the equilibrium theory and species–area relations have been considered relevant by other authors are threefold: (1) the benefits of single large reserves as opposed to a group of small reserves; (2) the best spatial arrangement of a system of reserves; and (3) the optimal shape of reserves. Figure 1 (after Diamond, 1975) represents, pictorially, the general principles put forward by Diamond (1975), Wilson & Willis (1975) and Diamond & May (1976). In each of the six cases, labelled A to F, species extinction rates are supposed to be lower, and the equilibrium number of species higher, for the reserve design on the left than for the one on the right. What follows is a discussion of the merits of each design. The general criticisms made above form a framework for this discussion.

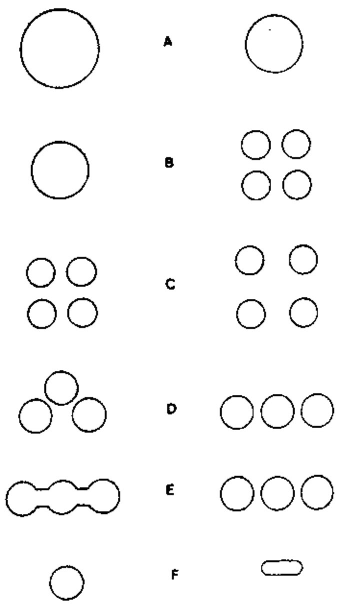

Fig. 1. Geometric design strategies, based on the equilibrium theory of island biogeography and the species–area relationship, proposed for the design of nature reserves, by Diamond (1975). For each of the six designs, A to F, extinction rates are said to be lower for the design on the left than that on the right, and the design on the left is said to hold more species at equilibrium than the design on the right.

Design A

There is no doubt that in most cases, a large area will encompass more species than a small one. In general, there can be no argument with this strategy: It is desirable to dedicate the largest possible land area to conservation since this provides some degree of protection for the future. However, where limited financial resources could more usefully be spent on management, education or some conservation policy other than the acquisition of reserves, there may be advantages in not protecting as large an area as possible.

Design B

The suggestion here is that one large reserve will conserve more species than a group of smaller reserves of the same total area, and will have lower overall extinction rates. Both sources of argument are used to justify this design, namely species–area relations and the equilibrium theory of island biogeography.

Abele & Connor (1979) consider this design, as a proposition to maximise species richness, to be predominantly based on the species–area relationship and as '. . . nothing more than an attempt to translate the long known monotonically increasing relationship between species number and area into a design strategy' (p. 89). They reiterate the point first made by Simberloff & Abele (1976) that the species–area relationship is actually ambiguous with regard to this. The difference between the number of species encompassed by a single large reserve and the number encompassed by a group of smaller reserves of the same total area depends on the slope of the species–area curve and the proportion of species in common between the group of smaller reserves. Higgs & Usher (1980) compared one large area of A units with two smaller areas of pA and $(1-p)A$ units $(0 < p < 1)$ using the statistic

$$Pv = p^z + (1-p)^z - 1$$

where Pv is the proportion of species in common on the two small reserves and z is the slope of the log–log (power function) species–area regression. They found that for limestone pavements in North Yorkshire, two small pavements always encompass more species than a single large one of equivalent total area. Higgs (1981) expressed the difference in the number of species on a single large reserve compared with the number on two small reserves, each half the size of the large reserve, as a ratio R. This ratio was modified by Higgs & Margules (1980) to incorporate two small areas of unequal size, still of the same total area as the large reserve, thus:

$$R = [p^z + (1-p)^z]/(1 + Pv).$$

They calculated this ratio from data given by Brown (1978) for birds and mammals on mountaintops in the North American Great Basin. The result is shown in Fig. 2: in most cases, two small mountaintops encompass more species than a single large mountaintop. They also calculated R using data from the atlases of breeding birds (Sharrock, 1976), higher plants (Perring & Walters, 1962) and mammals (Arnold, 1978) in Britain, by comparing successively larger groups of 10 km squares with the largest size, 64 10 km squares, in an area of Yorkshire. They found that either single large areas or two small areas could contain more species. Similar results have been obtained by Game & Peterken (1980) for woodlands in Lincolnshire, England, and Gilpin & Diamond (1980) for the New Hebridean (Vanuatu) Islands.

Thus, evidence from the species–area relationship yields conflicting advice as to the strategy likely to conserve most species, depending on the proportion of species in common between reserves and the slope of the species area curve.

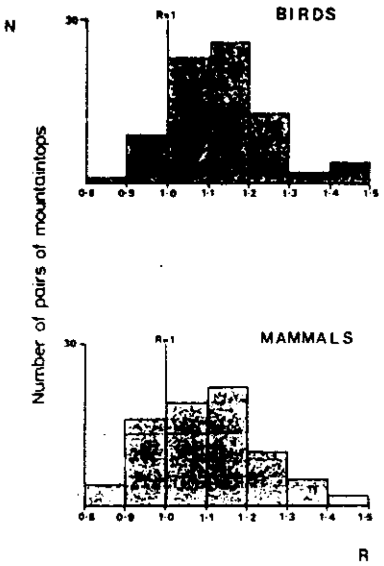

Fig. 2. Histograms of the distribution of values of R (see text for definition) for birds and mammals of mountaintops in the North American Great Basin (data from Brown, 1978). Two small mountaintops contain more species than one mountaintop of equivalent area in most cases. (From Higgs & Margules, 1980).

Part of the justification for this design rule is that one large area will result in fewer extinctions than several small areas. Diamond (1975) and Terborgh (1976) both contend that extinction rate is area-dependent. Abele & Connor (1979) could find no evidence for this contention and in a wider review, Gilbert (1980) concluded, 'There is no evidence that any extinctions in reserves have been due directly to any decrease in area' (p. 230).

Diamond (1975) himself makes the point, reiterated by Higgs (1981), that if competition contributes to extinction then two reserves may contain mutually exclusive guilds and so reduce the total number of extinctions. Frankel & Soulé (1981), however, could find no direct evidence for competition alone causing extinctions on islands, though they do note that some species do not coexist on very small islands. Equilibrium theory does not mention any possible effects of competition on species composition.

Finally, both options are, in many cases, irreversible. Once a decision has been taken to retain, say, a single large reserve in an area undergoing a major land-use change, it is not possible, at some future date, to revert to the option of a group of smaller reserves of equivalent area. The habitat involved will no longer exist elsewhere in the affected region. It would be a mistake with possibly serious long-term consequences for conservation to secure single large reserves in the belief that such a course is 'hedging bets' and can be changed if necessary.

Designs C & D

These designs assume that local immigration between reserves is important in maintaining species richness, and that local immigration between areas of so-called homogeneous habitat will be increased by the close proximity of sites. There is no doubt that immigration occurs, but there is little evidence on the effect of immigration and isolation in maintaining species numbers in reserves. In the case of certain birds and reptiles, Moore (1962) found that a distance of the order of 5 km appeared to be effective in preventing recolonisation of heathland areas. For higher plant species in woodlands, much smaller distances may be effective (Hooper, 1971). It is probable that for mobile species (such as most British birds) isolation of reserves, within certain limits, will not affect local immigration, but that for plants with poor dispersal mechanisms (e.g. vegetative propagation) and the more sedentary animals, isolation may be important. MacArthur (1972) cites an instance from the tropics in which a gap of 10 m appears to have prevented several bird species from spreading from one island to another.

In contrast, for the static situation at one point in time, Higgs & Margules (1980) show that for distributional data in the atlases of British flora and fauna, more distant areas may have fewer species in common, so that two more distant reserves might contain more species than two in closer proximity. Within Yorkshire, this reduction in the number of species in common with increased separation is significant in an east–west direction but not in a north–south direction (Table 1).

TABLE 1

THE EFFECT OF DISTANCE, D(km) ON THE PROPORTION OF GRAMINEAE SPECIES SHARED, Pv, BETWEEN PAIRS OF 10 km SQUARES IN YORKSHIRE. THE VALUES OF Pv WERE CALCULATED BY TAKING THE NUMBER OF RECORDS IN THE FIRST (MOST NORTHERLY FOR THE NORTH–SOUTH DIRECTION AND MOST WESTERLY FOR THE EAST–WEST DIRECTION) SQUARE OF EACH ROW OF AN 80 km × 80 km SQUARE, AND COMPARING THEM WITH THE OTHER SEVEN SQUARES IN THAT ROW.

Direction	*Regression*	*r*	*p*
East–West	$Pv = 0{\cdot}621 - 0{\cdot}143 \log D$	0·37	0·005**
North–South	$Pv = 0{\cdot}588 - 0{\cdot}0728 \log D$	0·22	0·103

This is probably a result of the greater environmental heterogeneity in an east–west direction, running from the coast, across the chalk wolds and the lacustrine deposits of the Vale of York to the sandstone and limestones of the Pennines. A parallel effect can be demonstrated for the higher plants on limestone pavements, a more or less uniform habitat with a low level of heterogeneity: although the distance between pavements does not affect the number of species, separation decreases the similarity between species composition. The regression equation,

$$Pv = 0{\cdot}413 + 0{\cdot}038A - 0{\cdot}0181 \log D \qquad (r = 0{\cdot}86,\ p < 0{\cdot}001)$$

shows the effect of area, A(ha) and distance, D(km) on the proportion of higher plant species shared, Pv, between 30 pairs of equal area limestone pavements in England, Scotland and Wales. Areas range between 0·02 and 4·9 ha, and separations between 3 m and 489 km. Floral composition increases in similarity as pavement areas increase and decreases with increasing separation. Most of the higher plant species that occur on limestone pavements also occur in a variety of other habitats, so that many of the communities surrounding the pavements act as source-pools for colonisation. The composition of this source-pool varies from place to place depending on the ecological conditions in that area and the geographic distributions of the species involved.

Thus, species–area relations and the equilibrium theory can support conflicting advice as to the optimal spatial arrangement of reserves intended to maximise species richness. Isolation almost certainly does affect immigration rates but the extent of this effect on species number and composition needs to be quantified for a variety of taxa in a variety of habitats before any general implications can be considered. In contrast, separation generally means greater variation in ecological and geographical heterogeneity, and thus, potentially, the number of species conserved within a reserve system.

Finally, we must emphasise the dangers of generalisations based on biogeographical concepts in areas with a long history of intensive land use such as the British Isles. Helliwell (1976) found that woods with the greatest 'conservation value' (based on the number and scarcity of higher plant species) were the small isolated fragments: larger blocks of woodland are generally more intensively managed for timber production.

Design E

Corridors or stepping stones of natural habitat between reserves may be important for some species as routes for local dispersal. MacArthur & Wilson (1967) state: 'It appears that even minute islands can significantly enhance biotic exchange providing they are able to support populations of the species in the first place' (p. 144). However, this is purely theoretical and empirical evidence is lacking.

MacClintock *et al.* (1977) found that a small forest fragment of 35 acres connected to a surrounding forest area of 10,000 acres by a disturbed woodland corridor, 15 acres in area, had an avifaunal composition that closely approximated that of much larger blocks of woodland. They conclude, not unreasonably, that the biogeographic position of this particular fragment accounts for the rich bird fauna. They go on to assert, however, that their results '... confirm the importance of minimal isolation and corridors connecting fragmented forest tracks for preservation of maximum biotic diversity' (p. 11). They do not attempt to separate the effects of the corridor from the effects of the close proximity of a major forest area. They have not satisfactorily demonstrated a significant contribution of the corridor to species numbers or composition on the fragment.

A major need for corridors or stepping stones does arise when dealing with migratory species. The National Wildlife Refuges in the USA are located according to a national strategy, and many of them form links in four chains of reserves that aim to protect each of the four major bird migration routes, the Pacific, Central, Mississippi and Atlantic flyways. All down the east coast, where the pressures of industry are most likely to be felt, they are closely spaced. In the west, an intensive agricultural belt like the San Joachin Valley is threaded with refuges to preserve a route to traditional wintering grounds (Mills, 1980).

Design F

The optimal shape of reserves is supposed to be circular to minimise dispersal distances within the reserve. Diamond (1975) suggests that if a reserve is too elongated or has peninsulas, dispersal rates to outlying parts of the reserve from more central parts may be sufficiently low to perpetuate local extinctions by island-like effects. Game (1980) argues theoretically that non-circular reserves may have both higher immigration and extinction rates, and that the optimal shape will depend on a balance between these two factors. However, there is no empirical evidence for the effect of reserve shape on local extinctions within reserves or on rates of immigration or extinction between reserves.

Long perimeters decrease the effective area of central habitat and reserves with long edges may have proportionally fewer species characteristic of the central area (Williamson, 1975). In contrast, edge species will benefit from reserves with high perimeter to area ratios. Thus, Moore & Hooper (1975) found that the occurrence of the blackcap *Sylvia atricapilla*, a bird of woodland glades and overgrown hedges (Peterson *et al.*, 1954), in woodlands shows a better correlation with the square root of the area than with area itself, suggesting that it is dependent on the margins of woods. However, many edge species may fare well in non-reserve habitats and it is the edge-intolerant species which are most dependent on reserves for survival. Limestone pavements clearly demonstrate the existence of edge zones where the specialist deep gryke habitat is reduced, and long thin pavements can be considered edge-zone throughout (Fig. 3).

Nevertheless, shape *per se* is unlikely to be considered as an important criterion by conservation bodies, and edge-zones are only liable to have a significant effect on very small reserves.

CONCLUSIONS

Design strategies to maximise species richness are based on the species–area relationship and the equilibrium theory of island biogeography. The species–area

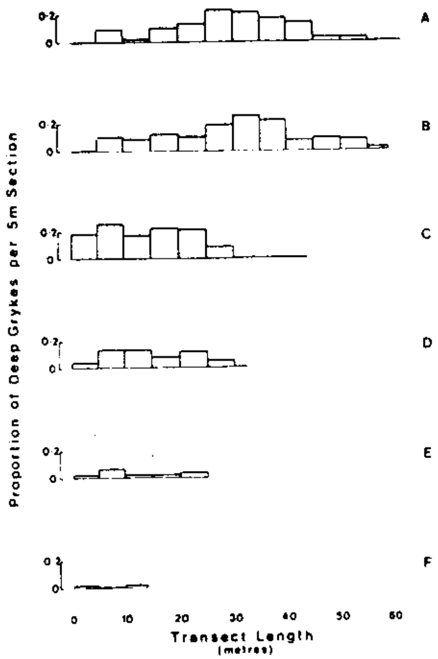

Fig. 3. Typical transects taken across the width of limestone pavements in the Yorkshire Dales, England, showing the proportion of deep grykes (weathered cracks along joint lines, depth/width ratio ≥ 2·0) per 5 m section. Pavements A, B and D exhibit physical 'edge-zones' on both sides where the limestone slopes under the surrounding grassland and the proportion of deep grykes decreases. Pavement C ends abruptly on one side in a small cliff and therefore has only one 'edge-zone'. Narrow pavements such as E and F can be considered as 'edge-zone' throughout.

relationship has been used to argue that single large reserves will encompass more species than single small reserves and more than a group of small reserves of equivalent total area. The equilibrium theory has been used to argue that small reserves, once isolated in surroundings of different habitat, will lose species more rapidly and, eventually a greater total number of species, than larger reserves. The ideas of species turnover and the effects of isolation on immigration and extinction, inherent in the equilibrium theory, have also been used to argue that regular, preferably circular, shaped reserves will retain more species than irregular shaped reserves. We have considered these arguments as well as recent reviews of the equilibrium theory and theoretical work on the species–area relationship. The following points emerge: (1) the equilibrium theory of island biogeography remains unsubstantiated. Most importantly, there is no evidence for extinction rate being area-dependent; (2) even if the equilibrium model did describe true islands, isolated or insular continental areas are so different from real islands that they might be very badly described by it; (3) the conclusions from the species–area relationship are equivocal; and (4) there is no empirical evidence to support the design strategies for whole communities. What little exists is only relevant to the particular species (mostly birds) investigated in those studies. We therefore urge caution in the application of general rules, such as the design strategies described above, to the practice of conservation.

This is not to suggest that a study of species–area relations cannot be valuable in conservation evaluation. Adriani & van der Maarel (1968) showed that the sand dune system of the Voorne was four times more species-rich than an average site in the Netherlands, per unit area. This proved to be a strong argument in favour of their conservation. Usher (1980a, 1980b) adopted a similar approach although he developed it to include factors such as typicalness and area for its own sake, as well as species richness. He fitted the power function model to data on the number of plant species on 49 limestone pavements near Malham, North Yorkshire. By plotting these pavements on a species–area scatter diagram and showing the regression line which resulted from fitting the model, the location of each pavement in relation to that line—the average species–area curve for all pavements—could easily be seen. Those with the greatest discrepancy in a positive direction have the most species per unit area (i.e. they are the most species-rich after area has been eliminated). Those falling on or close to the line are typical in their number of species and those about the upper end of the line are those of large area with a high number of species—the most species-rich in an absolute sense.

Quantifications of this sort are essential if truly accurate comparisons are to be made. Margules & Usher (1981) cite recent advances in quantifying some concepts important in conservation such as diversity (Pielou, 1975) and rarity (by way of mapping schemes such as *Atlas of the British flora*, Perring & Walters, 1962), and are optimistic about other advances in the coming decade. Techniques of numerical taxonomy, widely used in vegetation description and classification (e.g. Greig-Smith, 1964; van der Maarel, 1980) offer a hope of quantifying the concept of representativeness or typicalness, at least for vegetation communities.

We would like to affirm our support for the conservation ethic and the ideal of the preservation of maximum biological diversity. With today's high level of technology and rapidly changing patterns of land use worldwide, every conservation decision is potentially irreversible. This makes it imperative that all possible factors are taken into consideration when such decisions are made. Undue emphasis should not be placed on theoretical ideas which are unproven or equivocal.

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A land-bridge island perspective on mammalian extinctions in western North American parks

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In recent years, a number of authors[1-3] have suggested several geometric principles for the design of nature reserves based upon the hypothesis that nature reserves are analogous to land-bridge islands. Land-bridge islands are islands that were formerly connected to the mainland and were created by a rise in the level of the ocean. Land-bridge islands are considered supersaturated with species in that the ratio of island to mainland species numbers is higher than expected from the area of the island. As a result, the rate of extinction should exceed the rate of colonization on a land-bridge island, resulting in a loss of species that is suggested to be related to the size and degree of isolation of the island[4]. If nature reserves are considered to be similar to land-bridge islands, because most are slowly becoming isolated from their surroundings by habitat disturbance outside the reserves[4-6], several predictions follow. First, the total number of extinctions should exceed the total number of colonizations within a reserve; second, the number of extinctions should be inversely related to reserve size; and third, the number of extinctions should be directly related to reserve age. I report here that the natural post-establishment loss of mammalian species in 14 western North American national parks is consistent with these predictions of the land-bridge island hypothesis and that all but the largest western North American national parks are too small to retain an intact mammalian fauna.

I tested the land-bridge island predictions by examining the change in mammalian species number in 14 western North American national parks and park assemblages (Table 1) located within the Rocky Mountains, Sierra-Cascades and Colorado Plateau. A park assemblage is defined as two or more contiguous parks. The age of a park is defined as time since park establishment; the age of a park assemblage is defined as the mean time since park establishment for the individual parks. Analysis was limited to the orders Lagomorpha, Carnivora and Artiodactyla, because these orders had the most complete park sighting records. Species of these orders tend to be more frequently reported because of their relatively large body size, non-fossorial nature and 'popularity'.

I recorded for every species in each park, based upon park sighting records and the literature, the date of last sighting as of 1983/84 and the total number of sightings for the species if it had been sighted less than five times since establishment of the park. Species which had been sighted less than three times since the establishment of the park were excluded in the analysis of post-establishment colonizations and extinctions. Biases may exist in the sighting records because of their non-standardized nature, potential misidentification of species by observers, and a lack of equivalent sampling effort between parks. I have attempted to minimize these biases by using conservative methods (see below) for classifying a sighting as valid and determining the number of post-establishment extinctions.

With the exception of sightings made by biologists or park employees, a sighting was considered valid only if it was accompanied by an accurate description of the species. The number of post-establishment extinctions was determined by assuming that all species that had not been sighted for a minimum of 10 years by 1983 were extinct. In a few cases, there was solid evidence that several species had become extinct in a park since 1973. This method for determining the number of post-establishment extinctions excludes any species that have become extinct and subsequently recolonized the park naturally since park establishment. The number of post-establishment colonizations was determined by assuming a colonization had occurred if a species had not been reported within a park near time of establishment but was subsequently sighted at least three times since park establishment. The number of pre-establishment extinctions, considered hypothetical, was determined using three criteria. First, a species must have a historic range, as described in the literature, overlapping a park. Second, the park must currently meet known habitat requirements for a species. Third, a species must be documented as occurring either within a park or its vicinity before park establishment by a specimen, skeletal remains, pre-establishment sighting(s), post-establishment sighting(s) fewer than three times, or a post-establishment reintroduction by a park manager.

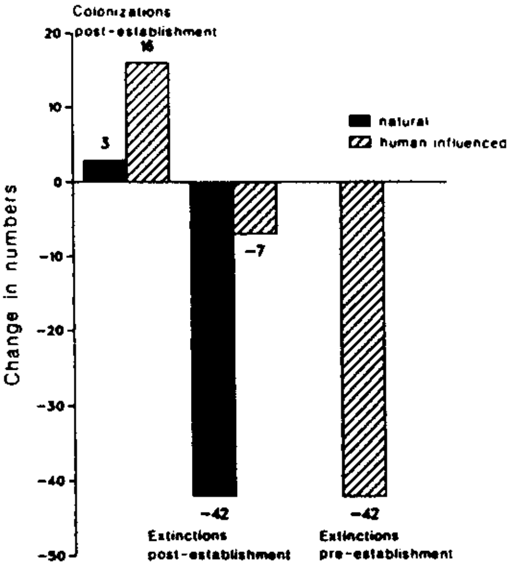

Fig. 1 Comparison of number of post-establishment colonizations with number of post-establishment and pre-establishment extinctions in 14 western North American national parks. Colonizations and extinctions are classified as either natural (solid bars) or human-influenced (hatched bars).

Colonizations and extinctions were classified as being natural or human-influenced. A natural extinction or colonization was an extinction or colonization that could not be related directly to human disturbance within a park. Conversely, a human-influenced extinction or colonization was one that could be

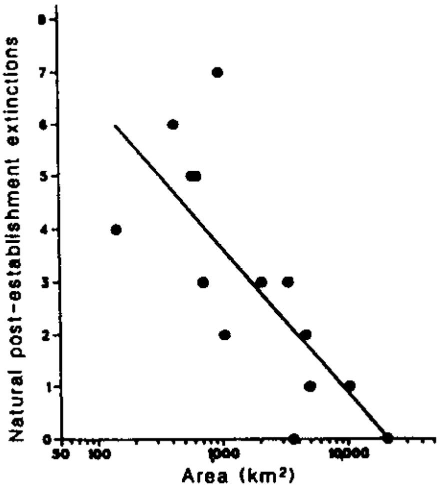

Fig. 2 Relationship between number of natural post-establishment extinctions and park area in 14 western North American national parks. Area is plotted on a logarithmic scale. The straight line shows the relationship $y = 11.95 - 2.76 \times (\log \text{area})$.

Table 1 Summary of pre- and post-establishment extinctions and colonizations, area and age for 14 western North American national parks

Park/Park assemblage	Proportional loss of total species found historically (%)	No. of pre-establishment human-influenced extinctions	No. of post-establishment natural extinctions	No. of post-establishment human-influenced extinctions	No. of post-establishment natural colonizations	No. of post-establishment human-influenced colonizations	Area (km^2)	Age (years)
Bryce Canyon	36	4	4	1	0	1	144	61
Lassen Volcanic	43	6	6	0	0	0	426	77
Zion	36	5	5	0	0	2	588	75
Crater Lake	31	5	5	0	0	2	641	82
Manning Provincial	26	4	3	0	1	1	712	43
Mount Rainier	32	1	7	0	0	1	976	85
Rocky Mountain	31	10	2	0	0	3	1,049	69
Yosemite	25	2	3	1	0	0	2,083	94
Sequoia-Kings Canyon	23	1	3	3	0	1	3,389	94
Olympic	6	0	0	1	0	2	3,628	75
Glacier-Waterton Lakes	7	1	2	0	1	1	4,627	81.5
Grand Canyon	18	2	1	1	0	0	4,931	76
Grand Teton-Yellowstone	4	0	1	0	1	1	10,328	83.5
Kootenay-Banff-Jasper-Yoho	0	1	0	0	0	1	20,736	84.5

Data from ref. 13.

potentially or directly related to human activities within a park (see below). Data are summarized in Table 1.

The number of cases (Fig. 1) of natural post-establishment extinctions of mammals ($n = 42$) has exceeded the number of post-establishment colonizations ($n = 3$). This result is consistent with the first prediction of the land-bridge island hypothesis. The natural colonizations resulted from range expansions by the raccoon (*Procyon lotor*) and the moose (*Alces alces*). Park managers have reintroduced 12 species that were found historically in the parks and four exotic species have colonized the parks from lands adjacent to the parks. I attribute the post-establishment human-influenced extinction of six species to predator control and one species to accidental poisoning. A large number of species ($n = 42$) were also lost before the establishment of most western North American national parks (Fig. 1). However, it is quite likely that many of the species that became extinct in the smaller parks before park establishment were transient populations. The pre-establishment loss of species is most probably attributable to human disturbance in the form of hunting, logging, grazing and mining which occurred in many of the western North American parks before their establishment[9]. Combining both pre- and post-establishment extinctions, up to 43% of all species of lagomorph, carnivore and artiodactyl (12 species) found historically within 14 western North American national parks have been lost within a given park (Table 1). Only the largest western North American park assemblage, the Kootenay-Banff-Jasper-Yoho park assemblage (20,736 km^2), still contains an intact historical mammalian faunal assemblage.

The number of natural post-establishment mammalian extinctions (Fig. 2) is significantly and inversely related to log park area ($r^2 = 0.56$, $P < 0.01$). The number of natural post-establishment mammalian extinctions is insignificantly correlated with log park age ($r^2 = 0.00$, $P > 0.97$). However, if the effects of park area are held constant, the number of natural post-establishment extinctions is significantly and positively partially correlated with log park age ($r = 0.57$, $P < 0.05$). Log park area (a) and log park age (g) when combined in a multiple linear regression model account for 71% of the total variation in numbers of natural post-establishment extinctions (e). The multiple regression model is: $e = -6.04 - 3.49(a) + 10.82(g)$ ($n = 14$, $F = 13.15$, $P < 0.002$). The results of the simple linear regression and the partial correlation are consistent with the second and third predictions of the land-bridge island hypothesis. In addition, the results of the simple and multiple linear regression indicate that park area is a more important determinant than park age of number of natural post-establishment mammalian extinctions in western North American parks.

The natural post-establishment loss of mammalian species is most probably attributable to the loss of habitat and the active elimination of fauna on adjacent lands or what has been described as short-term insularization effects[10]. This loss of habitat and the active elimination of fauna on lands adjacent to the parks have had a twofold effect. First, they have increased the probability of local extinction of species within the reserves because smaller parks tend to have smaller populations which in turn have a higher probablity of extinction[11,12]. Further support for this hypothesis is provided by the fact that population size is the most consistent predictor in a multivariate statistical analysis of life history characteristics of the probability of post-establishment persistence for populations of lagomorphs, carnivores and artiodactyls within 24 western North American national parks[13]. Second, this disturbance has reduced the potential for colonization from lands adjacent to the parks by increasing the distance or isolation of the parks from potential source areas. Openings as narrow as a road, open field, or clearcut have been shown to inhibit the movement of both large and small mammals[14-17].

Without active intervention by park managers, it is quite likely that a loss of mammalian species will continue as western North American national parks become increasingly insularized. Yet is is possible that even without further insularization, mammalian species may continue to be lost in these parks because of a lag between past disturbance and subsequent extinction. Augmentation of existing mammalian park populations by natural colonization, or what has been described as the rescue effect[18], probably will be limited to the most common species. The enhancement of populations for rare species will be largely dependent upon the active introduction of individuals by park managers.

A final factor that could explain the natural post-establishment loss of mammalian species in western North American parks is habitat change. It is widely acknowledged that fire suppression since the early 1900s has affected the vegetative structure of western North American national parks[19-22]. However if this vegetative change has had an influence on post-establishment mammalian extinctions, one would expect that species that are dependent upon early successional vegetation should be most prone to extinction. Of the 42 populations of species that have become extinct in 14 parks since park establishment, only 10 may be classified as being dependent upon early successional vegetation. Thus for most species, it appears that successional change is not the principal determinant of post-establishment local extinction of species.

The natural post-establishment loss of mammalian species in western North American national parks indicates that virtually all western North American national parks were too small to maintain the mammalian faunal assemblage found at time of park establishment. To reduce the potential loss of mammalian fauna in the future will most probably require that the mammalian fauna within the parks be more actively managed and that the parks be 'enlarged' either through the acquisition or the cooperative management of lands adjacent to the parks.

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Essay

Movement Corridors: Conservation Bargains or Poor Investments?

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Abstract: *Corridors for movement of organisms between refuges are confounded with corridors designed for other functions, obscuring an assessment of cost-effectiveness. The rationales for movement corridors are (1) to lower extinction rate in the sense of the equilibrium theory, (2) to lessen demographic stochasticity, (3) to stem inbreeding depression, and (4) to fulfill an inherent need for movement. There is a paucity of data showing how corridors are used and whether this use lessens extinction by solving these problems. Small, isolated populations need not be doomed to quick extinction from endogenous forces such as inbreeding depression or demographic stochasticity, if their habitats are protected from humans. In specific instances, corridors could have biological disadvantages. Corridor proposals cannot be adequately judged generically. In spite of weak theoretical and empirical bases, numerous movement corridor projects are planned. In the State of Florida, multi-million-dollar corridor proposals are unsupported by data on which species might use the corridors and to what effect. Similarly, plans for massive corridor networks to counter extinction caused*

Corredores para el movimiento: ¿Gangas de la conservación o malas inversiones?

Resumen: *Los corredores para el movimiento de organismos entre refugios son confundidos con corredores designados para otras funciones obscureciendo una evaluación sobre costo-efectividad. Las funciones atribuidas a los corredores para movimiento son (1) disminuir la tasa de extinción definida en términos de la teoría de equilibrio, (2) disminuir la estocasticidad demográfica, (3) contrarrestar la depresión endogámica y (4) satisfacer una necesidad innata de movimiento. Existe una carencia de datos que demuestren como son usados estos corredores y si este uso minimiza las extinciones al resolver estos problemas. Poblaciones pequeñas y aisladas no están necesariamente condenadas a una rápida extinción causada por fuerzas endógenas, como depresión endogámica o estocasticidad demográfica, si sus ábitats están protejidos de los humanos. En instancias particulares, los corredores pueden tener desventajas biológicas. Las propuestas sobre corredores no pueden ser juzgadas apropiadamente en forma genérica. Numerosos corredores para movimiento están proyectados a pesar de fundamentos teóricos y empíricos débiles. En el*

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by global warming are weakly supported. Alternative approaches not mutually exclusive of corridors might be more effective, but such a judgment cannot be made without a cost-benefit analysis.

estado de Florida, propuestas multimillionarias para corredores no están fundamentadas por datos que indiquen que especies usarian los corredores y con que propósito lo harían. En forma semejante, los proyectos de redes masivas de corredores para contrarrestar la extinción causada por el calentamiento global están pobremente fundamentados. Estrategias alternativas, que no son mutuamente excluyentes con los corredores, podrían ser mas efectivas, pero tales juicios no pueden ser hechos sin un análisis de costo-beneficio.

Introduction

A remarkable publicity campaign, much of it outside the bounds of mainstream science, has promoted corridors for conservation. Wilson and Willis (1975) originally proposed corridors based on the equilibrium theory of island biogeography (MacArthur & Wilson 1967); the suggestion was reprinted in *World Conservation Strategy* (International Union for the Conservation of Nature and Natural Resources [IUCN] 1980). With the imprimatur of the IUCN, the United Nations Environmental Program, and the World Wildlife Fund, the idea was widely accepted. The popular promotion of corridors entails lead articles in lay magazines (such as Arnold 1990), a videocasette (Suchy & Harris 1988), a pamphlet (Anonymous 1990*a*), the entire December 1986 issue of ENFO, and a special publication by Defenders of Wildlife (Mackintosh 1989). In Montana, a court has ruled that corridors are scientifically established as important (Breen 1991; Pace 1991). Keith Hay of the Conservation Fund argued that corridors "hold more promise for the conservation of the diversity of life than any other management factor except stabilization of the human population" (Chadwick 1990).

This hype is occurring in spite of a dearth of evidence of whether corridors will be useful in specific situations. "The workshops that discussed the values of corridors were certain that they were positive features despite the lack of supporting research" (Dendy 1987). That they facilitate movement "is now almost an article of faith" (Hobbs & Hopkins 1991). Saunders & Hobbs (1991*a*) believe that we do not have time to test the efficacy of corridors, while Noss (1992) argues that, in the face of uncertainty, it is prudent to maintain or restore "natural" kinds of corridors.

Discussion of corridors is confused (Anonymous 1986). We are concerned in this article with corridors for movement, but at least six senses of "corridor" appear in the conservation literature.

First, some habitats constitute corridors. A corridor may deserve protection as a distinct habitat, whether or not it aids movement (Simberloff & Cox 1987). For example, riparian communities are very threatened in some regions (Johnson 1989), but their value as habitats is independent of whether they allow movement between other habitats. To embed a discussion of riparian habitats in an argument about movement corridors (see Johnson 1989; Ames 1990) confounds assessment of strategies for land acquisition. Some linear artificial habitats, such as rights-of-way for highways (Adams & Dove 1989; Wilcox 1989), railroads (Noss 1992), and transmission lines (Anderson et al. 1977; Kroodsma 1982; Forman 1983), are also called "corridors," and can bolster animal populations and enhance urban and suburban green space (Adams & Dove 1989). Again, their utility as habitats is separate from their importance for movement.

Second, greenbelts and buffers are occasionally called "corridors," and their function of ameliorating the human environment is cited in discussions of movement corridors (see Gilbrook 1986; Budd et al. 1987; Adams & Dove 1989). Although such areas might aid dispersal, some envisioned uses (such as hiking and horse trails, boating, outfall for storm sewers) could impede their utility as either dispersal routes or habitats. In any event, the value of such constructs as aesthetic amenities is independent of their value for movement.

Third, Harris (1985) and Suchy and Harris (1988) call biogeographic landbridges such as the Isthmus of Panama "corridors." Such large regions have aided intercontinental movement of entire communities (Brown & Gibson 1983), but the relevance of this fact to maintaining viable populations in refuges is obscure (Simberloff & Cox 1987).

Fourth, a series of discrete refuges for migratory waterfowl is occasionally called a corridor (see Harris 1985; Anonymous 1991). Below we will suggest that such a system can be construed as an alternative to corridors or complementary to a corridor network.

Fifth, underpasses and tunnels are often now called "corridors." They are commonly used to allow animals to cross highways (reviewed by Bennett 1990*b*; Noss 1992), primarily to keep individuals from being killed on the road rather than to decrease demographic stochasticity, prevent inbreeding depression, or serve other population-level functions. Costs of such structures should be construed as part of road construction rather than as land acquisition.

Sixth, and our concern here, are strips of land intended to facilitate movement between larger habitats. Wilson and Willis (1975) and Harris and Scheck (1991), in the context of equilibrium theory, envision such movement as increasing immigration rates, thus raising the equilibrium number of species at each site. Harris (1984, 1985) suggested two other rationales for corridors. First, individuals of some species typically range widely; second, inbreeding depression will lead to extinction in small refuges. Recently, alleviation of demographic stochasticity has been a suggested benefit of corridors (see Merriam 1991; Thomas 1991; Noss 1992).

We are particularly concerned with the economic cost of corridors. Hobbs and Hopkins (1991) talk of corridors as adding an option to a sparse conservation repertoire, but options may be foreclosed if a particular corridor is reserved. Noss (1992 and personal communication) believes it is prudent to retain existing corridors, conceding that establishing new ones may be cost-ineffective. But even an existing corridor is not necessarily free, and prudence when all options cannot be pursued requires some sort of cost-benefit analysis of each.

Rationales for Movement Corridors

The Equilibrium Theory of Island Biogeography

The equilibrium theory of island biogeography states that species number is constant, but that local turnover changes composition. Thus, corridors are useful by virtue of maintaining more species. An odd aspect of the rush to found a technology of refuge design based on island biogeographic theory is that, exactly when the IUCN and others were popularizing refuge design based on equilibrium theory, the theory was increasingly heavily criticized (Gilbert 1980; Williamson 1981, 1989; Williams 1984, 1986) as inapplicable to most of nature, largely because local population extinction was not demonstrated.

Demographic Stochasticity and the Metapopulation

Although not cited in the original recommendations for corridors, demographic stochasticity has been widely recognized as a potential threat to small populations (references in Simberloff 1988), and its diminution is now viewed as a rationale for corridors (see Merriam 1991; Thomas 1991; Noss 1992). No unified theory combines genetic, demographic, and other forces threatening small populations, nor is there accord on the relative importance of these threats. Lande (1988) believes that demography will usually be more important than genetics to very small populations, while Goodman (1987*a*) sees demographic stochasticity as important only when just a "handful" of individuals remain.

The metapopulation paradigm (Levins 1970) has replaced equilibrium theory for habitat islands (Merriam 1991), partly because of absence of evidence for turnover. The metapopulation is seen as lessening or redressing extinction by demographic stochasticity of the component populations. As with the equilibrium theory, however, there is now a tendency to take the metapopulation paradigm as broadly representative of nature, rather than as a new and untested hypothesis. Such statements as, "Many or most species are distributed as 'metapopulations'" (Noss 1992) are simply unwarranted. There are few empirical data, no specification of the range of dispersal rates that qualifies a group of populations as a metapopulation, and a variety of untested metapopulation models (references in Hanski & Gilpin 1991), none of which has been demonstrated to represent many situations in nature. Even if the metapopulation model should be shown to apply to a particular situation, the model requires movement, not corridors (Merriam 1991).

Inbreeding Depression

A genetic argument for corridors extends the concept of movement to genes as well as individuals. Harris (1984, 1985) argues that gene flow is required to prevent inbreeding depression from causing extinction and that corridors are needed for this gene flow.

Although a degree of inbreeding depression is usually found in captive animal populations, its threat must be established empirically. Some species with little genetic variation suffer no inbreeding depression (such as Pere David's deer and the European bison [Frankel & Soulé 1981]). It is often said that such species were lucky—their populations probably shrank gradually, and natural selection removed deleterious alleles that cause inbreeding depression. This line of reasoning implies that inbreeding depression is likely if normally outbred species suddenly inbreed (Frankel & Soulé 1981), as might be induced by rapid habitat fragmentation. However, in these cases most of the population decline occurred in a few generations. Therefore it remains mysterious why some species have little or no inbreeding depression. In nature, evidence from animal populations is extremely scarce (Charlesworth & Charlesworth 1987). The oft-cited evolution of behavior that reduces inbreeding need not have been selected by inbreeding depression (Charlesworth & Charlesworth 1987). In higher plants in nature, a measure of inbreeding depression has almost always been found when sought (Charlesworth & Charlesworth 1987). However, adequate data have been collected from far too few species.

Finally, finding that small populations are threatened by inbreeding depression is different from demonstrating its existence (Lande 1988). To evaluate the threat from inbreeding depression, it is important to bear in mind that a loss in genetic fitness need not endanger a population. "Inbreeding depression" means that more inbred individuals are less fit than less inbred ones. Most populations of most species, however, generation after generation produce some individuals less fit than others, yet are not endangered. So it is not axiomatic that inbreeding, even if it should lead to inbreeding depression, is a major threat to small populations, relative to other threats (Lande 1988). In any event, even if inbreeding depression is found to threaten a population, the key question is whether corridors are the best way to stem it; we return to this point below.

Need of Individual Animals for Movement

The Northern Spotted Owl (*Strix occidentalis caurina*) has a median pair home range in most areas of 1200 to 2000 ha (Thomas et al. 1990). Home ranges are larger in areas with less old-growth forest habitat (references in Thomas et al. [1990]), suggesting that the crucial requirement is enough small mammal prey inhabiting this habitat. There is an indication that owls that do not get enough favored prey experience lowered reproduction rates, but there is no suggestion that failure of space for movement per se is limiting. Mortality of dispersing juveniles is severe, but Thomas et al. (1990) argue against even wide corridors specifically for owl movement on the grounds that predators may thrive in them. Spotted Owls appear to disperse in random directions, which also argues against a corridor strategy (Noss 1992). Rather, Thomas et al. (1990) suggest management of the entire matrix surrounding owl habitat conservation areas to make it suitable for owl dispersal.

Harris (1985) and Noss and Harris (1986) have adduced the large home ranges of Florida panthers (*Felis concolor coryi*) and black bears (*Ursus americanus*) as a rationale for corridors. Most conservation areas in Florida are too small to provide the approximately 80 km^2 covered by a male black bear (Lindzey & Meslow 1977; Wooding & Hardisky 1990) or the approximately 400 km^2 covered by a male panther (Belden 1989) each year, and Maehr and Harris (1986) believe that areas as large as 800 km^2 may not support viable populations of either species. However, black bear populations have persisted despite confinement to small areas (Lindzey & Meslow 1977). Corridors might allow some species to avoid potentially fatal intraspecific encounters. Territorial battles between male panthers and between male black bears are sometimes lethal (Kemp 1976; Belden 1989). There are instances of black bear cannibalism (Tietje et al. 1986), and young black bears establish territories more readily at low densities (Kemp 1976; Rogers 1987). Therefore if corridors actually aided dispersal, they might be beneficial, but there is little evidence that dispersal is mediated by such social interactions (Rogers 1987) or that bears use corridors to disperse.

No Florida panther restricts its movements to one protected area, and panthers use a "hardwood strand" corridor linking the Big Cypress National Preserve to unprotected habitat (Maehr 1990). Hardwood strands follow depressions and slow-moving watercourses in Florida (Maehr & Cox, unpublished data). This particular strand is less than 5 km long—much less than the daily ambit of a panther (Belden 1989)—and bounded by agricultural areas, which panthers avoid. How well panthers would use a much longer corridor is unknown. Long-distance dispersal by bears and panthers is not nearly as well documented. Maehr et al. (1988) describe one black bear dispersal of 120 km, but they also contend that well-defined corridors are not necessary for bears so long as habitat does not fully impede movement.

In sum, the need for movement per se is doubtful, though animals may be driven to move for specific purposes, such as finding food or avoiding conspecifics. The key questions are whether such movement is necessary in a specific refuge system and, if it is, whether corridors of specified characteristics are the best strategy to facilitate such movement.

How Inevitable is Quick Extinction of Small Populations?

Given the attention paid in recent conservation literature to threats to small populations, it might seem that any small, isolated population is doomed in the short term. Many go extinct (see Petterson 1985). But many small populations persist and cannot easily be dismissed as recently-reduced populations en route to extinction. Numerous endemic species of small islands are endangered primarily by either habitat destruction or introduced species (references in Simberloff 1986; see Craig 1991) but apparently thrived for millennia in the absence of humans, though many probably numbered at most in the low hundreds. Species in the highest trophic levels are particularly striking. For example, the Red-Tailed Hawk (*Buteo jamaicensis socorroensis*) of Socorro Island (southwest of Baja California) has had a stable population of about 20 pairs for at least the last few decades, and there is no reason to think the population was larger in antiquity (Walter 1990). Of course, we do not even know the fates of many isolated populations that disappeared in the absence of human interference, but rapid extinction is not automatic.

Evidence for Corridor Use

Simberloff & Cox (1987) found few empirical data on corridor use and discovered that most reported observations were ambiguous. These problems persist (Hobbs & Hopkins 1991; Nicholls & Margules 1991; Saunders & Hobbs 1991*a*). There are still few data, and many widely cited reports are unconvincing.

Probably the first advocacy of corridors based on specific data was for birds of forest patches in the northeastern U.S. (MacClintock et al. 1977). This study is often cited (see Greenberg 1990) as showing that corridors increase diversity. The study was uncontrolled; there were no isolated sites *not* connected by a corridor to a larger forest, and no data on corridor use for sites that were connected to a larger forest. A frequently cited (see Noss 1992) recent paper (Saunders & Ingram 1987) contends that "Comparison of breeding results from all five populations studied and the amount of native vegetation remaining in each area showed that Carnaby's Cockatoo [*Calyptorhynchus funereus latirostris*] can breed successfully in areas which have been extensively cleared provided there are corridors of native vegetation connecting patches of remnant vegetation." In fact, data from this paper do not show that corridors are more important than amount of vegetation in the remnant (Saunders, personal communication 1987). However, additional uncited data (Saunders 1980) showed that, at the one site where the cockatoo disappeared, feeding areas near railway and road verges were used but did not connect to a nearby reserve.

Bennett (1987*a*), studying the long-nosed potoroo (*Potorous tridactylus*) in Australian forest patches, concluded that forest strips along roads and creeks aid dispersal and allow persistence in a fragmented landscape. No data in this paper addressed this question, but the paper cited a dissertation (Bennett 1987*b*). There the conclusion rested solely on two animals trapped in forested corridors, while there were no traps outside of corridors. Bennett (1990*a*) similarly felt that narrow forested corridors "facilitate continuity between populations" of eight mammals in Australia but did not study movement outside of corridors. Suckling (1984) argued that forested roadside strips connecting woodland patches prevent local extinction of the sugar glider (*Petaurus breviceps*) in Australia. However, he did not trap outside corridors and forest patches, and the only unconnected patch of the three studied was less than half the size of the others. Thus there are no data on increased dispersal with corridors or increased extinction without them. Bennett (1990*b*) argued that "all known dispersal movements" of the sugar glider involved corridors; in fact, none were sought otherwise.

Assessing these claims was difficult, entailing correspondence and examination of an unpublished document (Bennett 1987*b*) in Australia that could not be procured by interlibrary loan in Florida. One cannot expect management personnel to expend such effort, yet without this examination one would be left with a misleading impression. For example, Ogle (1989) noted that a 1986 corridor proposal in New Zealand was questioned on the grounds of lack of evidence on corridor use, "notwithstanding the plausibility of the concept and a growing body of supportive data from overseas." There were, at that time, virtually no supportive empirical data, only a plethora of statements advocating the concept (Simberloff & Cox 1987). Ogle (1989) went on to cite new supporting data:

> Biological corridors have been the subject of considerable field research in Australia, and their importance for movements of fauna between otherwise discrete patches of habitat has been established on, for example, small marsupials (Bennett 1987) and Cockatoos (Saunders & Ingram 1987). Bennett showed that narrow strips of forest along road verges and water courses provide routes for the dispersal of adult long-nosed potoroo (*Potorous*) between remnants of native vegetation in agricultural lands of south-west Victoria. Saunders & Ingram have shown that Carnaby's Cockatoos (*Calyptorhynchus funereus latirostris*) in Western Australia nest in isolated forest remnants in agricultural land, and feed in remnants of native heathland. Native vegetation of road verges provides some feeding habitat and the routes (corridors) between nesting and feeding areas.

Ogle was at pains to show that corridors are critical for these species, but neither study cited demonstrated their importance.

Nicholls and Margules (1991) detail statistical difficulties of experiments to show that corridors enhance movement. Largely because of problems achieving sufficient experimental sample sizes, they acknowledge that observational studies could be useful. As the examples above show, however, many such studies are inconclusive, particularly because of failure to examine movement without corridors. That an animal uses corridors when these are present need not mean movement without them is impossible, or even less frequent. Of 36 papers in "The Role of Corridors" (Saunders & Hobbs 1991*b*), five present new data on animal movement (Arnold et al. 1991; Catterall et al. 1991; Date et al. 1991; Prevett 1991; Saunders & de Rebeira 1991). Of these, only Arnold et al. (1991) gathered data on movement between habitat patches without corridors. Only three (Arnold et al. 1991; Date et al. 1991; Prevett 1991) concluded that corridors have a very small role in conserving a particular taxon.

Regional Corridors to Alleviate the Effects of Global Warming

The interaction of fragmentation with global warming has led to a different sort of corridor proposal. Global warming can cause a species' present sites to change more quickly than the species can evolve (Peters & Darling 1985). During earlier climatic changes many species could shift their geographic ranges to remain in their favored habitat. As habitats have become fragmented, routes are increasingly blocked (Peters 1988).

Graham (1988), Hunter et al. (1988), and Harris and Gallagher (1989) suggest a vast network of corridors over North America. Hunter et al. (1988) feel that even a 300-meter-wide corridor stretching thousands of kilometers could be very useful. Few data are available to assess this plan. Whether a strip 300 meters wide would allow the range shifts that typified the Pleistocene has barely been discussed. Noss (1992) worries that the anticipated speed of temperature increase may render such corridors of little use for many species. Hobbs and Hopkins (1991) admit that the utility of corridors in counteracting effects of global warming is very uncertain, but they argue for going ahead anyway.

If a corridor is intended to preserve an entire community, as in the global warming recommendation, it is particularly important that it be wide enough to permit breeding as well as movement. One need only consider the limited mobility of many soil invertebrates and plants to realize that a range shift would be painfully slow and require many generations.

A corridor to permit survival and breeding is serving as more than a corridor for movement; it is a habitat in its own right. Such a requirement raises the stakes considerably. One must know if the interior of a corridor functions as the intended habitat rather than as edge. Both micrometeorological effects and biotic intrusions can propagate an edge effect far into the forest (see Levenson 1981; Janzen 1983, 1986; Wilcove et al. 1986; Kapos 1989). Nest predation studies (such as Wilcove 1985; Andren & Angelstam 1988) also point to a substantial edge effect. The modified habitat in thin corridors is the motivation for the Klamath Corridor Proposal (Pace 1991), which envisions a corridor 5.5 km wide, connecting two wilderness areas 26 km apart in the Klamath National Forest. This proposal specifically aims at a corridor that is a habitat, not just a travel route.

Potential Biological Disadvantages of Corridors

Genetic and Demographic Costs and Benefits

Although the possibility of inbreeding depression would likely be lowered if corridors were used, the possibility of loss of alleles to drift in an ensemble of refuges would increase (references in Simberloff [1988]). This trade-off is inevitable; which problem should be of more concern depends on the severity of inbreeding depression (an empirical matter) and how pronounced and dangerous the slowing of future evolution by drift will be. There is no unanimity on this matter (Simberloff 1988). Goodman (1987*b*) has argued that effects of demographic stochasticity can be greatly lessened by a modest amount of migration among refuges, though he gives no figure. Whether a corridor would be the only or even the best way to provide whatever movement is necessary would depend on information on how much movement would occur with and without corridors. Depending on metapopulation structure, as little as one breeding migrant per generation can render a population effectively panmictic (Lande & Barrowclough 1987), which raises the possibility that even if a corridor increased movement it might be unnecessary genetically.

Spread of Catastrophes

Phenomena such as fires, diseases, or introduced species can spread through a corridor (Simberloff & Cox 1987). For example, in New Zealand, introduced feral pigs may eliminate *Paryphanta* snails from large forest fragments but do not invade small, isolated ones (Ogle 1987). Similarly, introduced vertebrate browsers in New Zealand have almost eliminated mistletoe from large forest fragments, but not from isolated small groups of trees (Ogle & Wilson 1985). In most instances, however, the added risk of spreading catastrophes via corridors may be low because introduced predators or diseases can reach fragments without corridors.

Corridors as Reservoirs of Edge and Introduced Species

Several authors have suggested that corridors might be inimical as a habitat in their own right. For example, forest corridors have a high fraction of edge habitat and might attract edge-inhabiting predators (Ambuel & Temple 1983). The same concern is one reason for the disenchantment with corridors on the part of Thomas et al. (1990), and numerous other authors have pointed to this potential liability in particular systems (see Catterall et al. 1991). Others have warned that some corridors may favor movement by introduced species (see Forman 1991; Hobbs & Hopkins 1991; Panetta & Hopkins 1991).

Corridors as Traps or Sinks

Henein and Merriam (1990) and Soulé and Gilpin (1991) propose on the basis of simulation modeling that low-quality corridors could act as sinks, decreasing the size of a metapopulation. Field data on this proposition are nonexistent.

Discussion

The notion that corridors can't hurt, even if the possible biological costs could be discounted, is not necessarily always true. Much would depend on the relative costs and benefits of a proposed corridor and alternative uses of the funds (Simberloff & Cox 1987). Because there are so few data on the importance of movement through corridors, such an analysis will be very difficult. We believe no thorough analysis of this sort has ever been conducted. Possibly the most that can be done today is to say that some options are much less likely to be important than others, but even this attempt is rarely made. The enormous price of some corridor proposals surely implies that other options would not be pursued. For example, a 300-meter-wide corridor from south Florida to Canada, proposed by Hunter et al. (1988), would be approximately 720 km^2, enough for a very large refuge. If it were possible to buy conservation lands of this magnitude, would this corridor be the best possible purchase?

Florida provides examples of the uncritical advocacy of extremely expensive corridors. Florida's Conservation and Recreation Lands (CARL) acquisition program has an annual budget of approximately $50 million from the sale of real estate stamps and an additional $135 million from the Landmark Preservation 2000 bond program. Preservation 2000 bonds have been authorized for the first two years only, although the program is envisioned to extend ten years. Proposed acquisitions still far exceed available funds. For example, of 93 CARL proposals passing a stringent double review by 1991, a priority list of 60 had a tax-assessed value of $408,000,000 (fair market values are often twice tax-assessed ones). Thus, every acquisition means other land will not be acquired. Citizens of several counties have voted to tax themselves to acquire land. Many such counties apply for joint acquisition projects to the CARL program. County governments also face lists of projects far exceeding available funds.

The Florida Natural Areas Inventory submitted the Blackwater-Eglin Connector project to the CARL program in 1988 (Anonymous 1988). This 2400-ha corridor was intended to connect Eglin Air Force Base (187,500 ha) with the Blackwater River State Forest and the adjacent Conecuh National Forest (143,250 ha combined). Anticipated fair market value exceeded $5 million. The corridor was "to join three large publicly owned areas ... into a single, uninterrupted ecological unit of nearly one million acres; to assure perpetual opportunities for gene flow among all populations in these areas; to allow for direct movements of individuals of more vagile species..." (Anonymous 1988). The application spoke of the "urgency and desirability of developing systems of interconnected reserves for maintaining the full scope of biotic diversity" and stated that "connections between reserves create buffers against stochastic changes in populations, including local extinctions, and provide suitable pathways for 'natural' inoculations of new genetic material...."

No data showed that any species needed to move from one site to the other. Black bears are mentioned as potential users of the corridor, but they do not occur regularly in the Blackwater River State Forest or north of it (Brady & Maehr 1985). The corridor is complicated by Interstate 10, which separates Eglin from Blackwater. While small culverts run under the highway, there is no evidence that bears or other species use them or that they would substantially decrease highway mortality. Black bears are loath to cross interstate highways (Brady & Pelton 1989).

The Blackwater-Eglin Connector was also proposed to aid the movement of Red-cockaded Woodpeckers (*Picoides borealis*) (Anonymous 1988). The woodpeckers move up to 90 km (Walters et al. 1988*a*), but we doubt that this corridor would be effective. Of breeding females, 19% move per year, fewer than 5% of these move more than 5 km, and about 70% survive the year (Walters et al. 1988*b*). Therefore, the chance that a female will move that far and survive is about 0.7% per year. For all life-history categories together, the annual chance that a bird will disperse and survive is 4–8%. For breeding, this percentage is at least halved, because over 60% of dispersal is by first-year birds that produce only 20–67% as many fledglings as older ones.

Probabilities must be further reduced depending on the chance that a bird finds and uses the corridor. The distance traversed by the corridor is about 6 km, but midpoints of the two refuges are 45 km apart. Much less than 1% of the population monitored by Walters et al. (1988*b*) moved this far, so the great majority of dispersers will probably stay within their original refuge. The corridor itself is unsuitable for the woodpecker. Greatly altered by logging, it consists of streamside hardwoods and commercial pinelands. Several streams through the site have been impounded to create amenity lakes. It would surprise us if even 1% of dispersing individuals used this corridor, but if that many did, 0.04% of the population might reach the adjacent refuge and contribute to future generations. About 300 colonies inhabit both refuges (Wood & Wenner 1983), and each colony produces 1.2–1.7 fledglings per year (Walters et al. 1988*b*). So one successful dispersal might occur every 5–7 years. The corridor would thus be a very expensive way to move very few woodpeckers. It is unfair to ascribe the entire cost of a corridor to one or two target species when others would surely use it, but an expenditure of this size merits discussion of the full roster of species that would benefit.

This proposal was not approved by the CARL program. This fate contrasts with that of the Pal-Mar project, submitted to the CARL program in 1990 as a 8860 ha site in Martin and Palm Beach counties (Anonymous 1990*b*). Its fair market value was estimated at $22 million. The site is a large, relatively intact system of mesic/wet flatwoods and depression marsh/wet prairies containing many listed plant and animal species—perhaps the biggest relatively undisturbed functional wetland in south Florida east of the Everglades.

After the original application had been submitted, staff of the Florida Department of Natural Resources suggested expanding the project (Timmerman et al. 1991). They stated that the main thrust of a plan they had been developing to protect biological diversity in southeast Florida was establishment of two large corridors, and they suggested adding a corridor connecting Pal-Mar to Jonathan Dickinson State Park, which contains approximately 4850 ha. This corridor, subsequently added to the proposed Pal-Mar project, is 1.6 km wide and 10 km long, with one other section of land. The corridor is thus 18 km^2. It is bordered to the north by orange groves and to the south by residences. No estimate of cost was provided, but the proposed corridor contains substantial developable uplands, and its tax-assessed value is $21,000,000. Not only did the proposal request addition of a corridor (without biological data on which species would use it or why it is necessary), but it added that the corridor was key to the whole project and should be purchased *before* the original proposed acquisitions. The letter failed to mention that this corridor is traversed by two major highways. The final project design with recommended acquisition phasing has not yet been completed.

The detailed assessment of the Pal-Mar project, prepared by staff of the CARL land acquisition selection body (Anonymous 1990*b*), stated: "Acquisition of the Pal-Mar proposal will secure a corridor connecting J. W. Corbett Wildlife Management Area to Jonathan Dickinson State Park, and prevent otherwise inevitable development that would isolate the state park and *lead to faunal extirpations*" (our italics). Indeed, despite the fact that acquisition of the site proposed initially would protect a vast wetland system containing many state- and federally-listed species, the project assessment said, "Acquisition of the Pal-Mar tract would serve several purposes of regional significance, *the primary one* being the protection of a large portion of a proposed wildlife corridor that would link Jonathan Dickinson State Park to J. W. Corbett..." (our italics). The assessment even acknowledged that "Perhaps the most significant hurdle that this plan must overcome is the fact that wildlife routes between the state park and Pal-Mar are impeded by I-95 (six lanes) and the Florida Turnpike (four lanes), which run side by side less than a mile west of the park." Thus, even though large mammals have never been documented on the site and would need to cross ten heavily traveled lanes, the State of Florida is considering buying an 18 km^2 corridor on very expensive developable south Florida land.

We detail these examples because we feel that no abstract discussion of corridors can adequately guide acquisition and management decisions. There may well be specific cases in which a proposed corridor would be more effective than an alternative. For example, in parts of the American West, where many potential high-quality corridors are already in public ownership, one might expect acquisition costs to be low (Noss, personal communication) and use high. Noss (personal communication) suggests that elimination of below-cost timber sales in such sites might even save public money. However, the same benefits might derive from other land that might be set aside in the same region; are these the acres we would most wish a public agency to sequester? Noss (1987) believes that even major corridor costs can be met by the right sort of publicity and/or by peace dividends. We hope he is correct, but if he is, could not other conservation expenditures similarly increase? Surely costs and benefits of alternative strategies should be considered.

It is important to realize that there *are* general alternative strategies to facilitate survival where refuges are insufficient. Franklin (1989) has recently propounded the "new forestry," a collection of methods by which even logged forests in the American Northwest might be more useful for conservation than they are now. The key is that the entire landscape be managed as a matrix supporting the entire biotic community. The specific costs entailed in such management have not been tallied. In the longleaf pine forests of the American Southeast, topography and aspects of the biology of key species suggest that such an approach would not be prohibitively expensive (Simberloff 1992). The tablelands of northern New South Wales can be managed so that the entire landscape, not just reserves, contributes heavily to the conservation of the community (McIntyre 1991).

Numerous authors have pointed to the importance of small *un*connected patches of forest or even single trees for the persistence of populations (see Date et al. 1991; Prevett 1991). McDowell et al. (1991) call for a network of such "stepping stones" connected by corridors to minimize extinctions in the South African fynbos community. If resources are insufficient for both, which would be more useful? How dense and how large must a network of stepping stones be to be useful in this system?

Of course these strategies are not incompatible; corridors and stepping stones could be part of an entire landscape managed for both extraction and conservation. However, limited funds will almost certainly prevent the simultaneous adoption of all possible approaches, and it is simply not useful in practice to advocate "strategically placed larger reserves complemented by local or regional networks of smaller reserves and short connecting links between them in as many directions as possible" (Blyth 1991). One must be willing to set priorities, and these should be based on relative costs and benefits. We do not agree with Saunders and Hobbs (1991*a*) that we should preserve all corridors now because we do not have the time to find out if they are useful. If, by preserving them, we fail to pursue other options, such an approach is not prudent.

Finally, to the extent that this trend is encouraged by the fact that the concept of corridors is easily understood by the public and legislators (Harris & Gallagher 1989) or that "people feel they are doing something for conservation" (Bennett, in Stolzenburg 1991); it is not a scientific phenomenon at all; but it still has costs and benefits, and these are not being addressed. Is it good conservation biology to sell legislators and the public on the easiest program for them to understand, in the absence of evidence that it is the most effective one? Is it beneficial for people to feel they are doing something important for conservation by preserving narrow roadside strips (Bennett's corridors) in the absence of evidence that they really are doing something? Even if they are, is preserving such corridors sufficient? Does it foster the belief that one has done enough and need not preserve larger tracts of valuable habitat? We cannot answer such questions, but we believe that it is important to raise them.

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Introduction to Habitat Conservation Planning

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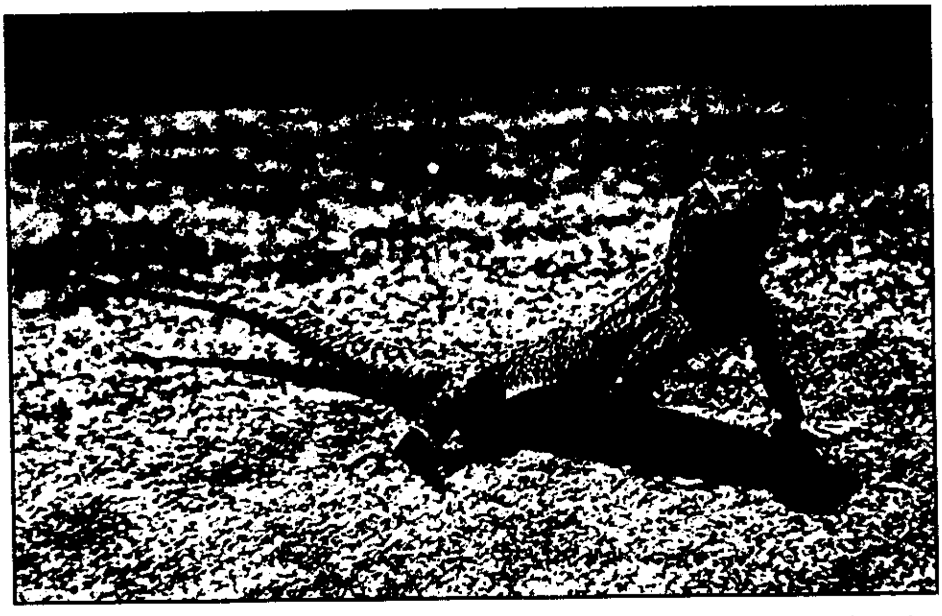
Habitat conservation plans (HCPs) have become an increasingly prevalent land management tool that seeks to balance the needs of endangered or threatened species with the needs of non-federal landowners. HCPs are voluntary agreements under the Endangered Species Act (ESA) negotiated between the federal government and private landowners or state and local governments, and, in some cases, other stakeholders. These agreements are designed to allow landowners to receive a federal permit—known as an incidental take permit—to unintentionally harm listed species in the course of completing proposed projects. In exchange for a permit, landowners agree to pursue specific management protections for endangered and threatened species.

HCPs are as varied and diverse as the habitats they aim to protect. HCPs range in size from a few acres to over a million acres. Some plans focus on a single species, while others focus on multiple species or ecosystems. Some HCPs are negotiated directly between the U. S. Fish and Wildlife Service (FWS) and the landowner; others involve a host of stakeholders, such as state and local governments, environmental groups, recreational groups, non-applicant landowners, and business organizations. HCPs also differ in their duration—permits range from one year to 100 years—and use a variety of funding mechanisms (Beatley 1994; FWS 1997b). Finally, HCPs vary in the means the parties to the agreement use to protect species: some HCPs focus on preserving key habitat areas while others require predator control, prescribed burning, or other mitigation measures.

One example of an HCP is the Coachella Valley HCP near Palm Springs, California (Beatley 1994). This HCP developed because rapidly expanding housing development on private land in the California desert increasingly threatened the habitat of the Coachella Valley fringe toad lizard (*Uma inornata*). Rather than go to court, the housing developers, federal and state agencies, conservationists, affected county governments, and other parties negotiated an HCP that was designed to allow development to continue and still protect key portions of the lizard's habitat. Completed in 1986, the HCP established three reserves totaling 17,000 acres, 8,000 acres of which is potentially occupiable lizard habitat. The parties acquired the reserve holdings using funds from The Nature Conservancy, the Federal Land and Water Conservation Fund, and other sources. Counting the reserve system and public lands in the valley managed as lizard habitat, the HCP protects roughly 15 percent of the total lizard habitat that remained in 1985. The rest of the lizard's range is open for development largely without restriction; counties do, however, assess a per-acre mitigation fee on all new development within the lizard's historic range. The FWS permitted the HCP for a period of thirty years, and it has largely been implemented as planned.

HCPs are likely to play an increasingly important role in species conservation in the United States. First, more attention is being paid to protecting listed species on non-federal lands, where conflicts between development and species are most likely to occur. According to a 1994 report by the General Accounting Office, over 80% of listed species reside in habitat on non-federal lands and nearly three-quarters of listed species have more than 60% of their habitat on non-federal lands (U.S. General Accounting Office 1994). Moreover, federal conservation efforts have begun to focus species recovery efforts on a number of "hot spot" areas, especially Florida, Southern California, Texas, and old growth forests in the Pacific Northwest, where high levels of endemism exist, and where biodiversity is jeopardized by rapid economic growth and development (K. Day, FWS, personal communication, Oct. 2, 1996; see e.g., Rodriguez et al. 1997). Approved HCPs are already most numerous in these areas and will continue to play important conservation roles there.



The Coachella Valley fringe toad lizard (*Uma inornata*) was one of the first endangered species covered under an HCP. Photograph by B. Moose Peterson/WRP.

HCPs are also important because they may help address weaknesses in the ESA. While the ESA has functioned well as a last ditch effort to prevent extinction, it has routinely failed either to address the habitat needs of species before they face extinction or to recover species to the point that they can be removed from the endangered species list (see e.g., National Research Council 1995). Both supporters and critics of the ESA have also identified the law's focus on individual species and lack of an overall habitat-oriented perspective as major weaknesses (Rohlf 1991). The lack of resources available for endangered species protection efforts has also been a continuing problem.

Many have pointed to HCPs as a promising tool to address these concerns (see e.g., Thornton 1991). For example, because HCPs can be designed as multi-party collaborative processes that can include both public and private lands and species other than those that are listed under the ESA, they can provide opportunities to protect species before they face extinction and to implement ecosystem-based management (FWS and NMFS 1996). HCPs can also function as a surrogate for community open-space planning, which may engage people who might otherwise not be concerned about endangered species in the process of protecting their habitats. Finally, HCPs may also provide opportunities to leverage significant private and public resources to implement species protection measures.

Legislative and administrative history

HCPs arise from Sections 9 and 10(a) of the ESA. Under Section 9 of the ESA it is illegal to "take" (i.e., kill, harm, or harass) a listed species. This prohibition against the take of species applies to private and public lands and has been interpreted broadly to include habitat destruction or modification. This prohibition has been particularly problematic for private landowners who could be subject to criminal and civil penalties for undertaking development activities that could harm or kill listed species on their lands (Beatley 1994). However, under Section 10(a) of the ESA, non-federal landowners who plan activities on their lands that may "incidentally take" (i.e., unintentionally harm) a threatened or endangered species may apply to the FWS or National Marine Fisheries Service (NMFS) for an incidental take permit (ITP) that exempts them from this strict Section 9 prohibition against take. In order to receive this ITP landowners must, among other things, prepare an HCP.

Congress was urged to create the Section 10(a) exemption by proponents of a conservation plan on San Bruno Mountain, California that was crafted in the early 1980s. In the conference report on the 1982 ESA Amendments, Congress specified that it intended the San Bruno plan to act "as a model" for future conservation plans developed under the incidental take exemption provision and that "the adequacy of similar conservation plans should be measured against the San Bruno plan" (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 31). Congress further noted that the San Bruno plan: (1) was based on "an independent exhaustive biological study" completed prior to the development of the plan; and (2) protected at least 87% of the habitat of the listed butterflies that led to the development of the HCP—enough habitat "to allow for enhancement of the survival of the species" (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 32).

To receive an ITP under Section 10(a), applicants must at a minimum submit a conservation plan that specifies (1) the impact which will likely result from their proposed incidental take; (2) what steps they will take to minimize and mitigate impacts, and the funding that will be available to implement such steps; (3) the alternative actions the applicant considered, and why they are not being used; (4) other measures required by the agency; and (5) procedures to deal with future unforeseen circumstances that may affect the health of the species or the success of the HCP (50 C. F. R. §§ 17.22, 17.32(b)(1)).

The habitat conservation planning process

The planning process has three general stages: development, approval, and implementation. The development of an HCP typically requires significant scientific baseline collection and analysis, often conducted by outside consultants hired by the applicant. The whole process can take many years and cost millions of dollars. Usually, district-level FWS or NMFS staff assist in the applicant's development of the HCP by providing clarification, scientific information, and feedback. For many large or complex HCPs, a steering committee representing affected stakeholders and scientific and agency interests is formed.

In the development stage, parties also negotiate the terms of the agreement. In return for allowing an incidental take of a species, the parties agree to pursue specific management protections for the species. Almost all HCPs share a basic central strategy of identifying and protecting certain high value habitat areas (Beatley 1994). In some cases, the landowner sets aside a portion of his or her own land for conservation purposes; in others, the landowner or independent parties (e.g., private land trusts; local, state, or federal government entities) purchase the habitat conservation areas. Local zoning restrictions have also been used to protect designated areas (Beatley 1994). In addition to these land protections, HCPs can also include other mitigation actions, such as public education campaigns, habitat restoration, land-use restrictions on nearby public lands, control of exotic species or predation, captive breeding, or changes to the design or density of landowners' projects (Beatley 1994).

The approval stage of the HCP planning process involves both internal agency analysis and external public review. The applicant usually submits four documents for agency approval: (1) a completed permit form which requests the specified amount and rate of incidental take; (2) the HCP, which includes the scientific information and details of the mitigation plan; (3) an implementation agreement which serves as a binding contract and details how

The gray wolf (*Canis lupus*) is covered by several multi-species HCPs. Photograph courtesy of U.S. Fish and Wildlife Service/John and Karen Hollingsworth.

the elements of the plan will be carried out, paid for, and monitored; and (4) the appropriate National Environmental Policy Act (NEPA) documentation (i.e., environmental assessment or environmental impact statement). The agency in turn will amend the NEPA documents if necessary and publish notice of the HCP and a minimum 30-day public comment period in the Federal Register. If the agency approves the HCP, it issues the applicant an ITP. This permit action qualifies as a federal agency action; thus, the agency must engage itself in a "self-consultation" process to evaluate whether the proposed action is in compliance with Section 7 of the ESA (50 Federal Register 39685, Sept. 30, 1985). State endangered species laws and environmental reviews, as well as local zoning or planning regulations, may require additional documentation or public review.

Implementing the HCP involves carrying out the prescribed mitigation actions, collecting funds, and monitoring take levels and overall species impacts. Funding for implementation of the HCP can take many forms and often involves some combination of federal, state, local, and private sources, such as per-unit fees on new development, community-wide taxes, contributions from participating groups (e.g., The Nature Conservancy), state wildlife funds, issuance of city bonds, and Federal Land and Water Conservation Fund appropriations (Beatley 1994). Monitoring responsibilities for approved HCPs are usually jointly shared by the applicant and the FWS or NMFS and often involve preparation of periodic reports documenting the amount of development that has occurred, number and type(s) of listed species taken, and the amount of money generated and spent to date (see Dohner and Smith, this issue).

The growth of HCPs

Landowners and the agencies initiated relatively few HCPs in the years following the creation of the Section 10(a) incidental take provisions in 1982. Traditionally, the agencies focused their efforts on those projects or actions that included federal lands or some federal permit approval. Since the Section 10 process is voluntary, most potential applicants chose not to participate and appear to have relied on lax enforcement of the Section 9 take prohibitions on private property (Houck 1993). Moreover, the HCP process was historically viewed as procedurally difficult, costly, plagued with delays, and risky in terms of regulatory assurances (Thornton 1994).

Habitat conservation planning, however, has changed dramatically in recent years. Growing scientific recognition of the role of private lands for endangered species recovery and the landmark 1981 District Court ruling in *Palila v. Hawaii Department of Land and Natural Resources* (639 F.2d 495, 9th Cir., 1981) both contributed to making Section 9 "a major force for wildlife conservation and a major headache to the development community" (Thornton 1991, p.610). Indeed, during the last decade there has been a significant rise in disputes concerning Section 9's application to private property (Thornton 1991).

Perhaps more importantly, the Clinton Administration has made several administrative changes in its ESA policies that have increased the incentive for landowners to engage in the HCP planning process and led to a dramatic increase in the number of landowners applying for and receiving approval for HCPs (see e.g., FWS 1995). Indeed, in an effort to encourage the broader application of HCPs and to deflate Congressional efforts to weaken the ESA, the Clinton Administration has sought to make Section 10 and HCPs "one of the ESA's most important and innovative conservation programs" (FWS 1995).

The result has been a dramatic increase in the number and scope of HCPs that have been proposed and approved. Prior to 1994 the FWS had approved a total of only 20 HCPs. However, after the Clinton Administration's efforts to streamline the planning process and increase landowner incentives to participate, the FWS approved 174 new plans between 1994 and 1996. At the end of 1996 there were approximately 200 HCPs at some stage of preparation, and the FWS expects to work on as many as 400 during FY 1998 (FWS 1997a, b). In addition, the scale and scope of HCPs have increased dramatically in recent years. The FWS and NMFS report that the majority of HCPs developed prior to 1995 were of less than 1,000 acres in area while HCPs in development in 1996 included 25 that exceed 10,000 acres, 25 that are more than 100,000 acres, and 18 that exceed 500,000 acres (FWS 1997b). By September 1997, the U. S. Department of Interior expects that more than 18.5 million acres of private land and over 300 species will be covered by HCPs (1997).

Administrative changes

The growth of HCPs and the policies that led to this growth raise several controversial issues that are the subject of articles in this issue. Our goal here is to provide background on these issues.

No Surprises policy

One of the most significant policy changes by the Clinton Administration was its adoption of the so-called No Surprises policy on August 11, 1994 (U.S. Departments of Interior and Commerce 1994). This policy assures landowners that once the agencies have approved an HCP, the landowner will not be required to accept new land-use restrictions or financial commitments beyond those agreed to in the HCP. Thus, if "unforeseen circumstances" reduce the likelihood that a species covered by the HCP will survive over the term of the permit, the agencies agree to bear the sole responsibility—both financial and logistical—of all recovery efforts above and beyond that required by the HCP. The policy further specifies that the agencies bear the burden of proving that unforeseen circumstances exist and that any additional future mitigation not called for in the original HCP be conducted within the geographic confines of the original HCP unless the permittee allows otherwise. Also under the policy, the agencies agree not to impose additional mitigation measures of any type on landowners whose HCPs are designed to have a net positive impact upon a species. Under current agency guidelines, all new HCPs must be consistent with this policy (FWS and NMFS 1996).

Approximately 74 of the HCPs issued after 1994 are thought to contain the No Surprises assurance (see Baur, this issue), although the agencies did not officially publish the No Surprises policy in the Federal Register until May 29, 1997. The agencies agreed to seek public comment on the policy and on any HCP that contains the No Surprises assurance when they settled a lawsuit filed by environmental groups unhappy with the process used to adopt the policy (62 Federal Register 29091, May 29, 1997).

Least Bell's vireo (*Vireo bellii pusillus*). Photograph courtesy of U.S. Department of Defense.

Other policy changes

The Clinton Administration has also adopted measures to encourage the development of large-scale, multi-species HCPs and to streamline agency procedures. In November of 1996, the FWS and NMFS released their Habitat Conservation Planning Handbook. While it is "not intended to supersede or alter any aspect of endangered species law or regulation" and serves only as a "guide," the Handbook does contain a number of important procedural changes aimed at expediting permit processing times, reducing the total number of permitting steps, combining required regulatory measures, and increasing coordination earlier in the HCP process. The Handbook focuses on how "to streamline the HCP process to the maximum extent practicable and allowable by law" but does not necessarily focus on how to make HCPs work better for species protection. Agency streamlining has taken a number of forms including "target" permit processing times, creation of a "low effect" category of HCPs that are exempt from full NEPA review, integration of permit and environmental review documents, use of template language, and concurrent agency review processes.

On June 6, 1997 the FWS and NMFS published regulations regarding prelisting agreements and its Safe Harbors policy (Department of Interior 1997). Prelisting agreements forestall listing of an imperiled species in exchange for landowner conservation efforts. The Safe Harbors policy encourages landowners to improve habitat for listed species on their property and attempts to reverse the incentive that landowners currently have to take endangered species before their land is regulated. Under the policy, the appropriate federal agency determines a habitat baseline condition and any increase in a listed species population above that baseline condition that results from the landowner's voluntary stewardship efforts would not increase their regulatory responsibility or affect future land-use decisions. For example, the FWS and a private landowner might agree to provide habitat for a certain number of red-cockaded woodpeckers (*Picoides borealis*) on the landowner's property. As long as the landowner continues to sustain that habitat and population baseline, he or she can actively log or otherwise manage that land without fear of prosecution under the ESA. The agency has been implementing this policy for some time even though it has not yet been officially approved. Currently, twenty-five Safe Harbor agreements cover more than 21,000 acres of private land and more than 10 species (Department of Interior 1997). Sixteen more agreements are in progress and are expected to cover another 14,000 acres.

Key issues

Recovery

While the overarching goal of the ESA is to recover species to the point at which its protections are no longer needed, the goal of species recovery does not currently drive the HCP planning process. In the Conference report to the 1982 ESA Amendments, Congress required the agencies to base their ITP decisions, in part, on "whether the taking will appreciably reduce the likelihood of the survival and recovery of the species in the wild," a standard very similar to the "jeopardy" standard in Section 7 of the ESA (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 29). Congress also suggested that the agencies consider "the extent to which the conservation plan is likely to enhance the habitat of the listed species or increase the long-term survivability of the species or its ecosystem" (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 31).

However, while encouraging species recovery, current agency policies require only that an HCP ensure the survival of all included listed species. The agency claims that HCPs are not legally required to either contribute to recovery or result in a net benefit to an affected species (see e.g., Taylor 1994; FWS and NMFS 1996). In the Habitat Conservation Planning Handbook, the agencies interpret Section 10(a) to "reflect the fact that HCPs were designed by Congress to authorize incidental take, not to be ... recovery tools" (FWS and NMFS 1996. p. 3-20). However, the Handbook also states: "...contribution to recovery is often an integral product of an HCP...." and "[i]n general, conservation plans that are not consistent with recovery plan objectives should be discouraged" (Id.).

Public involvement and peer review

Congress gave the agencies broad discretion in implementing Section 10(a). The agencies, in turn, have given a high degree of discretion to landowners in developing the scope, duration, and level of public involvement in the HCP, as well as the number of species covered by the plan (FWS and NMFS 1996). Congress also saw Section 10(a) and its HCP provisions as a means for promoting "creative partnerships between the public and private sectors" (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 30) and suggested that HCPs be "developed jointly between the appropriate federal wildlife agency and the private sector or local or state governmental agencies." It did not, however, explicitly envision an extensive participatory role in the HCP planning process for concerned citizens, independent scientists, or other interested publics. Indeed, the statute requires the agencies only to publish notice of each application and a 30-day comment in the Federal Register (16 U.S.C. § 1539(c); 50 C.F.R. § 17.22 (4)(b)(1)). Moreover, since Congress clearly intended its HCP provisions to address "the concerns of private landowners who are faced with having otherwise lawful actions ...prevented by Section 9 prohibitions against taking" (H.R. Rep. No. 835, 97th Cong., 2nd Sess. 32, 1982. p. 29) the extent of public involvement has often been left up to the discretion of the applicants.

In practice, applicants developing HCPs utilize a variety of public participation methods often depending on the type of land ownership(s) involved in the plan and local and state laws. In some cases an HCP may be negotiated directly between the landowner and the agency, with the 30-day comment period as the only public review of the plan. In other cases, outside stakeholders participate on an HCP steering committee and have more influence over the development of the plan.

Conclusion

As the 105th Congress considers legislation to reauthorize the Endangered Species Act, a number of controversial policy questions surrounding HCPs have not yet been adequately answered. While much has been written about early HCPs, there is a paucity of written material focusing on how HCPs created pursuant to the Clinton administration's policy changes deal with these questions. Given the tremendous growth in the number and scope of HCPs being implemented today, these questions deserve to be answered quickly—the existence of hundreds of endangered species is at stake.

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Ethical and Welfare Issues Associated with Keeping Wild Mammals in Captivity

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> *There was an exhibition at the Zoological Park in the Bronx yesterday which had*
> *for many of the visitors something more than a provocation to laughter. There were laughs in it enough, too,*
> *but there was something about it that made the serious minded grave. Even those who laughed the most*
> *turned away with an expression on their faces such as one sees after a play with a sad ending*
> *or a book in which the hero or heroine is poorly rewarded.*
> *"Something about it that I don't like," was the way one man put it.*
>
> NEW YORK TIMES, 9 SEPTEMBER 1906

"Something about it that I don't like." Those words were uttered in response to the remarkable sight of a Congo pygmy, Ota Benga, being exhibited in a cage at the Monkey House along with an orangutan that he had been given as a companion. Ota had previously been on display at the St. Louis World's Fair, along with thousands of other native people collected from around the world by early-twentieth-century explorers. This human exhibition was designed to be the anthropological counterpart of Carl Hagenbeck's enormous animal circus, also on display at the fair, and in addition was to serve an avowedly scientific purpose: to collect measurements that would enable scientists to determine the characteristics that distinguished "primitive" from "civilized" man. Hundreds of thousands of visitors flocked to see Ota Benga at the zoo until protests by the Baptist clergy (combined with Ota's unruly behavior) forced Bronx Zoo director William T. Hornaday to release him to the care of the Howard Colored Orphan Asylum (Bradford and Blume 1992).

"Something about it that I don't like." Thankfully, the exhibition of human curiosities is now a rare occurrence. However, modern zoo visitors may find themselves experiencing similar uncomfortable and contradictory feelings when they stand outside of an animal exhibit, particularly if the animal appears to them to be "bored" or "unhappy." Such feelings are symbolic of an important change in our ideas about the relationship between humans and animals, and indicate a progressive enlargement of our moral concerns beyond traditional boundaries such as nation, race, or species.

Historically, animals have been viewed in Western culture primarily in the context of their usefulness to human beings. Human needs for food, draft power, entertainment, enlightenment, or companionship have therefore been the paramount considerations in the treatment of animals, and this has been reflected not only in custom but in law. Domesticated animals were viewed as property, which could be purchased, used, and disposed of at the owner's discretion as long as the legal rights of other persons were not infringed in the process. Even wild animals did not escape notions of utility (Thomas 1983). This is not to suggest that cruel treatment of animals was considered acceptable.[1] However, kindness to animals was advocated not because it was a duty owed directly to animals themselves, but because it improved human character.

Although concern about the treatment of animals grew steadily (Thomas 1983), it was not until the nineteenth cen-

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[1] It may have been common, however, at least according to our current notions of cruelty. For graphic descriptions of human (mis)treatment of animals historically, see Carson (1972), Ryder (1989), and Turner (1992).

tury that attitudes toward animals began to change significantly. This change led ultimately to the growth of the organized animal protection movement, as well as to the adoption of legislation that regulated the treatment of animals with the explicit intention of diminishing the pain or suffering experienced by the animals.

A number of factors propelled this change (Turner 1980; Sperling 1988). Innovations in technology and manufacturing resulted in the growth of cities and a reduction in the labor force required for food production. A large urban middle class emerged that had little daily contact with food or pest animals, but that was affluent enough to keep animals primarily for companionship. There seems little doubt that the growth of pet keeping has both paralleled and fostered more empathetic views of animals (Serpell 1986).

A second factor was the growth of animal experimentation. By the nineteenth century vivisection was common in medical and veterinary schools in Europe, and physiologists like François Magendie conducted public demonstrations in which animals were subjected to procedures such as invasive surgery and slow suffocation. Since effective anesthetics (for either humans or animals) were not available until the 1850s, most of these experiments were carried out on fully conscious animals, provoking widespread revulsion and a heightened sensitivity to the issue of animal pain. The ensuing passionate arguments concerning the utility and morality of animal experimentation are still with us today.

But perhaps the most critical factor was the emergence of a new and explicitly scientific perspective on the natural world. The development of this perspective can be traced to the elaboration during the eighteenth century of a classification scheme based on the structural characteristics of animals and plants (Thomas 1983). This increased attention to structural relationships among organisms laid the foundation for Darwin's theory of evolution, which shattered long-held assumptions about human uniqueness. It is the growing appreciation of the continuity and commonalities between animals and humans resulting from the study of evolutionary biology that has fostered much of the current debate about the treatment of animals in our society.

ETHICS AND ANIMALS

Humans have long pondered the basis for their superiority over animals (Thomas 1983). Characteristics that have been suggested as distinguishing humans from animals have ranged from the fanciful to the serious: dancing, laughter, cooking, manners, religion, a convoluted gut (in order that sublime contemplation can occur during the leisurely digestion of food), hair that grays, ears that wiggle, cerebral laterality, an immortal soul, politics, an upright posture, a protruding nose, the use of tools, reason, and language. These distinctions have often been used to justify the unique legal and moral status of human beings.

Recently, however, philosophers have begun to ask whether traits like these are truly significant in the sense that they entitle humans to different ethical consideration. Why is it morally acceptable to use animals for scientific experiments or to keep them in zoos for educational purposes when it is not acceptable to use humans in this way? If it is because humans have speech or reason, then how should we view humans who do not have these attributes, for example, infants or individuals who are brain-damaged? Clearly, the answers to these questions will also have an effect on how society deals with difficult problems in human ethics such as abortion and euthanasia.

Two philosophers have been particularly prominent in this debate about the treatment of animals: Peter Singer, the author of *Animal Liberation* (1990), and Tom Regan, the author of *The Case for Animal Rights* (1983). Regan and Singer have been called the "midwives" of the animal rights movement in the United States (Jasper and Nelkin 1992), since they gave the movement a coherent agenda and an ethical foundation. They (and others) have posed a fundamentally new question about animals: In addition to their value to humans, do animals have a value in and of themselves, and do they therefore possess interests that entitle them to be treated as objects of moral concern? If so, what duties do we owe them?

Singer argues that the ability to experience suffering and pleasure *(sentience)*, which is shared by humans and many animals, is the necessary and sufficient condition for having morally relevant interests: "It would be nonsense to state that it was not in the interests of a stone to be kicked along the road by a schoolboy. A stone does not have interests because it cannot suffer. Nothing that we could do to it could possibly make any difference to its welfare . . . [but] a mouse, for example, does have an interest in not being kicked along the road, because it will suffer if it is."

Singer contends that all sentient creatures are entitled to have their interests in avoiding suffering and experiencing pleasure weighed equally with those of other sentient beings in situations in which a conflict of interest might occur, such as when animals are raised for meat production. According to Singer, denying such equal consideration on the basis of species alone constitutes *speciesism*, which is analogous to racism or sexism in that it uses arbitrary and morally irrelevant characteristics to define the boundaries of moral concern.

Tom Regan, on the other hand, views sentience as only one of the attributes that entitle animals to moral consideration. According to Regan, animals (particularly mammals) also have perceptions, memories, emotions, desires, beliefs, self-consciousness, intentions, and a sense of the future. As such, they are what Regan terms *"subjects of a life,"* who have a right not to be harmed by having their interests (whether those interests consist of choosing a mate, discovering a new type of food, or living a long life) disturbed by others.

It is worth emphasizing that neither Regan nor Singer is advocating equal treatment for animals, as is sometimes mistakenly claimed. Both are well aware that there would be little point in giving pandas the right to vote or dogs the right to a public education, since such rights are irrelevant to the animals and could not be exercised. Neither do they believe that the like interests of humans and animals are necessarily of equal weight. This is illustrated by Regan in one of his dog-in-a-lifeboat scenarios, in which four normal, healthy humans and a similarly healthy dog are in a lifeboat and one must be thrown overboard to ensure the survival of the rest. Justifying his choice of the dog, Regan states: "Now, the harm that death is, is a function of the opportunities for satisfaction it forecloses, and no reasonable person would deny that . . . death for the dog, though a harm, is not comparable to the harm that death would be for any of the humans."

Philosophers who criticize Regan and Singer dispute their view that animals have morally relevant interests on two general grounds. The first of these is based on differing views as to the nature of rights and morality. Rights have been defined as something "which can be claimed, demanded, asserted, insisted on, secured, waived or surrendered . . . a right is related to and contrasted with a duty, an obligation, a privilege, a power, a liability" (White 1984). Clearly, animals can neither claim rights nor carry out the duties associated with them. Contractualist philosophers such as Peter Carruthers (1992) argue that morality consists not of "givens," but of a (imaginary) contract between rational agents who are in agreement about claims and obligations. This places animals outside of the direct moral circle.

The second disagreement arises with respect to the traits or characteristics that are essential in order to have morally relevant interests. R. G. Frey (1980), for example, argues that animals cannot have interests because they do not have desires that can be thwarted or satisfied. According to Frey, in order to have desires one must also have beliefs about the world, and having beliefs requires both awareness and language. Carruthers (1992), on the other hand, contends that animals cannot suffer because their experiences of pleasure and pain, unlike human experience, are not conscious. In Carruthers's view, a conscious mental state is one that is available to conscious thought, which in its turn is also available to be thought about (what the ethologist Donald Griffin [1991] has called "thinking about the process of thinking itself").

It is plain that much of the current philosophical debate results from conflicting ideas about whether or not animals have subjective mental experiences and what the quality of those experiences might be. Until relatively recently, ideas about animal minds were bound up with ideas about the soul. Medieval theologians, while accepting that animals had souls, were careful to draw distinctions between humans and animals: Thomas Aquinas (1225–1274), for example, stated that humans had a soul that was superior in that it was intellectual and thus nearest to the divine likeness (Thomas Aquinas 1928). The idea that there was a distinction between humans and animals reached its peak in the writings of the French philosopher and scientist René Descartes (1596–1650), who discounted the idea of animal souls entirely.

Descartes conceptualized the soul as the seat not only of thinking but also of perceiving and feeling; in other words, of consciousness or the mind. As Stephen Walker notes (1983), this placed Descartes in an awkward position: animals had to be given all or nothing, souls or no souls, minds or no minds, not simply inferior minds. Descartes chose to give them no minds, for reasons that were influenced by his theological views about the soul: "There is none which is more effectual in leading feeble spirits from the straight path of virtue, than to imagine that the soul of the brute is of the same nature as our own, and that in consequence after this life we have nothing to fear or hope for, anymore than the flies and ants" (Descartes 1989, 16). Descartes instead postulated that animals were simply cleverly designed machines, automata without souls that responded to events in a programmed manner. Two characteristics served to differentiate men with souls from such automata: speech and voluntary action.

The more extreme implication of Descartes's view was that animals had no feelings and were therefore unable to experience pain. Although this view was by no means universally accepted, Descartes's lasting influence on the disciplines of biology and psychology is obvious. Until recently, researchers have generally adopted the principle known as Morgan's Canon when interpreting the behavior of animals: "In no case may we interpret an action as the outcome of an exercise of a higher psychical facility, if it can be interpreted as the exercise of one which stands lower on the psychological scale" (Morgan 1894). Even those who were willing to believe that animals had subjective mental states did not believe that those states could be studied scientifically. The study of psychological aspects of pain in animals, for example, is a very recent phenomenon (Bateson 1991).

Advances in the study of artificial intelligence and of the neurobiology of information processing in humans, however, have begun to show that mind is a property of the brain, although one that is poorly understood at present (Churchland 1986). Given the obvious similarities among vertebrates in the organization and function of the central nervous system, it seems probable that there is also an evolutionary continuity of consciousness or awareness. Darwin (1871) argued that animals feel pleasure and pain, experience excitement, suffer from boredom, demonstrate attentiveness and imagination, and are capable of reasoning. More recently, Donald Griffin (1974, 1992) has provided compelling evidence that animals show versatile behaviors and complex patterns of communication, indicating that they possess at least a rudimentary level of consciousness, which Griffin defines as the ability to think subjectively about objects and events.

Approaches to analyzing the behavior of animals that presume that animals have subjective mental states are not without their detractors (Kennedy 1992). Nevertheless, society seems increasingly inclined to give animals "the benefit of the doubt" and to assume that they have at least some level of awareness as well as certain morally relevant interests, such as an interest in being spared pain and suffering. This approach, however, raises the question of how the conflicts of interest between humans and animals that inevitably result can best be resolved. This topic deserves mention here, since the way in which we decide to resolve such conflicts has a crucial bearing on the types of animal use that society will ultimately find acceptable. It is also an area in which Peter Singer and Tom Regan diverge sharply in their approaches.

Singer, who is a utilitarian, believes that morally correct actions are those that result in the greatest aggregate good. This means that the costs and benefits to all sentient parties potentially affected by particular actions must be calculated, and the action taken that will maximize total pleasure and minimize total suffering. Thus, when contemplating testing a new drug on mice, researchers must weigh the costs to the mice in terms of suffering associated with captivity, testing, and death equally with the benefits that might accrue to humans if the drug proves to be an effective anticancer agent. In practice, many of us appear to use some such type of rough cost-benefit calculation when we make decisions about animal use (Galvin and Herzog 1992). Singer's philosophical position would therefore appear to be permissive of animal use in some situations. In practice, however, Singer is opposed to farming, animal experimentation, and most other uses of animals, arguing that the benefits rarely outweigh the costs.

Regan, on the other hand, argues that utilitarian calculations can result in our carrying out actions that run counter to our prevailing notions about morality. What, he asks, about his (hypothetical!) Aunt Bea, who is elderly, crotchety, and wealthy? Would not the greatest good be served by killing her and donating her fortune to a local children's hospital? Perhaps, but killing Aunt Bea would deprive her of her right to continue living; in this case, Aunt Bea's right to life "trumps" the aggregate good.[2] Regan argues that we should carry out those actions that ensure that the number of individual rights that are overridden is minimized, unless overriding the "rights of the few" will cause those few greater harm than overriding the "rights of the many." According to the rights view, the hapless mice referred to above should not be used to test the drug regardless of its potential benefits, since the value of the mice cannot be reduced merely to one of possible usefulness to humans.

By no means all philosophers who believe that animals have interests are opposed to animal use. Mary Midgley, for example, in her book *Animals and Why They Matter* (1983), suggests that we use a mixture of common sense and empathy when deciding how to treat animals. Bernard Rollin (1981) states that we must change the ways in which we care for captive animals in order to allow them to express their biological needs. These individuals articulate what we believe to be the current views and concerns of the public: that animals be spared pain and suffering (including suffering due to boredom, loneliness, and restriction of freedom) to the greatest extent feasible consonant with their use, that they experience a good quality of life while in captivity, and that they not be used for purposes that are "trivial." With these concerns as a backdrop, we now turn to a consideration of the nature and purpose of the zoo.

HISTORY OF HUMANS AND ANIMALS IN THE ZOO

The historical development of the zoo has been a mirror of these changing sentiments about the relationship between animals and humans. Zoological parks were an outgrowth of the privately held menageries that had been symbols of the wealth and power of the nobility since antiquity. By the late Middle Ages, however, menageries had also become a popular form of public entertainment in Europe. The display in London in 1254 of the first elephant to arrive in Britain attracted spectators from all over the country. Patrons who were too poor to pay the entrance fee to the menagerie established by Henry III at the Tower of London could have the fee waived by bringing a live cat or dog to be fed to the carnivores (Bennett 1829). Although menageries began to be unfashionable on the continent by the middle of the eighteenth century (Hahn 1967), an interest in collecting and observing exotic animals continued.

The first true zoological park was established at the Jardin des Plantes in Paris in the late eighteenth century, due largely to political circumstances but in part at the urging of prominent naturalists like Georges Louis Leclerc, Comte de Buffon. Buffon argued that the Paris botanical gardens were not complete as a living natural history museum without animals. This approach to integrating animals into the landscape had been adopted earlier (although with an aesthetic rather than a scientific purpose) by Louis XIV in his menagerie in the gardens at Versailles. The Jardin des Plantes was initially stocked with those animals that were not eaten by the starving population after their "liberation" from the private menageries during the French revolution by Jacobin sympathizers, who viewed the animals' incarceration as a representation of tyranny and denial of freedom (Loisel 1912). In keeping with the spirit of the age, the directors of the Jardin des Plantes stressed that the purpose of the zoological garden was scientific research rather than public entertainment, and many scientists did in fact avail themselves of the opportunities afforded by the collection (Hahn 1967).

The establishment of the Jardin des Plantes inspired Sir Stamford Raffles and Sir Humphrey Davy to found the Zoological Society of London in 1826, an event that was soon followed by the opening of the Regent's Park Zoo. Raffles envisioned a serious mission for the new zoo: it was to be "a scientific establishment . . . for teaching or elucidating Zoology" and a place where "new breeds, and races of animals [could be introduced] for the purpose of domestication" (quoted in Ritvo 1990). To foster this mission, admission to the zoo was originally restricted to the carefully selected members of the Zoological Society. Due to a pressing need for revenue, however, the zoo was soon opened to the public, and animal shows and "petting" zoos were incorporated to attract visitors (Ritvo 1990).

As the number of zoos grew throughout the nineteenth century, so too did protests against them. One area of controversy was the public feeding of live mammals to snakes and carnivores, which was opposed on the one hand by Charles Dickens, who thought it terrifying to the prey and demeaning to the spectators, and on the other by some so-

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[2] Actually, many utilitarian philosophers, including Singer, would also argue that killing Aunt Bea is wrong, although on different grounds than Regan. See Harris (1992) for a description of "Act" versus "Rule" utilitarianism and Goodin (1991) for information about preference utilitarianism.

called Darwinians who thought it wrong to feed "higher" animals to "lower" animals. Although public feedings were subsequently discontinued at the Regent's Park Zoo, wealthy patrons could still view private feedings by paying a fee to the keepers (Turner 1992).

Larger concerns, however, revolved around the treatment and care of zoo animals. There was a pronounced fascination with the intelligence and learning abilities of animals in the nineteenth century among both scientists and laypeople. This fascination resulted in a boom in the training of both domesticated and captive wild animals to perform tricks for public amusement and enlightenment. The training techniques used for wild animals were often painful, involving beating, burning, and the inducement of fear. Unruly zoo animals were controlled using similar techniques.

The outcry against the use of these techniques in Britain led to the passage of the Cruelty to Wild Animals in Captivity Act in 1900, which outlawed the teasing, abusing, or infuriating of captive animals (Ryder 1989). In the United States during this period the Jack London Club was formed to boycott trained animal performances. The club attracted more than 300,000 members, and Ringling Brothers, Barnum and Bailey chose to discontinue their animal acts from 1925 through 1929 as a result of the public pressure (Mighetto 1990). A beleaguered Hornaday, responding to complaints about the whipping of an elephant in musth at the Bronx Zoo, placed a sign on the elephant's cage that read, "Whipping an elephant *does not* hurt him; but he *thinks* it does," an interesting commentary on contemporary views of animals (cited in Bradford and Blume 1992).

There were equally vociferous protests about conditions in the zoological parks. After the opening of the Central Park Zoo in 1873 in a converted arsenal in New York, Henry Bergh, the founder of the American Society for the Prevention of Cruelty to Animals, posed the question: "What is the use or sense of penning those poor beasts up to gratify the curiosity of idle gazers . . . in the miserable shed in Central Park? . . . Neither public taste, education nor morals are benefitted" (quoted in Carson 1972).

Indeed, there was much to be concerned about in the early zoos. The lack of information available to the zoos about husbandry of exotic species was made graphically evident by Hornaday, who wrote: "Fame awaits the man who can discover a bill of fare on which Howling Monkeys, Sakis and Yerkees can live in captivity to adolescence, and repay their cost and care." Nevertheless, zoos were extremely popular, and Hornaday also made it clear that "So far as the available supply of captive primates will permit, these typical species will constantly be kept on exhibition, together with many others equally interesting" (Hornaday 1906).

Early capture, transport, and introductions of wild-caught animals to the zoo environment were governed by trial and error as zoos ventured to exhibit "never before seen" species (Hornaday 1906; Mann 1957; Zeehandelaar and Sarnoff 1971). Hunters, whalers, and military personnel could be commissioned to bring zoos living trophies of their expeditions. Foreign gifts to presidents, unwanted exotic pets, and circus donations were also a source of zoo animals (Bain 1989; Ehrlinger 1993; Mullan and Marvin 1987).

Mortality during capture and transport could be high. In 1900, the animal supplier Carl Hagenbeck captured 52 Przewalski's colts in Mongolia; only 23 survived the transport to Hamburg (Hornaday 1906). Although there were no professional or legal guidelines regulating exhibit animal welfare in transport until 1969 (except for quarantine, disease control laws, and endangered species regulations), some large animal wholesalers did provide insurance that the animal would survive at the facility for at least 30 days post-shipment (Zeehandelaar and Sarnoff 1971).

Mortality was also high after arrival at the zoo; the average life span of a carnivore in a zoo was only 2 years (Ritvo 1990). Physical conditions within the zoo were no doubt responsible for at least part of this mortality. Designed to give visitors the best possible view of the animal, most cages were small and barren, containing as few barriers between the animal and the visitor as possible (Mullan and Marvin 1987). Hornaday (1906) noted that some animals could become ill and die due to "sullenness" and "lack of exercise."

It soon became apparent to fledgling American zoos that improvements in basic care and husbandry were essential in order to maintain the integrity of the collection and perhaps allow for the vending or exchange of animals among institutions. Although the modern concept of animal welfare and its relevance to zoos was not yet formally defined, once an animal could be kept alive in captivity, its "comfort" and "satisfaction" could be addressed. Hornaday (1906), for example, wrote of comfortable quarters in terms of available floor space and heated retreats.

It was Carl Hagenbeck, however, who set the stage for new ideas about relationships between animals and humans in the zoo. Hagenbeck not only pioneered the use of positive training techniques, but also opened a revolutionary new type of zoo at Stellingen, outside Hamburg, that presented animals as he had seen them in the wild (Hagenbeck 1910). Hagenbeck attempted to recreate not only the physical aspects of habitat, such as topography, but also the thermal aspects. Hidden moats were substituted for the metal bars that had given the impression of incarceration. Many of Hagenbeck's ideas were imported by fledgling American zoos, such as the Bronx Zoo and the Cincinnati Zoo, where mixed-species naturalistic exhibits became commonplace.

Since this beginning, zoos have undergone a succession of changes in both philosophy and technological attainment that have resulted in their appearance changing, in the words of National Zoo director Michael Robinson (1989), from "art galleries . . . [to] penitentiaries, and later . . . public bathrooms," and in the "final stage in this progression [becoming] 'naturalistic' enclosures designed to meet the visitor's conception of nature." At the same time, zoos have increasingly been subject to federal legislation such as the Animal Welfare Act of 1970, as well as voluntarily adopted accreditation and ethical guidelines such as those written by the American Zoo and Aquarium Association (AAZPA 1990; AZA 1994).

THE ZOO IN PERSPECTIVE

Does the modern naturalistic and federally regulated zoo adequately address the concerns of the public about the care of captive wild animals? Compared with many other areas of animal use, zoos enjoy a high degree of public acceptance and approval. A recent nationwide survey of adults and children for the American Medical Association (1989) found that only 19% of those polled were opposed to keeping animals in zoos, in contrast to 25% opposed to the use of animals for food, 38% opposed to their use in scientific research, and 63% opposed to their use for testing household products (predictably, keeping animals as pets, an activity in which most people participate, scored the lowest negative rating: 3%). This approval is mirrored in zoo attendance: more than 100 million people visit zoos in the United States each year.

Nevertheless, zoos are vulnerable to criticism. The best zoo, after all, is still only a zoo. The natural habitat created in a zoo setting is an illusion. It is real to the visitor, but to the animal the enclosure is restrictive and monotonous, lacking most of the niches that would be found in the natural habitat. Predators, prey, parasites, conspecifics, thermal and daylight variation, and shifting resource availability are all integral aspects of the environments in which animals have evolved. Because of constraints in space and resources as well as the requirements of conservation and educational programs, the social, sexual, and parental behaviors of animals are often constrained and controlled. Zoo animals may experience stress when they are captured, transported, restrained, and/or exposed to or manipulated by humans, whether those humans are keepers, veterinarians, or visitors. Disciplining animals to cooperate in revenue-producing rides or shows poses additional ethical dilemmas (Kreger and Mench, in press).

The zoo community is acutely aware of these and other problems. Hutchins and Fascione (1991), for example, have detailed what they feel are four of the most potentially controversial ethical issues facing zoos today: the acquisition of animals for captive breeding programs, the disposal of surplus animals, basic animal care and husbandry, and the use of animals for research, education, and recreation. Similar issues have been raised by those critical of zoos (Fox 1986; Jamieson 1986; Midgley 1987; Haworth and Travers 1993). We will touch on some of these issues in the remainder of this chapter as we discuss zoo animal welfare and its relationship to the mission of the zoo.

The Mission of the Zoo

As previously emphasized, many of the zoos of the early twentieth century were established for more than simply public entertainment. Some were created with the missions that modern zoos share: research, conservation, education, and recreation (AAZPA 1986). In 1887, Hornaday, then a taxidermist at the Smithsonian Institution, proposed establishing a national zoo as a sanctuary for the American bison, which he feared would become extinct if not given protection in captivity. In 1889, the National Zoological Park was established by Congress "for the advancement of science and the instruction and recreation of the people" (Bain 1989).

The four missions of the zoo, of course, are inextricably interwoven. The recreational aspects of the zoo attract visitors, who are then available to be educated about natural history and the importance of wildlife conservation. Zoo research, although largely conducted out of view of the public, is central to the improved understanding of basic biology and behavior that is required to improve captive breeding and conservation efforts. But how successful are zoos in carrying out their stated goals? Although there are no clear answers to this question, the effectiveness of zoos is likely to have a major influence on public opinion about whether or not zoos should continue to exist in their present form. We have discussed some of the ethical and welfare issues associated with the zoo's recreation mission elsewhere (Kreger and Mench, in press). Here we will concentrate on education and conservation, which we believe to be the most important and visible missions of the zoo.

Education. As our knowledge of animals and the natural world has become more sophisticated, so too have the zoo's techniques for educating visitors. Few zoo directors nowadays would agree with the approach to education advocated by Hornaday (1906), who wrote that the orangutan "can easily be taught to wear clothes, sit at table, and eat with spoon and fork. . . . Such exhibitions are entirely germane to the educational purposes of a zoological garden or park, for they illustrate the mentality of animals, and their wonderful likeness to man, far more forcibly than the best printed statements." Instead of anthropomorphizing animals in this way, zoos now attempt (via graphics, demonstrations, and/or discussions) to provide accurate information about the distributions, habitats, and natural behaviors of animals.

Critics of the zoo like Dale Jamieson (1986) nevertheless contend that even naturalistic zoos continue to paint a distorted picture of animals, and that the zoo's educational objectives could be better fulfilled by using films, slides, or lectures rather than real animals. In fact, Jamieson asks, could not most of the "important educational objectives better be achieved by exhibiting empty cages with explanations of why they are empty?" This is a provocative question, since it cuts to the heart of the zoo's educational mission: not only to convey factual information about animals, but also to foster an appreciation of their dignity, uniqueness, and role in the ecosystem.

How successful is the zoo in fulfilling this mission? A survey of U.S. and Canadian residents showed that the public views the zoo as primarily an educational institution with children as its target audience (Hill and Knowlton 1987). Respondents rated the zoo highly in accomplishing this task. An October 1992 Roper poll reported in the "Testimony of the American Association of Zoological Parks and Aquariums and the Alliance of Marine Mammal Parks and Aquariums" before the Senate Committee on Commerce, Science, and Transportation, 1993, July, showed that 92% of U.S. residents believe that zoos, aquariums, and animal research facilities play an important role in educating the public about marine mammals and their conservation. However, Marcellini and Jenssen (1988) found that, of the time visitors spent in the reptile house at the National Zoo, only 8 minutes were spent looking at the exhibits, hardly enough time to absorb a great deal of information. Similarly, Wolf and Tymitz (1981) observed that while most visitors to the National Zoo did read at least some of the cage labels, many had erroneous conceptions about specific animals and their habitats.

That zoos often fail to convey factual information about animals is confirmed by the studies of Steven Kellert, who has conducted a number of surveys of contemporary attitudes toward wildlife. Kellert found that children whose learning experiences were derived from frequent zoo visits or discussions at school had the poorest scores on tests designed to measure their knowledge about wild animals. Children who had more interactive experiences with animals (like birdwatching or being raised on a livestock farm) had the highest scores (Kellert 1984/5). Adult zoogoers were also less knowledgeable about animals than were people who were members of animal activity groups such as conservation organizations (Kellert 1984).

Would the most effective zoo exhibits, then, be those that involve some kind of interaction between the visitor and the animal? In terms of changing attitudes toward animals, Morgan and Gramann (1989) found that, at least with snakes (species that many people have strong negative feelings about), while a slide show alone or exposure to an animal in an enclosure did not change attitudes, the presence of a human being with the snake (either themselves or the handler) significantly improved attitudes. There was no difference between allowing students to touch a snake and simply having them observe a handler holding the snake. There may be reason to suspect that visitors find the human-animal interaction more interesting, and therefore more educational, than animal-animal interactions, even with the best of graphics. Interactive learning experiences such as those provided in the National Zoo's Herp Lab (White and Barry 1984) have proved to be effective educational tools, as have shows such as the birds of prey show at the Washington Park Zoo, which was found to increase awareness, learning, and positive attitudes (Yerke and Burns 1991). Conversely, zoos should be aware that animal rides send an implicit message of human superiority and domination over other species.

Nevertheless, it should not be forgotten that, despite the best efforts of zoos, visitors will bring with them a set of values and attitudes toward animals that may be difficult (if not impossible) for the zoo to change. Our relationships to wild animals show an admixture of awe, fear, fascination, repugnance, and admiration. Describing nineteenth-century zoogoers, Ritvo (1990) remarked: "To win the permanent affections of the British public, a wild animal had to be impressive, whether in size like the elephant or hippo, or in mental power, like the chimpanzee, but it could not seem too dangerous or independent." This situation has probably changed little in the past hundred years.

People tend to dislike or fear animals that are small, unattractive, slimy, predatory, dangerous to humans, sudden in their movements, or that have an appearance that differs markedly from the human form. In contrast, they are attracted to animals that are large, intelligent, neotenic, and similar to humans in appearance or behavior (Bennett-Levy and Marteau 1984; Burghardt and Herzog 1989). Burghardt and Herzog suggested that such responses may be biologically based, and can be categorized according to four general considerations that shape our ethical attitudes toward specific animals: the animal's perceived benefit to humans; our degree of empathy toward the animal based on its perceived similarity to us; the animal's rarity, diversity, and place in the ecosystem; and human psychology, including religious and aesthetic preferences. These considerations are reflected in public attitudes toward wildlife protection (Optow 1993; Plous 1993) and may dictate zoo effectiveness to a much greater extent than zoos are able to dictate attitudes. As zoos and conservation organizations know only too well, it is much easier to generate support for the conservation of a "charismatic megavertebrate" like the panda than for a small fish like the snail darter.

Returning to Jamieson's question about the educational value of empty cages: realistically, it is unlikely that people would bother to visit a zoo full of empty cages. Coe (1985) has suggested that what the zoo visitor wants is anticipation, lack of distraction, novelty, fulfilled expectations, emotional involvement, and reinforcement, and that all of these are necessary to make zoogoing a memorable experience. When the visitor enters a novel environment full of unfamiliar sounds and sensations, such as a rainforest exhibit, and suddenly encounters an animal close by that appears not to be behind a barrier, that person will probably remember the visit and reinforce the concepts learned (e.g., the animal's behavior and habitat) by telling others about it.

The challenge to the zoo is to provide this type of learning experience without demeaning the animal: several studies have shown that wild animals are perceived by people to be more dignified and less passive than their zoo counterparts, even when the zoo animals are presented in naturalistic settings (Rhoads and Goldsworthy 1979; Finlay, James, and Maple 1988). A complicating consideration is that the presence of zoo visitors may in itself cause confined animals to behave abnormally (Glaston et al. 1984; Chamove, Hosey, and Schaetzel 1988; Carlstead 1991; Mitchell et al. 1992).

Conservation. Since the 1960s zoos have increasingly viewed the conservation of threatened or endangered species as one of their most important functions. Considerable emphasis has been placed on the development of reproductive technologies for captive animal propagation and on techniques for genetic management to ensure the maintenance of genetic diversity. Zoos occasionally remove whole populations of an endangered species from the wild for "last chance" captive breeding programs, with the goal of eventual reintroduction when the cause of the species decline is removed (Hutchins and Weise 1991). This has been done for Przewalski's horse, ***Equus przewalski,*** the black-footed ferret, ***Mustela nigripes,*** and the Arabian oryx, *Oryx leucoryx*.

There have been a few notable conservation successes. The reintroduction of the golden lion tamarin, *Leontopithe-*

cus rosalia, in Brazil, for example, represents the culmination of an effort involving captive management, field research, habitat restoration, and conservation education (Kleiman et al. 1986). But despite such successes, important questions are being raised about the overall effectiveness of, and even the necessity for, zoo-based conservation efforts.

Varner and Monroe (1991), for example, have criticized captive breeding programs on several grounds. They note that such programs tend to focus only on particular (appealing) species even though the preservation of all (or most) of the component species in an ecosystem is essential if that ecosystem is to be preserved. In addition, they state that most reintroduction programs are unlikely to be successful because of continuing habitat destruction and the reduced competence and adaptability of captive-bred and captive-reared animals. Varner and Monroe argue that money would be far better spent on in situ conservation efforts designed to preserve habitats.

Supporters of zoo conservation programs contend that concentrating on "flagship" species generates public support for broader conservation efforts, thus protecting many other incidental species that might otherwise become extinct (Hutchins and Wemmer 1991). They also argue that zoos can genetically manage captive species in order to avoid the inbreeding that has been shown to occur in declining wild populations (Lacy 1993). Finally, they point out that most zoos are supported by city and state governments; the likelihood that these governments would channel their funds to in situ conservation efforts rather than zoos is slender (Hutchins and Fascione 1991).

An additional ethical issue related to captive breeding deserves mention here: that of disposal of surplus animals. As a result of past indiscriminate breeding, attempts to increase genetic diversity, and limitations in contraceptive technology, zoos have produced many surplus animals (Fox 1986; Lindburg 1991; Hutchins and Fascione 1991; see also Graham, chap. 28, this volume). Due to limited space and resources, these animals have to be sold, transferred, or euthanized. Despite the apparent paradox involved in some animal protection groups (unenthusiastically) supporting euthanasia for unwanted pets but opposing its use in zoo animals (Fox 1986), zoos must realize that the public may well react negatively to the prospect of healthy captive animals being killed, and may also perceive the zoo as having a responsibility to ensure that animals are provided with appropriate care throughout their lifetimes. In fact, the public tends to view zoos as "custodians of the ark," the first place to contact to dispose of an unwanted exotic pet or an orphaned or injured wild animal. Proactive approaches to the surplus problem include the continuing development of reliable and reversible chemical contraception and enforcement of the AZA prohibition of sales of animals to anyone unable to care for them adequately or who uses them for "canned hunts."

Costs and Benefits: Zoo Animal Welfare. The basis of these disagreements about zoo conservation programs, as well as the other missions and practices of the zoo, is perhaps best summed up by Mary Midgley (1987): "[T]he welfare of existing animals is supposed to give way systematically, not just to human interests, but also to the surmised future interests of their own possible remote descendants. If this is to be justified, the prospects of success had better be good." Midgley here poses the central question of whether or not the benefits of zoos to both animals and humans outweigh the costs to the zoo animal. This is an extremely complex question that zoos will continue to wrestle with in the coming decades.

If zoos are effective, their benefits in terms of improving public understanding of animals and ecosystems and preserving habitats and genetic diversity could be considerable. In fact, some environmental ethicists, such as Baird Callicott (1992), argue that species and ecosystems also have a value in and of themselves and that animal rights and animal welfare advocates have taken an overly narrow view in emphasizing only moral obligations to individual animals.

But what are the costs to animals in the zoo? We have already described some potential costs in the section above on the history of the zoo. In practice, however, given our current knowledge, it is as difficult to assess the costs of captivity to animals as it is to assess its benefits to individuals, species, and ecosystems.

As the chapters in this book attest, the attention that zoos have paid to the care of captive wild animals has resulted in significant improvements in their physical comfort and nutritional and health status. As a result, mortality and morbidity in zoos have declined significantly (Chiszar, Murphy, and Iliff 1990). As has been pointed out elsewhere (Hutchins and Fascione 1991), zoos also provide animals with benefits in terms of protection from predators, disease, starvation, and other stressors that they would normally encounter in the wild. However, it is clear that confinement must also impose some costs on animals. Current concerns about the rights and welfare of animals focus not so much on failure to meet their physical needs in captivity, but on the failure to meet their behavioral and psychological needs. The way in which the debate about these needs has developed in the farm animal community provides an interesting model for zoos.

In 1964, in response to public pressure, the British government established a committee (the Brambell Committee) to investigate the welfare of intensively farmed animals. After examining many farming systems, the members of that committee concluded that animals had behavioral needs that were frustrated by confinement. They recommended that, at a minimum, animals be provided with what they called the "five basic freedoms": to turn around, lie down, stand up, stretch, and groom without restriction (Thorpe 1969). This report stimulated a great deal of scientific research on animal welfare, and in turn a significant reformulation of those five freedoms: freedom to display most normal patterns of behavior as well as freedom from thirst, hunger, and malnutrition, physical and thermal discomfort, injury and disease, and fear (Spedding 1993).

These five "new" freedoms obviously place much greater emphasis on the psychological well-being of farm animals. Defining psychological well-being and assessing the mental states of animals, however, are extremely difficult tasks, which require that we view the world from the animal's perspective rather than our own. A variety of new techniques (for example, preference testing) are being developed to address questions such as whether or not animals have space, time, and self-awareness, to explore the nature and intensity of their emotions, and to look at the interactions between behavior, motivation, and rearing environments (Dawkins 1990; Mench 1993). The answers to these questions will provide insight into the mental lives of animals that will be instrumental in addressing the concerns raised by philosophers like Regan and Singer about the rights and value of animals.

The answers also have a more immediate relevance for zoos because they are important not only for improving the welfare of captive animals but for facilitating reintroductions into natural habitats. Successful reintroductions require individual animals to be able to forage, identify predators, and recognize and assimilate with wild counterparts (Wemmer and Derrickson 1987). Animals that are deprived of the opportunity to learn particular behaviors at particular times may be poor candidates for reintroduction, since they will have difficulty adjusting to the variable environments found in the wild.

Zoo biologists have been pioneers in the study of the psychology of captive animals. Heini Hediger, director of the Zurich Zoological Gardens (1968), demonstrated that abnormal or maladaptive behaviors could be the result of factors such as rearing environment, lack of environmental cues and stimulation, and inadequate space. The concept of environmental or behavioral enrichment and its potential use in zoos was introduced by Hal Markowitz in his book *Behavioral Enrichment in the Zoo* (1982). Zoos are placing increasing emphasis on environmental enrichment. The recently revised *Accreditation Standardized Guidelines* of the AZA (1994, 5) state, "All animal enclosures, including hospital facilities (quarantine/isolation), must be of a size to allow for the social and psychological well-being of the animals; and exhibit enclosures must include provisions for the behavioral enrichment of the animals." Encouraging ethological research should be a high priority for zoos, since such research provides the best approach to investigating questions about animal perspectives and animal-centered environmental design.

As society is becoming more affluent and many of the basic needs of human beings are increasingly being met, we are beginning to reflect on our obligations to the larger natural world. These reflections are likely to lead to profound changes in the ways in which we use and treat animals. The public has a great regard and affection for zoos. It is the responsibility of the zoo community to retain that regard and affection by understanding the changing societal consensus about animals and by designing zoo environments that meet the needs that the animal *itself* perceives to be important. Integrating these design changes with the other missions of the zoo will be a challenging and rewarding task for the future.

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THE ROLE OF ZOOS AND AQUARIUMS IN AMPHIBIAN AND REPTILIAN CONSERVATION

ROBERT J. WIESE* AND MICHAEL HUTCHINS*

Introduction

THE "IUCN RED LIST OF THREATENED ANIMALS" includes 93 reptilian and 63 amphibian species (IUCN 1990). Due to the combined effects of habitat alteration, pollution, and overexploitation, however, the actual number of endangered or threatened taxa may be considerably higher. Indeed, the preservation of biological diversity seems to be an overwhelming task, and success will only be possible through the cooperative efforts of numerous individuals and organizations (Prescott and Hutchins 1991). North America's zoos and aquariums are trying to do their part, and our intent is to summarize a number of the current efforts.

In 1980, the American Association of Zoological Parks and Aquariums—a nonprofit organization representing 160 of North America's finest zoological institutions—identified wildlife conservation as its highest priority. The role of professionally managed zoos and aquariums in conservation is multifaceted; however, they contribute in at least six ways by:

(1) Providing a refuge for threatened and endangered species by maintaining genetically and demographically healthy populations as reservoirs of genetic material and as an insurance policy against extinction;

(2) Propagating animals for reintroduction to areas where they have been extirpated, and developing successful reintroduction techniques;

(3) Conducting veterinary, nutritional, reproductive, behavioral, and other research, both basic and applied, which increases our ability to manage and conserve both captive and wild populations;

(4) Developing and testing technologies that can be applied to field conservation;

(5) Educating the general public in an attempt to change attitudes and lifestyles that affect wildlife and the environment; and

(6) Providing direct or indirect support for in situ conservation programs that may or may not involve a captive-breeding component.

Captive-Breeding Programs

Herpetology departments in zoological institutions throughout the world have long worked to develop effective and efficient husbandry protocols for the care and reproduction of reptiles and amphibians. This effort has led to an immense body of knowledge that can be applied to the development of successful breeding programs for endangered and threatened species. During 1988–1989, more than 69 amphibian and 575 reptilian taxa were bred in captivity, many of which are listed as endangered, threatened, or rare (Olney and Ellis 1991*a*, 1991*b*). The Captive Breeding Specialist Group of the International Union for the Conservation of Nature and Natural Resources's Species Survival Commission presently recognizes five regional captive breeding

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Acronyms used in this chapter:

AAZPA	American Association of Zoological Parks and Aquariums
CAMPs	Conservation Assessment and Management Plans
CBSG	Captive Breeding Specialist Group
CPR	Captive Propagation Rescue
IUCN	International Union for the Conservation of Nature and Natural Resources
SSAR	Society for the Study of Amphibians and Reptiles
SSC	Species Survival Commission
SSP	Species Survival Plan
TAGs	Taxon Advisory Groups

TABLE 1. Reptilian and amphibian species with SSPs and the year that each program was established.

Common name	Scientific name	Year
Chinese Alligator	*Alligator sinensis*	1982
Radiated Tortoise	*Geochelone radiata*	1982
Aruba Island Rattlesnake	*Crotalus durissus unicolor*	1982
Dumeril's Ground Boa	*Acrantophis dumerili*	1983
Puerto Rican Crested Toad	*Peltophryne lemur*	1984
Mona Island Boa	*Epicrates monensis*	1990

programs, which cover Australasia, Europe, Japan, North America, and the United Kingdom. A number of other regions, such as Central America, Brazil, India, China, and Africa, are presently in the process of organization. While many of these programs share similar strategies and philosophies, considerable differences in their approaches exist. We will concentrate primarily on the strategies developed within the North American captive-breeding community, specifically the AAZPA Conservation Program. (Readers interested in the European Endangered Species Program and a similar program for the United Kingdom should consult Tudge [1992].)

The focal point of the AAZPA Conservation Program is the Species Survival Plan (Foose 1983; Hutchins and Wiese 1991). Through the Species Survival Plan program, member zoos and aquariums in North America work cooperatively to maintain genetically and demographically viable populations of endangered or threatened species as a hedge against extinction. Of course, captive-breeding programs are not a panacea for the endangered species problem and should only be implemented as part of a holistic effort to preserve species in their natural habitats (Hutchins and Wiese 1991). Thus, the ultimate goal of the SSP is to reinforce natural populations, not replace them (Foose 1983). As part of this holistic approach, it is also important that the original causes of decline in nature be addressed simultaneously with the development of captive-breeding programs (Gibbons, this volume, page 119).

With regard to amphibian and reptilian conservation, there are currently six species addressed by an SSP program and several others are likely to be added in the near future (Table 1). Each SSP program is overseen by a species coordinator with the assistance of a studbook keeper, a propagation group consisting of elected representatives of participating zoos and aquariums, and various scientific advisors. Without the dedication of these hard-working volunteers, the program would not be possible. The AAZPA Executive Office and Conservation Center in Bethesda, Maryland, and the AAZPA Wildlife Conservation and Management Committee oversee all SSP and related conservation and scientific programs and provide scientific, legal, public relations, and other services to species coordinators and propagation groups, as needed.

Basic population data on species of concern, including age, sex, and reproductive history are maintained in studbooks that allow analyses and specific management decisions to be based on populations of known pedigree (Glatston 1986). The AAZPA currently has 21 approved studbooks for various amphibian and reptilian taxa, including the SSP species listed in Table 1. A current list of all non-SSP species with approved studbooks is shown in Table 2.

The primary goal of the SSP is to preserve as much genetic variation as possible within the restrictions of the "captive carrying capacity" (Foose 1983). This translates into a balance between maximizing genetic diversity at the population level (equalizing relative founder lineage contribution)

TABLE 2. Non-SSP reptilian and amphibian species with AAZPA-approved studbooks.

Common name	Scientific name
Annulated Boa	*Corallus annulatus*
African Spurred Tortoise	*Geochelone sulcata*
Asian Brown Tortoise	*Manouria emys*
Galapagos Tortoise	*Geochelone elephantopus*
Pancake Tortoise	*Malacochersus tornieri*
Sideneck Turtles	*Podocnemis* sp.
Dwarf Caiman	*Paleosuchus palpebrosus*
Cuban Crocodile	*Crocodylus rhombifer*
Morelet's Crocodile	*Crocodylus moreletii*
Siamese Crocodile	*Crocodylus siamensis*
False Gharial	*Tomistoma schlegelii*
Gharial	*Gavialis gangeticus*
Madagascar Tomato Frog	*Dyscophus antongilii*
King Cobra	*Ophiophagus hannah*
Louisiana Pine Snake	*Pituophis melanoleucus ruthveni*
Black Pine Snake	*Pituophis melanoleucus lodingi*
Chinese Crocodile Lizard	*Shinisaurus crocodilurus*
Prehensile-tailed Skink	*Corucia zebrata*
Rock Iguanas	*Cyclura* sp.

and maximizing heterozygosity at the individual level (minimizing inbreeding).

Once studbook data have been analyzed, using the latest genetic and demographic software, recommendations are made concerning which animals should breed, with which individuals, and how many offspring should be produced (Foose 1983). Overrepresented lineages are identified so that breeding can be curtailed. For a captive population, it is as important to slow breeding in overrepresented lines as it is to stimulate breeding in underrepresented lines. These analyses and recommendations are then compiled and reported in a master plan. Master plans are updated regularly because the population structure changes as a result of management decisions.

Through responsible management and breeding, it is hoped that zoos and aquariums will be able to contribute significantly to the conservation of many species at risk. Captive populations act as reserves in the event that conditions change and wild populations decline or disappear. In addition to assisting endangered species, captive breeding also sustains populations of common species, thus minimizing the need to remove animals from the wild.

The threat to biological diversity is growing, and because of space limitations, captive-breeding programs will only be able to assist a small fraction of the species at risk (Soulé et al. 1986; McMahan 1991). Therefore, as responsible stewards, we must prioritize species and make our selections carefully, so that as much diversity as possible is ultimately preserved. This essentially amounts to a form of triage (Knowles 1986; Hutchins and Wiese 1991). For this purpose, specialized committees called Taxon Advisory Groups have been developed. In fact, the TAG concept had its beginnings within the North American zoo herpetology community with the establishment of the Crocodilian Advisory Group in 1986 (J. L. Behler, pers. comm.). The primary function of a TAG is to prioritize species for SSP and studbook designation and develop a regional strategic-collection plan (Hutchins and Wiese 1991). The TAGs also address more general issues, such as ethical concerns, husbandry protocols, research needs, and other topics that are common to an entire taxon. Working TAGs presently exist for amphibians, chelonians, crocodilians, snakes, and lizards.

Establishing priorities for future SSPs and studbooks is a complicated process and must include consideration of many different factors. Important resources include, when available, Action Plans produced by the IUCN/SSC and Conservation Assessment and Management Plans produced by the CBSG of the IUCN/SSC (Foose et al. 1992). Action Plans give the current conservation status of each species and information on their natural history, while CAMPs include general recommendations about which species are most in need of captive-breeding programs. CAMPs are formulated in consultation with the appropriate IUCN/SSC Taxonomic Specialist Groups, regional TAGs, and other relevant conservation organizations (Hutchins and Wiese 1991). Some of the factors considered include the degree of endangerment in the wild, availability of adequate founder stock, previous success with captive breeding, taxonomic uniqueness, probability of recovery, and ability to serve as a flagship species to help protect endangered ecosystems (Hutchins and Wemmer 1991).

While many SSP programs will need to manage populations in captivity for an extended period of time, this is not always the case. Short-term projects, often referred to as Captive Propagation Rescue, are designed to quickly reestablish natural populations, but they require that the original reasons for endangerment be eliminated (Conway 1989; Gibbons, this volume, page 119). CPR projects should receive more attention by zoos and aquariums than they do now. Members of the SSP for the Puerto Rican Crested Toad (*Peltophryne lemur*; Johnson 1990, and this volume, page 243) are currently trying to establish a CPR project for this species. With short-term CPR projects, species can be maintained and bred in captivity until sufficient habitat is acquired, preserved, or restored and the species is returned to a self-sustaining natural status. In these instances, zoos and aquariums act as temporary way stations for species on the road back to viable natural populations. With respect to many amphibians and reptiles, CPR projects may prove to be the most productive approach.

Captive-breeding and reintroduction programs for amphibians and reptiles have certain advantages relative to those for mammals and birds. First, many amphibians and reptiles have a relatively high reproductive potential allowing them to recover quickly from population bottlenecks. If a population can rebound quickly, there is a lower probability that allelic diversity will be lost due to genetic drift (Falconer 1981; Wiese 1990). Therefore, if adequate numbers of founders can be acquired and bred, it is possible to retain much of a population's natural evolutionary potential. This is especially true for species that experience high mortality during the egg or juvenile stage. In such cases, captive breeding may greatly increase survivability, thereby further increasing the population's growth potential. Of course, captive environments should duplicate natural conditions as closely as possible to minimize artificial selection in species maintained for conservation purposes (Frankham et al. 1986).

Second, the behavior of amphibians and reptiles is relatively "hard wired" when compared to mammals and birds (Warwick 1990; Chiszar et al., this volume, page 147). Thus, in many cases, it will be unnecessary to train the animals to identify appropriate foods or habitat or to interact appropriately with conspecifics. It is important to note, however, that this generalization may not always be true (Warwick 1990). Reintroduction efforts should therefore be monitored closely and techniques developed on a species-by-species basis (Dodd and Seigel 1991; Burke 1991). Because familiarity with the home range is important in some species, it may be beneficial to release individuals at a young age, perhaps soon after the egg or juvenile stage. It is also critical that the potential to spread pathogens from captive to free-ranging populations be carefully evaluated before any releases take place (Hutchins et al. 1991; Jacobson, this volume, page 109).

A third advantage comes from the relatively small area required to maintain a viable population of many amphibians and reptiles, both in captivity and in nature. Because the home ranges of many species are relatively small compared to those of mammals and birds, it is often feasible to set aside or purchase adequate habitat to maintain viable populations. Because such populations are small and fragmented, however, all are at risk from demographic catastrophes (Foose 1983). Thus, several wild populations will have to be established before a species can be considered out of danger. Furthermore, a healthy captive population may need to be maintained as a hedge against future catastrophic events.

Zoo and Aquarium Research

For captive breeding and reintroduction to be successful, managers must have accurate knowledge of a species' basic biology (Hutchins 1988; Murphy and Chiszar 1989; Warwick 1990). Information from a variety of disciplines including physiology, behavior, nutrition, reproduction, disease, and genetics are important to a program's success. In some instances, the knowledge gained and husbandry techniques developed are even more valuable than the captive populations themselves. This is especially true when common taxa are used as models to develop techniques for endangered or threatened species.

Collaboration between zoos, universities, and government wildlife agencies is not new to the field of herpetology (Murphy and Collins 1980). In fact, this cooperation has resulted in numerous research advances. The Society for the Study of Amphibians and Reptiles should be commended for recognizing this potential and being one of the first scientific societies to have and promote an official zoo liaison. The *Journal of Herpetology* and *Herpetological Review* contain numerous studies conducted by zoo and aquarium scientists or by university scientists in collaboration with zoo and aquarium personnel. SSAR has recently established a new series, *Herpetological Conservation*, dedicated to such issues.

Research on captive populations can assist conservation efforts and promote animal welfare in several ways. More specifically, it can aid in the:

(1) Development of successful husbandry protocols for a wide variety of species (documentation of normal physiological, nutritional, reproductive, and behavioral parameters is particularly useful in this regard);

(2) Clarification of pedigrees and resolution of taxonomic status (specific and subspecific) through detailed genetic analysis;

(3) Development of veterinary procedures that may help both wild and captive populations; and

(4) Development of capture, restraint, identification, monitoring, and other techniques for use in field conservation and in captive-breeding programs.

Development of Husbandry Protocols

When a species or population is threatened with extinction, immediate action needs to be taken. If captive-husbandry and propagation techniques have been previously established, a species' prospect for survival is often greatly enhanced. If zoo managers are faced with both a limited gene pool and a lack of knowledge concerning the species' basic biology, however, the chances of recovery are slim. This argues for the establishment of an experimental captive population well before a species becomes critically endangered. For example, the development of successful husbandry protocols for the Bog Turtle (*Clemmys muhlenbergii*) has been extremely valuable now that the species is threatened in nature (Tryon and Hulsey 1977; Herman and George 1986). Although more research is needed, husbandry protocols presently exist for a number of threatened or endangered reptiles and amphibians. A small sampling of these species include the Japanese Giant Salamander, *Andrias japonicus* (Kuwabara et al. 1989); Pancake Tortoise, *Malacochersus tornieri* (Darlington and Davis 1990); Morelet's Crocodile, *Crocodylus moreletii* (Hunt 1980); West Indian rock iguanas, *Cyclura* sp. (Noegel 1989; Duval and Christie 1990); Louisiana Pine Snake, *Pituophis melanoleucus ruthveni* (Reichling 1988); Puerto Rican Crested Toad, *Peltophryne lemur* (Miller 1985; Paine et al. 1989); San Francisco Garter Snake, *Thamnophis sirtalis tetrataenia* (Cover and Boyer 1988), and the Western Swamp Turtle, *Pseudemydura umbrina* (Kuchling and DeJose 1989). Breeding programs to assist the recovery of these species have a better chance of success because of the pioneering work that has already been accomplished.

Basic research on captive animals can complement field studies. For example, many amphibians and reptiles are secretive and their normal social behavior, feeding habits, and reproductive biology are often difficult to study under field conditions (Fitch 1987; Hutchins 1988; Warwick 1990). Captive populations allow for intensive physiological and behavioral data to be gathered in a more systematic manner. This may lead to new insights that would have been difficult or impossible to obtain in the field (Chiszar et al., this volume, page 147). Standard physiological values are also more easily obtained from captive animals in cases in which blood, tissues, venom, fecal, and other samples can be collected on a regular basis. Of course, data collected on captive populations should be verified with comparable data from wild populations when possible (Murphy and Chiszar 1989; Zimmermann 1989).

Resolution of Pedigree and Taxonomic Status

If captive-breeding programs are to assist in the long-term conservation of endangered and threatened species, they must retain as much of the original genetic variation available in the founding animals as possible (Allendorf 1986; Ralls and Ballou 1986). As mentioned previously, this requires careful management of a population and its reproduction, an essential component of which is the determination of the parentage of each individual in the population (Foose et al. 1986).

Establishing parentage is a fairly simple objective with species that form pair bonds and require only one pair of animals per enclosure. When several males are required for courtship or when sperm storage is possible, however, determining the exact parentage is not always simple. The Dumeril's Ground Boa (*Acrantophis dumerili*) SSP group has just recently completed a DNA study that targeted several animals of unknown parentage. As a result of this study, a number of holes in the pedigree were filled allowing for more efficient and accurate breeding recommendations to be made (R. D. Hudson et al., pers. comm.). Similar DNA fingerprint studies were used to illuminate the pedigree of Galapagos Tortoises, *Geochelone elephantopus* (Ryder et al. 1989).

Populations can possess co-adaptations to local environments and/or to other genes or chromosomes. Disruption of these co-adapted complexes may have devastating effects on reintroduction attempts (Templeton et al. 1986). DNA studies to determine the similarities or differences among species and subspecies, therefore, are potentially important to the success of reintroductions (Ryder et al. 1989).

Improving Veterinary Care

Veterinary advances have been an important result of zoo- and aquarium-based research. The ongoing efforts by members of the SSP for the Aruba Island Rattlesnake (*Crotalus durissus unicolor*) to develop a vaccine for reptilian *Paramyxovirus* is an excellent example (Odum and Goode, this volume, page 363). The knowledge gained from detailed necropsies is critical to the development of effective diagnostic and treatment protocols for both captive and free-ranging wildlife (Murphy and Shadduck 1979; Hutchins et al. 1991).

Innovative clinical techniques that were developed for human health care, such as endoscopy, have been used in the sexing of reptiles (Schildger and Wicker 1989). Artificial insemination is another important technique that provides a powerful management tool in captive-breeding programs in which specific individuals are designated to breed. Such techniques have been used for crocodilians (Larsen and Cardheilhac 1984) and snakes (Mengden et al. 1980; Quinn et al. 1989).

Development of New Technologies

Research on captive populations has led to the development of many technologies now commonly used in herpetological studies. The squeeze-box technique for safely obtaining accurate measurements of snakes was developed using captive specimens (Quinn and Jones 1974). Investigations of egg development and physiology require standardized, reliable, and simple artificial incubation protocols. Many laboratory incubation protocols in use today employ vermiculite—a substrate originally developed for use in captive propagation (Tryon 1975).

In addition to helping sustain captive populations, technologies developed and tested in zoos and aquariums can also benefit field conservation efforts. For example, biologists who employ radiotelemetry often test receivers or implantation and attachment procedures on captive animals before transferring them to field use (Asa 1991; Kingsmill 1991).

To reach their full potential, however, zoos and aquariums will need to increase their commitment to scientific research. Increased cooperation between scientists working for zoos, aquariums, and universities has the potential to further our present knowledge and to enhance our combined efforts to assist amphibians and reptiles threatened with extinction (Murphy and Chiszar 1989).

In Situ Conservation

In situ conservation efforts must also receive increased attention by the zoo and aquarium community. Zoos have been involved with several reintroduction efforts and these are important aspects of several SSPs. Members of the SSP for the Puerto Rican Crested Toad (Johnson 1990, and this volume, page 243) and that for the Virgin Islands Boa, *Epicrates monensis* (Tolson, this volume, page 353), have initiated reintroduction projects. The Jersey Wildlife Preservation Trust has also been a leader in the in situ conservation of threatened and endangered amphibians and reptiles (Bloxam and Tonge 1986; Reid et al. 1989).

Reintroduction may prove to be an important conservation tool. Captive programs must also expand their current scope, however, to include habitat protection (Hutchins and Wiese 1991). Many of these projects will likely be in conjunction with short-term CPR programs. In fact, a number of zoos and aquariums are already working with governmental agencies and other local, national, and international conservation organizations to protect critical habitat for endangered amphibians and reptiles. Current efforts to save the endangered Bog Turtle provide an excellent example. Several zoos, including the Knoxville Zoological Park, Zoo Atlanta, and the New York Zoological Park, are devoting considerable resources to the survival of this species, which has declined drastically due to habitat destruction and illegal collection for the pet trade (J. L. Behler et al., pers. comm.).

The Knoxville Zoological Park has recently entered into a renewable, eight-year agreement with the Tennessee Wildlife Resources Agency, The Nature Conservancy, and private landowners to protect some of the last remaining Bog Turtle habitat in Tennessee. Captive-breeding programs are also underway to provide a source of animals to establish new populations. This work is possible today because methods for captive breeding were established long before the threat became overwhelming (Tryon and Hulsey 1977; Herman and George 1986).

Similar programs are underway for many other species, including the Piebald Chuckwalla, *Sauromalus varius* (Lawler et al., this volume, page 333), Louisiana Pine Snake, *Pituophis melanoleucus ruthveni* (S. Hammack, pers. comm.), and Kirtland's Snake, *Clonophis kirtlandii* (W. McMahan, pers. comm.).

Public Education

The importance of conservation education cannot be overemphasized. Public education, both within North America and abroad, is extremely important to the success of various recovery efforts. While there are a number of advantages to working with amphibians and reptiles in zoos and aquariums, their public appeal is not as high as it is for mammals and birds (Hoff and Maple 1982; Steinhart 1984; Kellert 1989). Education programs are especially needed to change negative attitudes and to call attention to conservation issues surrounding reptiles and amphibians (Murphy and Mitchell 1989). The Dallas Zoo's graphics display of the rattlesnake roundup tragedy (Warwick et al. 1991) is an excellent example of what can be done to call the public's attention to specific conservation issues. Additional conservation topics about which institutions need to inform their constituents are the global decline of amphibians (Barinaga 1990; Borchelt 1990; Pechmann et al. 1991), the increased threat of micro- and macro-pollution (Hutchinson and Simmonds 1992), and the pet and animal products trade (International Union for the Conservation of Nature and Natural Resources 1989; Swingland and Klemens 1989; Das 1990; Hirth and Rohovit 1992).

Education programs are also extremely important to the success of reintroduction projects (Durrell and Mallinson 1987; Kleiman 1989). If attitudes of local people cannot be changed and an appreciation of wildlife fostered, then reintroduction efforts are unlikely to be successful. Therefore, local people must be educated concerning the ecological role and value of the species in question. Although not a zoo-based program, Dagmar Werner's captive-breeding program to save the Green Iguana (*Iguana iguana*) in Panama and Costa Rica provides an excellent model for other countries. Through intensive media and educational programs, local people now understand their natural heritage better and manage sustainable populations of this species. As a result, many acres of tropical forest have been preserved for Green Iguanas and other species (Cohn 1989; Vietmeyer 1989).

The SSP for the Puerto Rican Crested Toad (Johnson 1990, and this volume, page 243) has been highly successful with respect to education as well. Cooperation between the SSP and the Puerto Rican government has led to an intensive educational effort. Today, children of the Guánica region, where the toads are found, are well aware of this important part of their endemic fauna. Educational posters were distributed as part of a public relations campaign to inform Puerto Ricans about the importance and uniqueness of this species. Ownership of all captive toads has been retained by the government of Puerto Rico in order to ensure a sense of participation in and shared responsibility for the program. Members of the SSP for the Aruba Island Rattlesnake have adopted a similar strategy, that of educating the people of Aruba about the importance of their native wildlife. There is also a program to train medical doctors in the treatment of snake bites (Odum and Goode, this volume, page 363).

Summary

There is much work to be done if we are to assist even a fraction of the species currently at risk. Through the successful use of captive-breeding and reintroduction programs in conjunction with strategic collection planning, scientific research, in situ conservation efforts, and public education, professionally managed zoos and aquariums can play a significant role in amphibian and reptilian conservation.

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Limitations of Captive Breeding in Endangered Species Recovery

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Abstract: *The use of captive breeding in species recovery has grown enormously in recent years, but without a concurrent growth in appreciation of its limitations. Problems with (1) establishing self-sufficient captive populations, (2) poor success in reintroductions, (3) high costs, (4) domestication, (5) preemption of other recovery techniques, (6) disease outbreaks, and (7) maintaining administrative continuity have all been significant. The technique has often been invoked prematurely and should not normally be employed before a careful field evaluation of costs and benefits of all conservation alternatives has been accomplished and a determination made that captive breeding is essential for species survival. Merely demonstrating that a species' population is declining or has fallen below what may be a minimum viable size does not constitute enough analysis to justify captive breeding as a recovery measure. Captive breeding should be viewed as a last resort in species recovery and not a prophylactic or long-term solution because of the inexorable genetic and phenotypic changes that occur in captive environments. Captive breeding can play a crucial role in recovery of some species for which effective alternatives are unavailable in the short term. However, it should not displace habitat and ecosystem protection nor should it be invoked in the absence of comprehensive efforts to maintain or restore populations in wild habitats. Zoological institutions with captive breeding programs should operate under carefully defined conditions of disease prevention and genetic/behavioral management. More important, these institutions should help preserve biodiversity through their capacities for public education, professional training, research, and support of in situ conservation efforts.*

Las limitaciones de la cría en cautiverio en la recuperación de especies en peligro de extinción

Resumen: *El uso de la cría en cautiverio para la recuperación de especies ha crecido enormemente en años recientes, pero sin un crecimiento concurrente en el reconocimiento de sus limitaciones. Los problemas con (1) el establecimiento de poblaciones cautivas autosuficientes, (2) el escazo éxito en la reintroducción, (3) los altos costos, (4) la domesticación, (5) la exclusión de otras técnicas de recuperación, (6) los brotes de enfermedades, y (7) el mentenimiento de la continuidad administrativa han sido todos signifivativos. Esta técnica ha sido frucuentemente invocada en forma prematura y no debería ser usada normalmente sin antes llevar a cabo una cuidadosa evaluación a campo de los costos y beneficios de todas las alternativas de conservación y de determinar si la cría en cautiverio es esencial para la supervivencia de la especie. Demostrar sim-*

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plemente que una población de una especie esta declinando o ha caído por debajo de lo que sería del tamaño viable mínimo, no constitutye un análisis suficiente como para justificar la cría en cautiverio como medida de recuperación. Debido a los cambios genéticos y fenotípicos inexorables que se producen en ambientes de cautiverio, la cría en cautiverio debería ser una medida última instancia en la recuperación y no una profiláxis o solución a largo plazo. La cría en cautiverio puede jugar un papel crucial en la recuperación de algunas especies, para las cuales no se encuentran a disposición alternativas efectivas en el corto plazo. Sin embargo, esta no debe desplazar a la protección del hábitat y del ecosistema, así como tampoco debe ser invocada en ausencia de esfuerzos comprensivos para mantener o reestablecer poblaciones en hábitats naturales. Las instituciones zoológicas con programas de cría en cautiverio, deberían operar bajo condiciones cuidadosamente definidas en cuanto a la prevención de enfermedades y manejo genético/etológico. Aún mas importante, estas instituciones deben ayudar a la preservación de la biodiversidad a través de su capacidad para la educación pública, el entrenamiento profesional, la investigación, y el apoyo a la conservación in situ.

Introduction

In recent years there has been a tremendous increase in the use of captive breeding for recovering endangered species. Captive breeding techniques have been improving continuously, as have techniques for reintroducing captive-bred animals into the wild. For some species, such as the California Condor (*Gymnogyps californianus*), the Mauritius Kestrel (*Falco punctatus*), the black-footed ferret (*Mustela nigripes*), and the Guam Rail (*Rallus owstoni*), captive breeding has clearly represented the difference between survival and extinction in the short term (Snyder & Snyder 1989; Derrickson & Snyder 1992; Jones et al. 1995; Miller et al., in press).

Despite the important role that captive breeding has had in the recovery of some species, we are concerned that it is being promoted as a recovery technique for many species that may not benefit from it. We note in particular that the World Conservation Union's (IUCN) Captive Breeding Specialist Group, renamed the Conservation Breeding Specialist Group (CBSG), has recently generated a series of Conservation Assessment and Management Plans (CAMPs) that call for long-term captive breeding of numerous taxa. For example, the draft CAMP document for parrots (Seal et al. 1992) recommended long-term captive breeding for roughly half of the 330 parrot species in the world. For vertebrates in general, Seal et al. (1993) recommended captive management for a staggering 1192 (34%) of the 3550 taxa examined. Furthermore, captive breeding is recommended in a remarkable 64% of the 314 approved recovery plans for U.S. endangered and threatened wildlife (Tear et al. 1993). Of special concern are a number of "ark" paradigm proposals that envision long-term preservation of numerous species through captive breeding, followed, perhaps centuries from now, by reintroductions to the wild (Soulé et al. 1986; Foose et al. 1992; Tudge 1992).

Because the implications of such large-scale reliance on captive breeding are profound and because some proposals currently before Congress would revise the Endangered Species Act to greatly emphasize captive breeding, we believe a review of the overall advisability of this technique in species recovery is appropriate. We examine the role of captive breeding in the recovery of endangered animal species, focusing on seven often overlooked limitations of the technique. Although we do not consider plants, we believe our discussion also has relevance to plant conservation (cf. Ashton 1988; Allen 1994; Hamilton 1994). Captive breeding for recovery purposes (i.e., for ultimate reintroductions to the wild) should not be confused with captive breeding for other purposes, such as exhibit, conservation education, or research. Although these latter captive breeding programs may also have conservation value, they have quite different characteristics and entail different precautions.

Our primary conclusion is that captive breeding has a legitimate role to play in the recovery of only a limited number of endangered species and should be employed only when other viable alternatives are unavailable. When it is employed, it should always be tightly coupled with recovery objectives for wild populations and should not be proposed as a long-term solution.

Limitations of Captive Breeding

Achieving Self-sustaining Captive Populations

It is often assumed that self-sustaining captive populations can be readily established for most endangered and threatened taxa. However, only a small percentage of vertebrate or invertebrate taxa have bred in captivity (Conway 1986; Rahbek 1993), and obtaining consistent reproduction and survivorship under captive conditions has proven difficult with many species (Table 1). Failures to breed well in confinement can be traced to a variety of causes, including the lack of psychological, physiological, or environmental requirements (Millam et al. 1988; Merola 1994), inadequate diet (Setchell et al. 1987), effects of hand-rearing (Myers et al. 1988), behav-

Table 1. Examples of endangered species breeding programs that have encountered significant problems in achieving self-sustaining captive populations.

Species	*Problems*	*Reference(s)*
Whooping Crane (*Grus americana*)	low numbers, high mortality, infertility, incompatibility	Lewis (1990)
Kakapo (*Strigops habroptilus*)	low numbers, poor survival	Merton and Empson (1989)
Puerto Rican Parrot (*Amazona vittata*)	low fertility, incompatibility, inbreeding (?)	Snyder et al. (1987), Brock and White (1992)
Hawaiian Crow (*Corvus kubaryi*)	low numbers, low fertility, high mortality, incompatibility	NRC (1992)
Aye-Aye (*Daubentonia madagascariensis*)	low offspring survival	Sterling (1993)
Giant panda (*Ailuropoda melanoleuca*)	low numbers, poor neonate survival, incompatibility	Hu and Wei (1990)
Northern white rhino (*Ceratotherium simum cottoni*)	low numbers, low conception rate	Svitalsky et al. (1993)

ioral incompatibility (Yamamoto et al. 1989), and inbreeding depression (Ralls & Ballou 1983; Danielle & Murray 1986). Identifying these factors can be extremely difficult, and for many endangered taxa effective captive management and husbandry regimes are still unknown even after years of experimentation. Because of poor reproduction, self-sustaining captive populations may never be achieved for some endangered species. For others, large numbers of individuals must be held in captivity to attain the production needed to sustain reintroduction efforts.

Reintroduction

In a recent review of 145 reintroduction programs of captive-bred animals, largely vertebrates, Beck et al. (1994) found only 16 cases (11%) of successfully established wild populations (although with some programs still in progress, this rate may rise over time). Captive-bred stocks also fared relatively poorly in the reintroduction programs reviewed earlier by Griffith et al. (1989). These results suggest major difficulties with establishing wild populations from captive-bred stock.

The causes of failure in reintroductions of captive-bred animals vary greatly from case to case and range from a failure to correct the factors originally causing extirpation to significant behavioral deficiencies in released animals, especially with respect to foraging, predator avoidance, and social behavior. Such deficiencies have been documented in a wide variety of captive-bred animals (e.g., Lyles & May 1987; Kleiman 1989; Miller et al. 1990; Wiley et al. 1992; Fleming & Gross 1993; Snyder et al. 1994). These deficiencies seem especially frequent in species that learn most of their behavioral repertoires and in animals that lack opportunities to associate with wild individuals in natural settings during critical learning periods. Reintroduction attempts with captive-bred individuals of species facing appreciable predation threats in the wild often fail. It is noteworthy that a substantial fraction of the successful reintroductions considered by Beck et al. (1994) involved large species, such as the Arabian oryx (*Oryx leucoryx*) and plains bison (*Bison bison*), that were reintroduced in areas without predators.

Logically, behavioral problems seem least likely in reintroductions of species that lack parental care. However, as a caveat to this assertion, releases of captive-raised juvenile sea turtles, to establish new breeding colonies or reestablish extirpated colonies, have been conducted for decades without documented success (National Research Council 1990). In species with extended parental care the behavioral deficiencies of captive-bred stock have sometimes been overcome by conspecific fostering (Snyder et al. 1987; Wiley et al. 1992). Unfortunately, opportunities for conspecific fostering are few or absent for many endangered species. The alternative of cross-fostering young to adults of other species can lead to behavioral problems in species recognition (Harris 1970; Lewis 1990) and is usually best avoided.

It is still early for safe generalizations, but we suggest that in the absence of fostering, the survival of released captive-reared individuals may often be best with species whose behavior is instinctive, species at the top of food chains or species introduced to predator-free or predator-deficient environments. Results to date suggest that for species whose behavioral repertoires are largely learned, it may be difficult to reestablish wild populations if all individuals are drawn into captivity at any point and if releases are limited to captive-bred individuals (Snyder et al. 1994).

Domestication

Many of the problems affecting captive preservation and reintroduction of endangered species are results of genetic and phenotypic changes that occur in captivity. Modern, conservation-oriented breeding programs attempt to ameliorate the genetic effects of inbreeding, drift, and adaptation to the captive environment through the deliberate and careful control of reproduction, population size, and population demography (Foose & Ballou 1988; Allendorf 1993). This is a difficult task, however, given (1) the practical limitations of controlling reproduction; (2) the dynamic nature of evolutionary forces in small populations; (3) the types of genetic variation to be maintained; and (4) the uncertain nature of selection in the captive environment (Lande 1988; Simberloff 1988). We are particularly concerned that the usual strategy to slow down genetic change—equal breeding of founder family lines—is impractical for many species that do not breed readily in captivity, especially those that are reluctant to accept forced pairings and are resistant to manipulative techniques such as artificial insemination. Even in those critically endangered species for which genetic management is relatively feasible, it is not always implemented (Miller et al. in press).

Captive environments differ greatly from wild environments, and evolutionary processes do not stop because species are in cages (Spurway 1955; Kohane & Parsons 1988; Allendorf 1993). Species become progressively more adapted to captivity even when comprehensive genetic management is practiced. Given a number of generations, one can expect to see populations that differ from wild stocks in significant ways, with most, if not all, of these differences having deleterious effects on fitness in the wild (Mason et al. 1967; Fleming & Gross 1993). Upon release such captive stocks may be incapable of producing viable wild populations and/or may exert deleterious genetic pressures on remnant wild populations (Fleming 1994; Philippart 1995).

Selection for traits such as tameness can often be strong in captivity regardless of whether it is intentional or not. And when selection is strong, major changes can occur quickly. For example, in only 20 generations Belyaev (1979) was able to produce almost fully domesticated forms of silver foxes (*Vulpes fulva*), exhibiting typical dog-like characteristics such as two breeding periods per year, drooping ears, erect tails, and behavioral traits such as tail-wagging and a tendency to lick hands and faces of humans (all characteristics that are absent from wild fox populations).

Domestication can be especially rapid in certain fishes and invertebrates (Moyle 1969; Myers & Sabath 1980; Swain & Riddell 1990; Johnsson & Abrahams 1991), possibly due to the high potential fecundity of individuals and short generation times. Many insects, for example, quickly undergo major changes in behavior and morphology under captive conditions. Because of the magnitude of such changes, efforts to reestablish the large copper butterfly (*Lycaena dispar*) in the United Kingdom have focused on use of endangered wild stocks from other countries rather than available captive-bred stocks (Pullin 1993).

Behavioral traits that are learned or culturally transmitted are especially prone to rapid loss in captivity, and genetic management provides no relief from these losses. For many species captive populations may become resistant to reestablishment in the wild for behavioral reasons alone, and within very few, sometimes only single, generations. For example, in species in which young learn long, annual migrations by associating with experienced individuals, the first captive-produced generation may not migrate properly in the absence of a wild population or even in the presence of a wild population if it does not include parental individuals (Akçakaya 1990). Behavioral changes induced by captivity may be the most significant problem when and if we try to unload the "ark" (Lyles & May 1987).

How reversible is domestication? Feral populations of domestic cats (*Felis catus*) have become established from captivity in many regions and with phenotypes reverting to wild appearance relatively quickly. But, feral populations of many domesticated forms are unknown, except in predator-free environments. For example, chickens (*Gallus gallus*) and canaries (*Serius canarius*) have failed to establish wild populations anywhere except on predator-free islands (Derrickson & Snyder 1992). The inability of Wild Turkeys (*Meleagris gallopavo*) to form wild populations after only a few generations in captivity has been thoroughly examined (Leopold 1944; Knoder 1959). In this species domestication effects are apparent in certain features of the endocrine and nervous systems. Size of the adrenal glands rapidly declines in captive flocks and seems closely tied to a loss of the physiological and behavioral traits essential for survival in the wild (Knoder 1959).

We believe the implications of progressive genetic and phenotypic changes are considerably more serious than commonly recognized. Proposals based on the "ark" paradigm are built on a misconception of constancy or near constancy of captive populations through time. For many species long-term captive breeding, despite all efforts to slow changes, may result in domesticated forms with low reestablishment potentials.

Because of progressive domestication, we should abandon any general expectations that we can "preserve" endangered species in captivity without significant change over the long term and limit captive breeding programs to short-term situations where animals will be returned to the wild as soon as possible. Thus, captive breeding programs for reintroduction should not be started any sooner than is clearly necessary, and "prophylactic" captive breeding should be avoided.

Disease

Some evidence exists that endangered species may have enhanced susceptibility to disease because of reduced genetic diversity that can result from small population size (O'Brien & Evermann 1988; Thorne & Williams 1988). Whether or not this is true, disease problems

Table 2. Examples of recent epizootics in captive populations of endangered species.

Species	*Disease*	*Reference(s)*
Whooping Crane (*Grus americana*)	equine encephalitis	Dein et al. (1986)
Red-crowned (*Grus japonensis*) and Hooded (*G. monacha*) Cranes	inclusion body disease	Docherty and Romaine (1983)
Mauritius Kestrel (*Falco punctatus*)	herpes virus, hepatitis	Cooper (1993)
Mauritius Pink Pigeon (*Nesoenas mayeri*)	herpes virus	Snyder et al. (1985)
Puerto Rican Plain Pigeon (*Columba inornata wetmorei*)	coccidiosis, capillaria	Arnizaut and Perez-Rivera (1991)
Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*)	sarcocystis	D. Thomsen, pers. comm.
White-winged Wood Duck (*Carina moschata*)	avian tuberculosis	Cromie et al. (1989)
Bali Mynah (*Leucopsar rothschildi*)	avian pox, atoxoplasmosis	Landolf and Kocan (1976), Partington et al. (1989)
Addax (*Addax nasomaculatus*) and spider monkey (*Ateles geoffroyi frontatus*)	pseudotuberculosis	Welsh et al. (1992)
Black-footed ferret (*Mustela nigripes*)	distemper	Carpenter et al. (1976)
Green sea turtle (Chelonia mydas)	chlamydiosis	Jacobson (1993)
Aruba Island rattlesnake (*Crotalus durissus unicolor*)	ophidian paramyxovirus	Odum and Goode (1994)

have been common in captive populations of endangered species (Table 2).

The frequency of disease outbreaks in captive collections is partly a result of enhanced exposure, especially to exotic pathogens. The prevalence of international wildlife trade and the normally close juxtaposition of diverse species in zoos and private collections have brought many species into contact with diseases and parasites for which they have little resistance (Derrickson & Snyder 1992; Bush et al. 1993; Jacobson 1993). Although disease risks also exist for wild populations, such risks often involve diseases to which the populations have had previous exposure and have developed some resistance. When serious disease problems arise for wild populations (e.g., sylvatic plague and distemper for black-footed ferrets), the diseases involved are often suspected or known to be of exotic origin (Miller et al., in press).

Funding for the study of wildlife diseases has been poor, diagnostic capabilities are not on a par with those for human diseases, and sophisticated tests and vaccines are not available for many pathogens (Worley 1993). Further, standard quarantine periods are too brief for reliable detection of many slow-acting diseases. Some serious diseases can remain latent in asymptomatic carriers for long periods and suddenly manifest themselves when animals come under stress (Partington et al. 1989). Cleansing a facility contaminated with environmentally persistent pathogens can necessitate facility demolition, soil and substrate removal, and euthanasia of potentially infected individuals (Gough 1989).

Because of the existence of slow-acting, yet serious diseases that cannot be detected reliably in carrier individuals (e.g., psittacine proventricular dilation syndrome, avian tuberculosis, paratuberculosis, salmonellosis, Pacheco's disease and other herpes infections), there are always risks that release programs may inadvertently infect wild populations with pathogens to which they lack resistance, even with intensive pre-release screening for diagnosable diseases. These risks are presumably greatest when reintroduction programs use individuals from open, multi-species facilities outside the normal range of the species or when reintroductions use confiscated animals with unknown histories. Although risks also exist for translocations of animals from one wild location to another, the chances of contact with exotic diseases is generally less in such releases than in releases from open, multi-species captive environments as long as transfers are made within historic populations.

Many reestablished populations of Wild Turkeys in the midwestern U.S. are infected with a hematozoan parasite (*Plasmodium kempi*), apparently resulting from translocations of infected birds (Castle & Christensen 1990). Similarly, a virulent upper respiratory mycoplasma disease in wild desert tortoises (*Xerobates agassizii*) and gopher tortoises (*Gopherus polyphemus*) is believed to have resulted from releases of infected captive individuals (Jacobson 1993). Woodford and Rossiter (1994) list many additional cases of inadvertent introductions of diseases into wild populations through releases of contaminated captive-bred or translocated wild-caught animals. Clearly there are appreciable risks to wild populations through releases of captive-bred or translocated wild animals (cf. Snyder et al. 1994), and these risks are often not limited to the species reintroduced (examples in Woodford & Rossiter 1994).

Griffith et al. (1993) reported that animals were not subjected to physical examinations by a professional biologist or veterinarian in 24% of the reintroductions they reviewed. In the survey by Beck et al. (1994) medical screening was practiced in only 46% of the reintroduction programs. Because of the potential significance of disease problems, the CBSG and the American Zoo and Aquarium Association hosted a symposium in 1992 to develop health screening protocols for reintroductions (Wolff & Seal 1993). Unfortunately, because screening methods do not exist for many slow-acting pathogens and because new diseases continue to crop up, the only way to minimize disease risks during reintroductions is to (1) screen intensively for diseases that can be detected and (2) be certain that released stocks have had a long history of non-exposure to potential disease carriers. The latter is effectively impossible in the open, multi-species environments that characterize most public and private zoological collections.

Basic veterinary principles suggest that captive breeding for recovery should be done under the following conditions: (1) captive populations should be maintained in isolated single-species facilities that do not regularly exchange stocks with other facilities; (2) captive breeding should be conducted within the natural range of the species to reduce exposure to exotic pathogens and in at least two geographically separate facilities; (3) founder stock should not be drawn from open, multi-species facilities, but should be taken directly from the wild or from single-species facilities within the natural range that have good histories of disease prevention; and (4) facilities should be closed to the public, and staff should practice rigorous disease-prevention methodology, including strict avoidance of contact with other captive stocks.

These recommendations are based on the position advanced by Ashton and Cooper (1989) that exclusion of pathogens is a much more effective way to avoid problems than attempting to eliminate pathogens once they are established. Thus, strong efforts should be made to prevent exposure of captive stocks to microorganisms and parasites not normally present in their wild populations (we are not, however, advocating maintenance of stocks under completely sterile conditions). Unless such efforts are made, the risks of introducing exotic pathogens into captive and wild populations are substantial.

Most of the precautions we advocate are employed by some captive breeding programs for endangered species (such as California Condor; Puerto Rican Parrot [*Amazona vittata*]), but few are employed by the majority of programs. Unfortunately, comprehensive disease precautions substantially inflate the costs of captive breeding, especially the needs for isolated facilities and separate staffs to care for the animals. Few zoological institutions can afford to practice these precautions and most rely mainly on a quarantine of incoming stock for 30-60 days to reduce the chance of disease outbreaks. Such quarantine can reveal only a fraction of disease-infected animals, and disease outbreaks remain common in open, multi-species institutions (Shima & Osborn 1989).

Our orientation and emphasis on disease risks are a consequence of (1) repeated personal experiences with serious diseases in a variety of captive-breeding and reintroduction programs in which the above precautions were not taken; (2) a virtual absence of such problems in our experience with programs taking many of the above precautions; and (3) a growing realization that the failure of many programs to implement thorough precautions represents a significant risk to wild populations. We are not opposed to all reintroduction efforts from a disease standpoint, and we recognize that disease risks may vary substantially from one taxonomic group to another. Nevertheless, costs of comprehensive disease precautions should be accepted as intrinsic to all captive-breeding efforts for reintroduction. The potentials for future disasters like the chestnut blight, Dutch elm disease, whirling disease of trout, and mycoplasma disease of tortoises should engender an attitude of considerable caution and humility, not one of denial. The recent decision of the U.S. Fish and Wildlife Service to abandon plans to move highly endangered Puerto Rican Parrots to an open, multi-species environment on the mainland (Wilson et al. 1994) is exactly the sort of disease-risk assessment that should become routine throughout the conservation community.

Financial and Physical Resources

The costs of captive breeding programs for recovery of endangered species sometimes run on the order of a half-million dollars per year per species (Derrickson & Snyder 1992). Further, zoological institutions do not have enough space to accommodate viable captive populations for all species that are threatened with extinction (Conway 1986; Soulé et al. 1986; Rahbek 1993)—assuming that captive breeding might be advisable for all these species. If captive breeding for endangered species were to be limited to closed, single-species facilities, as we believe it generally should be, the shortfalls in space and financial resources would be even more daunting.

To counter the space limitations in zoological institutions, Foose and Seal (1992) advocated the concept of nucleus populations. Although these populations (generally under 100 individuals) would be too small to maintain long-term genetic diversity, diversity would be maintained through periodic importations of wild stock. However, Willis and Wiese (1993) showed that the frequency of importations required to maintain genetic diversity in nucleus populations is at least an order of magnitude greater than assumed by Foose and Seal (1992) and is impractical for many species.

Some costs of captive breeding endangered species can be met by institutional revenues. To the extent that institutions limit themselves to showy endangered species, captive breeding can make economic sense. Unfortunately, most endangered species are visually unspectacular, so there is little potential to pay for captive propagation of these species from their own exhibit earnings.

Private breeders are often proposed as an alternative to zoos for breeding endangered species (Clubb 1992), but effective long-term conservation programs are unlikely to come from this sector. Like most zoological institutions, private breeders have been generally unwilling to maintain single-species facilities and separate staffs for endangered species. In addition, genetic management of captive stocks has typically been lax among private, captive breeders, with widespread deficiencies in record-keeping (for example, clouded leopard [*Neofelis nebulosa*], S. Millard, personal communication) and a fascination with hybridization of species and races (such as blue iguana [*Cyclura nubila lewisi*], Burton 1993). Conflicts of interest over ownership of animals and reluctance of individual breeders to cooperate with one another continue to impede programs (Clubb 1992).

In general, the financial resources needed for comprehensive captive breeding of endangered species are not likely to be available either in zoological institutions or among private captive breeders. Both sectors are eager to breed endangered species, but neither can be expected to do it comprehensively without a major infusion of funding from other sources. Unfortunately, financial support from government and private sources is quite limited and usually materializes only for species with substantial public appeal.

In comparison, the monies needed for effective in situ conservation efforts are often much more modest (Leader-Williams 1990; Balmford et al. 1995). Although we recognize that some in situ conservation efforts are costly, the general emphasis on habitat protection inherent in in situ approaches means that multitudes of species beyond particular target species are simultaneously conserved. Consequently, the costs involved should generally be considered those of saving entire ecosystems, rather than those of conserving a single species. From this viewpoint, the true cost differentials between in situ and ex situ approaches may often be much greater than the single order of magnitude calculated for large mammals by Balmford et al. (1995).

Preemption of Other, Better Techniques

Much has been said about difficulties in moving funds between ex situ and in situ approaches (Conway 1995), and in some cases we agree that funds are nontransferable. It is also valid to suggest that in some cases funds for in situ efforts have originated largely as an extension of funding for captive breeding. Nevertheless, in diverse conservation programs, in both public and private sectors, we have frequently dealt with situations of funding competition between these approaches and are acutely aware of how one approach often preempts the other, sometimes to the detriment of crucial in situ needs.

For example, despite requests over a period of years from the California Condor Recovery Team, the U.S. Fish and Wildlife Service has until recently declined to fund a proposal to conduct toxicity studies of alternatives to lead bullets, which could solve the problem of lead poisoning in Condors in the wild (see Wiemeyer et al. 1988; Snyder & Snyder 1989). Meanwhile captive breeding and releases have continued to be funded at more than $1.0 million annually (including contributions from zoological institutions). Fortunately, the modest funding (~$30,000) needed for the toxicity studies has now been secured (Anonymous 1994).

For another example, highlighting a black-footed ferret captive breeding and reintroduction program has made it easy for the federal government to deflect attention away from the destruction of ferret habitat through prairie-dog eradication campaigns. In fact, the U.S. Fish and Wildlife Service has determined recently that the captive ferret population is the only "essential" ferret population, in spite of a clear mandate from the Endangered Species Act to recover the species in the wild (Miller et al. in press). Although captive breeding of ferrets, like that of California Condors, is clearly a necessary conservation activity, both species' programs have suffered in recent years from a lack of balance between efforts aimed at captive breeding and reintroduction and those aimed at ameliorating limiting factors in the wild.

Thus, captive breeding can divert attention from the problems causing a species' decline and become a technological fix that merely prolongs rather than rectifies problems (Frazer 1992; Meffe 1992; Philippart 1995). Long-term solutions are often politically more difficult than captive breeding solutions, so it is tempting for managers to deemphasize efforts for wild populations once captive populations are in place.

When captive breeding is tightly coupled with efforts to save wild populations, it can help lead to habitat preservation by serving as a focus for generating public interest in the plight of a species (Durrell & Mallinson 1987; Mallinson 1988). Unfortunately, in practice the connection between captive breeding and habitat preservation is sometimes tenuous. Captive breeding can become an end in itself and may undermine rather than enhance habitat preservation by reducing the urgency with which this goal is pursued. The existence of a captive population can give a false impression that a species is safe, so that destruction of habitat and wild populations can proceed. Certain recent proposals to breed sea turtles and Spotted Owls (*Strix occidentalis*) in captivity have likely been put forth with exactly this objective in mind.

Preemption of other conservation alternatives is an acute problem when decisions are made to bring all members of a species into captivity before causes of endangerment are well understood. The chances of success in subsequent reintroductions are greatly reduced under such conditions. A decision to bring all Puerto Rican Parrots into captivity in 1972 was fortunately never carried out (Snyder et al. 1987). Research into population-limiting factors has since led to slow recovery of the wild population, whereas captive breeding has yet to become a fully successful enterprise (Wilson et al. 1994).

Ensuring Administrative Continuity

During the past 20 years we have participated in captive-breeding and reintroduction programs for a diverse array of endangered species. The level of success in these programs has depended heavily on the degree of commitment and expertise characterizing program administrators. Yet one of the most alarming features of virtually all these programs has been a high degree of instability in the quality of efforts. In particular, many unintended effects have resulted from personnel changes over the years. Such changes are inevitable and often occur for reasons that have little to do with the goals of maximizing program performance.

Multiple changes in administrative personnel will occur during the lifetimes of many conservation programs because of the often slow rate of recovery of endangered species. For "Millennium arks," the personnel turnover will be truly extraordinary. Captive breeding programs for endangered species are not unique with respect to their susceptibility to variations in administrative quality. However, these programs are vulnerable to the effects of such variations because they are input intensive and because serious mistakes, once made, may be impossible to correct. Complex in situ efforts are also vulnerable to effects of administrative decay. But when straightforward species or habitat protection is adequate for species conservation, in situ efforts can have a significant advantage in long-term stability.

In practical terms, the difficulties in ensuring adequate administrative continuity are among the most serious problems faced by most breeding programs, governmental or private. Yet, this subject has been almost completely ignored (Clark et al. 1994). The general assumption seems to be that programs will always proceed in a rational, goal-maximizing manner. Real-life deviations from this assumption are frequent and should be weighed heavily against presumed benefits of captive breeding in decisions regarding the initiation of captive breeding programs likely to last more than a few years.

Conclusions

The short-term successes in conserving a few endangered species through captive breeding have led to extraordinary enthusiasm for this technique in parts of the conservation community (Rahbek 1993). This enthusiasm has reached an apogee in the "ark" paradigm that envisions preservation of legions of vertebrate species in captivity for up to hundreds of years—to be someday reestablished in the "wild." This view assumes success rates in breeding and genetic/behavioral management in many species that are unattainable, probabilities of successful reintroduction to the wild that are unrealistic, and a sustained availability of resources that is unlikely. Perhaps most unconvincing of all is an unwarranted confidence in the continued viability of human institutions to safeguard species in captivity under social and economic conditions that can be expected to vary from benign to chaotic over the long term. In short, we believe the ark paradigm is fundamentally flawed and diversionary.

The scope of problems inherent in conducting comprehensive captive breeding programs for species recovery, the great expense involved in these programs, and the fundamental limitations of these programs to produce long-term conservation benefits suggest strongly that captive breeding should generally be viewed as a last-resort recovery strategy. In contrast to the basically prophylactic approach to captive breeding taken by the CBSG and by many recovery plans, we believe that captive breeding should not normally be recommended or initiated in recovery efforts before careful field studies have been completed and a comprehensive determination has been made that preferable conservation alternatives are not immediately available and that captive breeding is essential for near-term survival of a species. Captive breeding should not be a long-term conservation strategy and, when adopted as a recovery technique, should always be integrated with simultaneous efforts to maintain, augment, or reestablish wild populations. Although captive breeding does have an important and positive role to play in a small percentage of recovery programs, attempts to use this technique as a panacea uncoupled from conservation efforts for wild populations can be expected to be detrimental. Clearly, every proposal to establish a captive population for recovery merits thorough evaluation and objective peer review.

Captive breeding should not be invoked as a species recovery tool simply because a wild population falls below what may be determined to be a minimum viable size. Such populations may still be far more viable than captive populations given the many problems associated with captive breeding and reintroduction. Although population viability analyses have been used frequently to justify captive breeding, none to our knowledge has ever made rigorous comparisons of the long-term viability of wild and captive populations or acknowledged many of the aforementioned factors affecting the viability of captive populations. In many cases alternative, non-captive approaches may be more effective, economical, and safe than captive approaches in achieving recovery. Usually there is enough time to investigate promising alternatives before initiating captive breeding, and conservation organizations should emphasize such investigations as a high priority.

All recovery programs incorporating either reintroductions of captive-bred stock or translocations of wild animals should incorporate rigorous disease prevention and screening procedures. The disease precautions we advocate for recovery captive breeding populations are restrictive and may be sufficiently expensive to preclude captive breeding as a recovery approach for many species. However, many of the species that have been recommended for recovery captive breeding (Seal et al. 1992) do not merit this approach in the first place. Further, not only disease risks, but also overall costs (e.g., labor, construction, transportation) can generally be minimized by conducting recovery captive breeding programs in countries of origin rather than in ex situ environments in developed nations. Locating captive programs for endangered species within their countries of origin can simultaneously provide a unique foundation for additional, synergistic conservation programs aimed at research, training, public education, and habitat preservation.

In today's era of "animal rights" many zoological institutions are under severe attack and view their own survival as tied closely to their involvement in captive management of endangered species. As long as such institutions limit their efforts to species that truly need captive breeding and ensure that these efforts are properly carried out and closely integrated with protection of wild populations and habitats, we see great benefit in their participation in recovery programs.

Although we believe captive breeding of endangered species for recovery should not be conducted in open multi-species facilities outside of the species' native range, this should not be construed as an anti-zoo orientation. We strongly support the efforts of zoos to establish recovery captive populations in appropriate facilities in countries of origin of endangered species when such programs are advisable and are desired by local governments. Further, we strongly support the efforts of zoos to pursue other "nonrecovery" forms of captive breeding of endangered species; for example, to ensure supplies of animals for exhibition. In addition, we firmly believe that zoological institutions have an important role to play in endangered species conservation through their support of public education, professional training, research, and in situ conservation programs. Many zoological institutions directly support field studies and education programs in both native and foreign countries, and their traditional role as institutions for display of exotic creatures is changing rapidly (Mallinson 1988; Wemmer et al. 1994; Conway 1995; Hutchins et al. 1995). These in situ conservation and education programs may ultimately contribute far more to the overall preservation of biodiversity than breeding programs aimed at single species.

It is no exaggeration to say zoological institutions are one of the major hopes for the future of conservation of biodiversity. At the same time, we fear that by focusing on recovery captive breeding as their central role in conservation, some institutions may fall short of their full conservation potential. It would be tragic if these considerable potentials were frittered away in ill-conceived and expensive attempts to create and maintain captive breeding programs for species that are much better conserved by other approaches.

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29

Reintroduction Programs

DEVRA G. KLEIMAN

This chapter outlines the conditions that make a reintroduction program using captive mammals of a threatened or endangered species an appropriate conservation strategy, and presents some basic guidelines for such an effort. IUCN (1987) also provides criteria for these and related efforts.

Reintroduction is an approach that is attractive to zoo conservationists, as well as to the general public, but such a program should be undertaken only with a clear understanding of the costs and benefits. Because reintroduction is a complex endeavor that usually involves both a long-term financial commitment and active collaboration by governmental and nongovernmental agencies and institutions, it is not a viable option for the majority of endangered species held in captivity. Indeed, attempts to reintroduce a species, if poorly conceived or implemented, may actually obscure the conservation issues that led to the decline of the species in the first place—and thus may detract from, rather than add to, a species' chances of survival (IUCN 1987).

The first step in considering a reintroduction is to define the long-term conservation goals of the program and the criteria for success. Aims vary according to (1) the status of each species in captivity and in the wild and (2) the political situation within the receiving country. Generally, major goals include increasing the size of the wild population, establishing additional wild populations, and/or preserving or enhancing available habitat. Ideally, reintroduction could also be used to enhance the demographic and genetic management of both wild and captive populations. While criteria for success vary depending upon the aims of each program, a program is likely to be judged a success if the status of a species is significantly improved by the reintroduction, even if every single released individual dies. Reintroduction solely as a solution to the problem of surplus captive animals is inappropriate; an integrated plan to promote the preservation of the species in the wild is also needed.

The success of many early attempts to reintroduce mammals into natural habitats cannot be fairly evaluated since there has been limited post-release monitoring, especially for primate reintroductions (Aveling and Mitchell 1982; Borner 1985). There have been some clear successes with ungulates, including the American bison, *Bison bison*, and the European wisent, *Bison bonasus* (Conway 1980; Campbell 1980), although those efforts also involved minimal monitoring.

In the remainder of this chapter I will concentrate on outlining those factors that should be considered in planning and implementing a reintroduction program involving the release of threatened or endangered captive mammals. There have been many more reintroduction programs for bird species (Campbell 1980), although they are neither less complicated nor less expensive than reintroduction programs for mammals. Long (1981) estimated, in a review of translocations, reintroductions, and introductions, that approximately half of the attempts failed. Cade (1986), Wemmer and Derrickson (1987), Kleiman (1989), Stanley Price (1989), Gipps (1991), and Beck et al. (1994) provide reviews and bibliographies on reintroduction programs for captive birds and mammals.

A description of a release of animals into a natural habitat needs to specify (1) whether the release occurs within the species' original geographic range, (2) whether there is a preexisting free-ranging population at the release site, and (3) the history of the specimens released (i.e., wild- or captive-born, currently in the wild or in captivity, previous experience in the wild). There are differences among authors in their use of terms (Konstant and Mittermeier 1982; IUCN 1987; Stanley Price 1989). I am defining *reintroduction* here as the release of either captive-born or wild-caught animals into an area within their original range where populations have declined or disappeared. Reintroductions may involve moving *(translocating)* wild-caught animals or releasing naive captive animals (both wild- and captive-born), and may have a conservation or an economic purpose. Goals may include improving the status of the wild population by increasing numbers (sometimes termed *restocking*) or changing the population's genetic makeup. The latter goal may be appropriate when the species exists in small groups in insular habitats that preclude outbreeding.

WHEN IS REINTRODUCTION APPROPRIATE?

Reintroduction may be appropriate when the demography and genetics of the wild population suggest that a species could go extinct and that a boost in population size or genetic diversity would protect its future. Such a judgment must be based on a thorough knowledge of the species' biology, distribution, and ecological requirements, as well as an understanding of the original factors causing the population decline.

With the condition of the wild population ascertained, there must exist a viable, self-sustaining captive population with broad genetic representation. The captive population must be sufficiently robust to sustain the loss of many animals for a prolonged period while reintroduction techniques are perfected. Animals chosen for a release program must be surplus to the future needs of the captive population and able to interbreed with animals in the wild population. There are numerous species, such as owl monkeys, *Aotus trivirgatus*, in which distinct populations appear morphologically identical, but are so different genetically that individuals cannot interbreed (Ma et al. 1976). Shields (1982) has suggested that outbreeding depression may be a more common problem than expected.

Another requirement is the existence of suitable habitat with sufficient carrying capacity (Brambell 1977) to sustain the growth of the reintroduced population. Habitat suitability can be assessed only by detailed studies of the habitat preferences, movements, shelter requirements, and foraging and feeding behavior of free-ranging wild-born animals. Critical resources may not always be self-evident. Coimbra-Filho and Mittermeier (1978) correctly identified tree holes for sleeping as a critical resource for the golden lion tamarin, *Leontopithecus rosalia*. We preceded reintroductions of this species with an evaluation of the numbers of trees with sufficient girth to provide tree holes for nocturnal nesting (J. M. Dietz, D. G. Kleiman, and B. B. Beck, unpub.). Preferred habitat should have no, or a very reduced, resident population, but be within the natural range of the species.

Since habitat loss and alteration are the paramount causes of the decline of most species, the lack of suitable protected habitat is the major ecological reason to reject proposals for a reintroduction program. Thus, a prerequisite for a reintroduction program is the existence of legally protected areas, such as national parks or equivalent reserves, with real and effective protection (Campbell 1980; U.S. Fish and Wildlife Service 1982; Aveling and Mitchell 1982; Borner 1985; Oliver 1985). There must also be the expectation that the protected areas will survive intact into the future. Without a long-term commitment, there will be a constant (and probably losing) battle to protect not only the animals but also the habitat. For example, difficulty in finding a politically safe habitat for releasing red wolves, *Canis rufus*, has been one of the major obstacles to the Red Wolf Recovery Plan (U.S. Fish and Wildlife Service 1982; Parker 1986), as it has been for the release of sea otters, *Enhydra lutris* (K. Ralls, pers. comm.).

Currently, one of the most impressive reintroduction programs involves the release of captive-born Arabian oryx, *Oryx leucoryx*, in Oman (Fitter 1984; Stanley Price 1989). The Sultan of Oman has personally taken an interest in the program and is supporting it financially and providing equipment. Furthermore, individuals from local tribes are employed by the project, and thus directly benefit from it (Stanley Price 1986, 1989). This effort is likely to be successful, as long as the support remains at the level of government policy and the local citizenry is kept aware and involved.

While sufficient protected habitat is of paramount importance for the development of a reintroduction program, other reasons for a species' decline must also be identified and eliminated prior to the release of captive-bred animals (Brambell 1977). Hunting or poaching for food, fur, trophies, or other body parts has been a major factor in many species' decline, especially for birds and the large charismatic mammals. In other cases, species have declined or been lost due to predation, food competition, or habitat destruction caused by the introduction of nonnative species, including domestic cats, dogs, rats, rabbits, goats, and snakes. Birds and reptiles endemic to islands have suffered greatly from these causes.

Diseases that can rapidly wipe out a population (and a species, if it already exists in small numbers) may also be introduced through other carriers. Kear (1975) describes several cases in which avian species have been decimated through accidentally introduced viruses.

Free-ranging animals should not be present in an area targeted for a reintroduction if the wild population is severely endangered. It is not usually appropriate to intermix the wild and captive populations unless the species' future survival absolutely depends upon an "injection" from the captive gene pool. First, the captives may carry disease agents to which they, but not the wild individuals, are immune, a problem pointed out by many authors (Brambell 1977; Caldecott and Kavanagh 1983; Aveling and Mitchell 1982). The wild population can be protected by first releasing captives in habitats that are devoid of free-ranging animals. Alternatively, captives can be shipped to the country of destination and quarantined. Prior to release, selected free-ranging individuals can be introduced to the quarantined captives and act as "guinea pigs" to test for the presence of possible disease vectors. Prerelease screening by veterinarians of the captives' blood, urine, feces, and ectoparasites, followed by appropriate treatment, may also reduce the potential for disease transmission. However, veterinary evaluations of specimens destined for release is necessary regardless of the existence of overt health problems or the likelihood of contact between a reintroduced and a wild population.

Another reason for reducing contact between reintroduced captive-born animals and the wild population is to protect the genetic integrity of either or both populations. For example, the red wolf is currently considered extinct in the wild due to extensive crossing with the coyote, *Canis latrans* (U.S. Fish and Wildlife Service 1982, 1986; Parker 1986). To prevent further hybridization, the reintroduction program releases captives on islands or in areas known to be devoid of coyotes and hybrids.

Releasing animals into a saturated stable natural population is known to cause social disruption and stress (Brewer

TABLE 29.1. Decision Making Concerning the Reintroduction of Lion Tamarins (*Leontopithecus*): Do the Necessary Conditions Exist?

	Leontopithecus		
	rosalia	*chrysomelas*	*chrysopygus*
1. The reasons for the reduction in species numbers have been eliminated (e.g., hunting, deforestation, commerce)	?	No	No
2. Sufficient habitat is protected and secure	Yes?	No	Yes
3. Available habitat exists with low densities of or without native animals	Yes	Yes?	?
4. It is certain that the release of animals will not jeopardize the existing wild population	No	No	No
5. Sufficient information exists about the species' biology in the wild to evaluate whether the program is a success	5	1.5	3
6. Conservation education exists	5	2	4
7. The population in captivity is secure, well managed, and has surplus animals	Yes	No	No
8. Knowledge of the techniques of reintroduction exists	3	3	3
9. Resources for postrelease monitoring are available	Yes	No	No
10. There is a need to augment the size/genetic diversity of the wild population	Yes	No	Yes?
IS REINTRODUCTION RECOMMENDED?	YES	NO	NO

Source: Based on material provided by C. and S. Padua, A. Rylands, C. Alves, J. and L. A. Dietz, J. Ballou, F. Simon, B. Beck, and J. Mallinson at the *Leontopithecus* Management Workshop, Belo Horizonte, Brazil, June 19–23, 1990.

Note: Scale: 5, best; 0, worst.

1978; Carter 1981; Aveling and Mitchell 1982; McGrew 1983; Borner 1985; Harcourt, in press). For newly released animals (as singletons or groups) unacquainted with an area and without established home ranges or territories, a confrontation with adapted wild animals in natural social groups may result, at best, in flight and dispersal to a marginal habitat. At worst, the native animals may attack and seriously wound or kill the newcomers (Harcourt, in press; McGrew 1983). There are several documented cases in which young chimpanzees, *Pan troglodytes*, have been attacked after release into the territory of an established group (Brewer 1978; Carter 1981; Borner 1985).

Captives may also be unacquainted with the etiquette of social interactions in natural habitats, and may overreact upon meeting a wild conspecific. For example, groups of wild golden lion tamarins regularly interact at territorial boundaries. Although the interactions have aggressive components, they rarely result in injuries (Peres 1986; pers. obs.). However, groups of newly released captive-born tamarins were very aggressive toward each other during their first conspecific encounters, resulting in the flight and loss of some individuals (D. G. Kleiman, J. M. Dietz, and B. B. Beck, unpub.).

Decision Making: A Concrete Example

This section (see also Kleiman 1990) provides a concrete example of how to decide whether the appropriate conditions exist to recommend (or argue against) reintroductions of captive-born animals or translocations of wild individuals or groups.

The lion tamarins (genus *Leontopithecus*) derive from the Atlantic Coastal rainforests of Brazil. All species are endangered, mainly due to habitat destruction and alteration. There are captive populations of three species, each at different levels of development.

Table 29.1 lists ten conditions that should be met in order to recommend a reintroduction/translocation program. Additionally, it evaluates the position of the three lion tamarin forms with respect to each condition. Finally, a general recommendation is presented concerning whether a program of reintroduction is warranted for each of the three forms (this material was prepared in 1990).

The major reason for the decline of the lion tamarins has been deforestation. There has also been a thriving commerce in these forms because they are favored as pets. The reasons for the decline of *L. chrysopygus* and *L. chrysomelas* have not been eliminated, thus dictating against a reintroduction at this time. It is questionable whether or not the reasons for the decline of *L. rosalia* are now fully under control.

There is likely sufficient protected habitat available for *L. chrysopygus*, but not for *L. chrysomelas*. Protected habitat exists for *L. rosalia*, although in insufficient quantities for its future survival.

To prevent social disruption and disease transmission, it is preferable to use areas that have small or no populations of wild tamarins. This condition exists for *L. rosalia*, and probably for *L. chrysomelas*. There are many available confiscated *L. chrysomelas* that cannot be absorbed easily into the captive population; reintroduction may be a viable option for this small subset of wild-born animals. The situation for *L. chrysopygus* is unknown at this time.

Reintroductions should be encouraged only when there is some certainty that the release of animals from other regions (both captive and wild-born) will not jeopardize the existing native population through transmission of disease or social disruption. We do not have this confidence for the three forms of lion tamarins at this time due to our limited knowledge of their biology and status.

The evaluation of the success of a reintroduction can be accomplished only by long-term monitoring and must be based on a thorough knowledge of a species' biology, distribution, and ecological requirements. On a scale of 1–5, with 5 being the best-case scenario, I suggest that there is sufficient information available for *L. rosalia*, and totally insufficient information available for *L. chrysomelas*, with *L. chrysopygus* somewhere in between.

A conservation education program in conjunction with a reintroduction can attract and inform the local populace and may well result in greater community support for the effort. Both *L. rosalia* and *L. chrysopygus* conservation programs have strong educational components. The education program for *L. chrysomelas* is developing.

A prerequisite to the reintroduction of animals currently in captivity (whether captive or wild-born) is a secure, well-managed captive population with a long-term Masterplan and available surplus animals. This condition is met in *L. rosalia*, but not yet in *L. chrysomelas* and *L. chrysopygus*.

We have much still to learn about the methodologies of preparation, adaptation, and release of lion tamarins. With so many unanswered questions about the techniques that will ensure success—for example, for the injection of single animals into established reproductive groups—I suggest that we still consider reintroduction an experimental approach.

Access to the resources necessary to monitor the activities and survivorship of released animals is essential for a reintroduction effort, especially since we have not yet perfected our preparation and release techniques. The conservation programs for *L. chrysomelas* and *L. chrysopygus* are not yet sufficiently developed, with respect to financial support and the necessary infrastructure, to warrant a reintroduction effort. The *L. rosalia* program has a well-developed infrastructure and considerable resources to monitor the activities of released animals.

One major purpose of a reintroduction program is to augment the numbers or genetic diversity of a population. *L. rosalia* currently needs such augmentation, while the situation for *L. chrysomelas* and *L. chrysopygus* is not clear at this time.

Weighing the degree to which the necessary conditions are met for each species suggests that while reintroduction efforts may be appropriate for *L. rosalia*, they are not yet appropriate for *L. chrysomelas* or *L. chrysopygus*.

HOW DO YOU START?

Negotiations

Most reintroductions start with individual interests but ultimately involve multiple organizations, both governmental and nongovernmental, local, national, and multinational. The first step is to obtain the support and involvement of the appropriate governmental agencies, especially those that provide permits for the movements of threatened and endangered species. Collaboration should also be sought from the staffs of zoos, local universities, and conservation organizations in as well as outside the host country.

Continued success depends upon having the program eventually involve local people rather than outsiders, regardless of its location. There should be obvious benefits to the community, or support will be half-hearted or nonexistent. An abstract benefit, such as saving a species from extinction, is often not a compelling argument to a government official without resources who is under pressure from starving landless peasants. Economic benefits are obviously a strong incentive for cooperation. In Oman, local tribes are employed in the monitoring program for the Arabian oryx (Stanley Price 1986, 1989). Educational benefits (e.g., providing advanced training abroad) and the transfer of technology are additional inducements that also accelerate the transfer of the management of the program into local hands.

There must be a signed document containing the aims and objectives of the program as well as the criteria for its success. The signed agreement should also state the expectations, responsibilities, and degree of authority of each party, preferably with a preliminary schedule of work. At the outset, the responsibility for decision making at each stage of the process must be made clear, and a set of guidelines for making decisions should be provided. For example, animals may die or be born after the candidates for reintroduction are chosen, but before release. The authority for changing the list of release candidates in these circumstances must remain with a single person. Similarly, only one person should decide whether to "rescue" an animal that is doing poorly after the release. Another issue that must be included in the formal agreement is the ownership of the specimens (will they continue to be owned by the provider or be transferred to the receiver?).

Financial Support

A reintroduction program requires the long-term commitment of many individuals, including professionals living in the field for extended periods. Substantial funding is consequently required for (1) salaries; (2) field headquarters and subsistence; (3) vehicle(s), including fuel and maintenance for transport in the area of the reintroduction; (4) animal caging and shipping costs; (5) equipment and supplies for monitoring the released animals, such as binoculars, radiotelemetry equipment (receivers, antennas, and transmitters), materials for marking animals, and traps for capturing animals; (6) travel for the principals; and (7) long-distance communication. Kleiman et al. (1991) provide examples of costs for the Golden Lion Tamarin Conservation Program, which includes a reintroduction component. Expenses mount considerably when the project involves additional components, such as a conservation education effort, habitat protection, prerelease preparation and training of animals, and extensive field studies of the status and behavioral ecology of the free-ranging wild population.

Reintroduction programs for large mammals that normally range over great distances may be prohibitively expensive, since keeping track of the released animals may require the use of aircraft for radiotelemetry (Stanley Price 1986, 1989). Cost alone can prevent reintroduction programs from being used for the preservation of most species (Brambell 1977). Wildlife protection, habitat preservation, and conservation education may be more cost-effective conservation measures than reintroduction (Borner 1985).

Field Studies and Site Selection

Initial field surveys will clarify the status of the population in the wild and the availability of suitable habitat to support the reintroduced animals *and their descendants*. Releases should cease as the carrying capacity of the habitat is reached, as may soon be the case for the orangutan, *Pongo pygmaeus*, in Malaysia and Indonesia (Aveling and Mitchell 1982), where rehabilitation centers for wild-born orphans have been operating for many years.

A suitable release site should be completely protected and accessible and should have a small (or no) resident population of the target species, unless the goal of the reintroduction is to increase genetic diversity within an insular population. Planners should know whether the reserve area can sustain a genetically viable population in the future, and of what size. Field surveys may be time-consuming and complex, especially if little is known of the behavioral ecology and habitat preferences of the species. But field surveys are crucial since they may identify the causes of a species' decline in the wild and provide information necessary to eliminate the threats. If preliminary field studies indicate that there is insufficient suitable habitat or continued major threats to the species, planners must be prepared to abandon the proposed reintroduction unless they can show that the benefits of proceeding outweigh the costs.

Regular status surveys also allow for evaluation of the potential effects of the reintroduction on the native population. Similarly, information concerning behavioral ecology allows for the immediate evaluation of habitat suitability and the eventual comparison of released and wild animals. These comparisons are absolutely critical for the continued evolution of reintroduction methodology and procedures.

Choosing Animals

The choice of specimens for release derives from the project's objectives. For example, if the intent is to release only a small quantity of "genetic material" into an inbred population, then the only selection criterion might be an individual animal's genetic background. However, since most reintroductions aim to bolster the wild population's numbers significantly, the choice of animals is usually much more complicated. Biologists must also ensure that none of the selection criteria will negatively affect the genetic or demographic composition of the captive population.

The genetic characteristics of the candidates for reintroduction should be as close as possible to those of the original wild inhabitants of the region so that genetic adaptations to particular ecological characteristics of the area will be present in the released animals (Brambell 1977). For example, Stromberg and Boyce (1986) criticize the release of swift foxes, *Vulpes velox*, from Colorado stock in Canada because they believe that hybridization between the northern and southern populations will swamp the remaining fragile population of northern foxes and that the Colorado foxes will be unable to survive the cold winters of the north. Herrero, Schroeder, and Scott-Brown (1986) provide a convincing rejoinder and review the bases for their decision.

Biologists must determine the age and sex classes most appropriate for reintroduction, as well as the size and composition of groups to be reintroduced. Previous studies of the mating system, social organization, and the spatial relationships of individuals will provide guidelines for making these decisions. For example, based on such information, the groups of Jamaican hutias, *Geocapromys brownii*, golden lion tamarins, and Arabian oryx chosen for reintroduction were stable and cohesive; the hutias and tamarins were in monogamous families and the oryx in polygynous herds (Oliver 1985; Kleiman et al. 1986; Stanley Price 1986). Red wolves have been released as mated pairs (U.S. Fish and Wildlife Service 1986; Point Defiance Zoo and Aquarium 1988), and European otters, *Lutra lutra*, as trios of a single male and two females (Jeffries et al. 1985). Except for the otters, these were all reintroductions conducted in locations devoid of the species.

In saturated areas a different strategy is necessary. For example, gorilla, *Gorilla gorilla*, ecology and social behavior suggests that adult males or adult females with young are not good choices for release due to the likelihood of aggression from established groups; adolescent and adult females are probably the best candidates (Harcourt, in press). Early experiences with chimpanzee reintroductions suggested that cohesive groups should be released in already populated areas (Borner 1985). Finally, in some cases it might be best to reintroduce captive-born animals in the company of one or more wild-born individuals, rather than in a group composed only of captives.

Other decisions include the choice of season for the release, the distance between release sites, and the timing of the release(s)—that is, whether all releases will occur simultaneously or at predetermined intervals. The season chosen for release(s) should not be one in which critical resources are unavailable. Timing of releases depends in part on social organization if the animals will ultimately be occupying territories adjacent to each other.

The choice of animals and groups for reintroduction is a complex process that may require alternative strategies and considerable experimentation. Ultimately, the aim is the combination of animals that will survive best with the least preparation and cost, since a major criterion for success is a viable, free-ranging, self-sustaining population. The research and development phases of a reintroduction program may be very costly.

Cooperating Institutions

If only a single institution is holding the captive animals scheduled for reintroduction, then animals need only be moved between that institution, a halfway house quarantine facility (if necessary), and the release site. If several zoos are holding animals to be reintroduced, then coordination is more complicated, especially when substantial prerelease preparation is planned. As the individuals constituting the captive population of an endangered species are often distributed widely to minimize extinction risks, coordination will undoubtedly be complicated. In all cases, veterinary screening and treatment prior to release is necessary and is best done at a single institution for consistency.

Cooperating zoos must obtain health and import/export permits and arrange transport well in advance of the shipment itself. Institutions at the receiving site must be fully involved in the scheduling of shipments, especially if the receiving agency needs to prepare facilities or holding cages for prerelease acclimation.

Public Relations and Education

Public education and a broad base of public support are the only long-term solutions to conservation problems in both developing and developed countries. Since the local community often contributes significantly to the decline of a species through hunting or other activities that result in habitat degradation, a strategy involving the local community as collaborators rather than as obstacles to the program is the most likely to achieve success. Carley (1981) and Dietz and Nagagata (1986) describe conservation education programs acting in conjunction with the experimental release of red wolves in South Carolina and the reintroduction of the golden lion tamarin in Brazil, respectively.

Conservationists need to be sensitive to the pressures affecting the activities of local individuals, especially government officials, so that the latter are not put in impossible or compromising positions due to the activities of the reintroduction program. Although a successful conservation program clearly requires considerable basic biological knowledge, it demands public relations and political skills even more. Harcourt (in press) suggests, and I strongly agree, that the politics of reintroductions are as important as the release methodology.

A good reintroduction program involves local collaborators with a stake in its future success. In a developing country, there should be a commitment to train a future cadre of professional biologists in zoo biology, reintroduction methodology, wildlife biology, and conservation (Kleiman et al. 1986). To this end, a percentage of the project's total budget should be allocated for student support (or other forms of professional training) (see Kleiman et al. 1991).

Habitat Protection and Management

The degradation of habitats is the chief cause of species losses. A successful reintroduction requires a secure site; therefore an active program for habitat protection must exist. In some cases, habitat protection will derive from the activities of the reintroduction program (Aveling and Mitchell 1982). Additionally, reintroduction programs may need to become involved in aggressive management of land and animals or even the restoration of destroyed habitats. This need for aggressive management derives from the islandlike quality of so many reserve areas, whose ecological balance is easily upset due to their small size. The management and restoration of habitats in the Tropics are major challenges for the future (Ehrlich and Ehrlich 1981).

THE REINTRODUCTION

Preparation of Animals

We have very little experience in reintroducing captive mammals into their native habitats. No general guidelines exist for preparing species from the various taxa for reintroduction. However, there are at least six major areas of behavior to consider in the development of any preparation scheme. To survive, candidates for reintroduction must be able to (1) avoid predators; (2) acquire and process food; (3) interact socially with conspecifics; (4) find or construct shelters and nests; (5) locomote on complex terrain; and (6) orient and navigate in a complex environment. Preparation also may involve acclimatization of release candidates to the habitat and climatic conditions at the release site for some time prior to the reintroduction.

Species differences in the amount of prerelease conditioning required are likely to be significant. Herbivores may need little training in food acquisition and processing, while omnivores and carnivores may require extensive training. Species that normally live in herds or are solitary in the wild may need less preparation in the rules of social etiquette than forms that live in groups with a complex social structure. Arboreal species may need more preparation in locomotion and orientation than terrestrial forms. Migratory species or those with large home ranges may need to learn how to navigate and develop routes through natural habitats; territorial forms may need to learn how to define the limits of their ranges. We do not know which of these behaviors are learned and thus require training, and which are genetically hard-wired. Examples of different approaches to preparation (both recommended and tested) are given by Kleiman et al. (1986); Beck et al. (1991); Beck et al. (in press); Box (1991); Miller et al. (1990a, 1990b); Stanley Price (1986, 1989); Oliver (1985); Oliver et al. (1986); Parker (1986); Harcourt (in press); Rijksen (1974); Scott-Brown, Herrero, and Mamo (1986); and U.S. Fish and Wildlife Service (1982).

To prepare golden lion tamarins to forage and feed, Beck developed a feeding protocol that involved the gradual replacement of a single bowl of food with food that was distributed in different locations and hidden in "puzzle boxes," thereby forcing the animals not only to search for food, but to work to extract it. To improve locomotor ability and spatial orientation, animals were exposed to exceedingly complex three-dimensional environments that were regularly dismantled and rebuilt. The overall survival rates of prepared and unprepared tamarins did not differ (Beck et al. 1991; Beck et al., in press). Living for several months in a free-ranging condition on the zoo grounds, however, seemed to confer an advantage on tamarins after release, especially with extensive post-release support through provisioning and post-release training (Beck et al. 1991).

Red wolves have been preadapted to hunting by exposing them first to carcasses and then to live prey before reintroduction (U.S. Fish and Wildlife Service 1982). Miller et al. (1990a, 1990b) conducted one of the very few experiments to test the effects of training protocols on the behavior of captive animals with the ultimate aim of applying the techniques to the preparation of endangered black-footed ferrets, *Mustela nigripes*, for reintroduction. They used nonendangered Siberian polecats, *Mustela eversmanni*, as a model species to examine the development of predator avoidance and prey location skills in naive captives. The captives in general spent more time in surface activity than in burrows when searching for food. They also showed little evidence of a capacity for long-term memory of a negative experience with a potential predator.

For many species, social preparation is of considerable importance. Castro et al. (in press) have noted that the auditory communication skills of captive-born golden lion tamarins differ from those of wild tamarins, which could affect the ability of released captive-born individuals to interact properly with wild conspecifics.

For great ape reintroductions (and introductions), the major preparation has been social, in that candidates have been housed with conspecifics prior to release (Wilson and Elicker 1976; Pfeiffer and Koebner 1978) after being housed alone for long periods. Great ape releases have also often involved providing animals with exposure to a natural environment while still keeping them under human care. Hannah and McGrew (1991) summarize great ape rehabilitation projects, including some preparation techniques.

Incorporating preparation techniques into the normal zoo environment might result in more naturalistic and complex habitats for captive animals. At the National Zoological Park, tamarin groups scheduled for reintroduction are now released on zoo grounds during the spring and summer months. They are free-ranging for several months prior to shipment (Bronikowski, Beck, and Power 1989).

Beck (1991) points out that our attitudes toward animal welfare may be an obstacle to providing an enriched environment that would prepare captive-borns for survival in the wild. Real preparation would include exposure to food shortages, parasites and disease, predators, dramatic fluctuations in ambient conditions, and dangerous objects. To most keepers and veterinarians, such practices would simply be unacceptable.

Preparation has not generally been considered an essential element in most reintroduction programs, possibly because the training technology is not yet available. An alternative to prerelease training may be the pairing of captive-born animals with experienced wild-caught individuals prior to release, with or without post-release training.

Release and Monitoring

The reintroduction of captive-born animals into the wild signifies a change in the relationship between the animals and the animal manager, even if each specimen is outfitted with a transmitter and followed for 24 hours each day. Captive animals are the total responsibility of their caretakers; their diets, shelters, companions—indeed, most aspects of their environment—are controlled and controllable. Once the release occurs, this control is lost. Project personnel must decide whether and under what conditions to intervene if an animal begins to fail. The decision depends upon many factors, such as the political situation (can animals be allowed to die with everyone's full knowledge?); the value of the individual animal to the project because of its social, experiential, or genetic background; the perceived reason for the animal's problem (e.g., disease, predation, social conflict, human error); and the availability of captive housing for rescued individuals. If guidelines governing the rescue of reintroduced animals are clearly spelled out before the release, project personnel can avoid making a rushed decision in a confused and possibly emotionally charged climate.

The long-term monitoring of released animals is a crucial component of any reintroduction program. The zoos providing the animals for reintroduction have a special interest in the results of monitoring since it is important for them to keep their constituencies informed about the progress of individuals from their collections that have been reintroduced. Intensive monitoring can also facilitate the collection of carcasses for pathological study and thus clarify causes of death of released animals. A monitoring program will indicate how and when the behavioral repertoire of captive-born animals becomes comparable to that of wild specimens. All of this information can then be fed back into the management of the captive population.

Most reintroduction programs have included the provision of essential resources such as food, water, and shelter, both to provide support for the animals and to control their movements. Golden lion tamarins, Jamaican hutias, and Arabian oryx were all released from enclosures with shelters, with the hope that the animals would remain in the vicinity (Kleiman et al. 1986; Oliver et al. 1986; Stanley Price 1986, 1989). Sites where food and shelter are provided can be used for trapping and examining the specimens.

When to eliminate support is a major decision. It is extremely important to challenge the animals, but is also easier to control their movements if critical resources like food are provided. Achieving a wild state may mean developing fear and avoidance responses to humans, a condition that most animal managers find difficult to promote in their "charges." For each reintroduction, because of species differences and differences in goals, there will be complex decisions to be made for which there are no clear guidelines. To what extent and for how long should food supplementation continue? To what extent and for how long should humans be an important part of the lives of the released specimens? How much intensive monitoring is necessary, and how long should it continue? A common thread and a common problem will be reducing the human-animal contacts and encouraging the animals to avoid people, all while the project personnel continue to monitor the animals.

Defining Success

There are no established criteria for calling any given reintroduction a success. Griffith et al. (1989) evaluated those variables that led to the success of intentional introductions and reintroductions of native birds and mammals (not all endangered or threatened) to the wild in Australia, New Zealand, Canada, and the United States (including Hawaii) between 1973 and 1986. Greater success was associated with releasing larger numbers of individuals; extending the program duration; releasing animals into excellent habitat and into the core of their historical range; using wild-caught individuals; releasing herbivores rather than omnivores or carnivores; and releasing animals into areas without competitors. Stanley Price (1989) discusses the characteristics that make animals the most reintroducible: large animals living in cohesive groups, explorer species, nocturnal species, and species tolerant of habitat change or extreme environmental variation.

Beck et al. (1994) suggest that a reintroduction project should be counted as successful if the wild population reaches 500 individuals that are free of provisioning or other human support, or if a formal genetic/demographic analysis predicts that the population will be self-sustaining. By these stringent criteria, they found that only 16 (11%) of 145 animal reintroductions were successful. However, many of these projects are ongoing, and their success or failure cannot yet be evaluated. Also, a reintroduction attempt can have indirect, longer-term conservation benefits, such as increased public awareness, professional training, and enhanced habitat protection (Beck et al. 1994).

Beck et al. (1994) noted that the successful programs (by their definition) were longer and released more animals than the unsuccessful programs (as did Griffith et al. 1989). They also provided local employment and had community education programs. Finally, the successful projects used medical screening and post-release provisioning *less* than unsuccessful projects, a counterintuitive result.

One issue requires clarification. All reintroduced animals will eventually die, as will all captive animals. The success or failure of a program should not be measured by the mortality of the original reintroduced cohort. More important is the number and genetic variation of the surviving descendants of the released animals and the degree to which their genetic material is integrated with that of the original wild population.

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Successful Reintroduction of Captive-Raised Yellow-Shouldered Amazon Parrots on Margarita Island, Venezuela

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Abstract: *The Yellow-shouldered Amazon (*Amazona barbadensis*) is one of the most endangered species of parrots in Venezuela. An integrated conservation program has focused on reversing the causes of parrot population decline on the Macanao Peninsula in Margarita Island. As a result, the parrot population on the island has increased to about 1900 individuals in 1996 from an estimated population of 750 in 1989, when the project started. Cooperation from national and local authorities and the project's community outreach have resulted in several confiscated chicks. Whereas most confiscated chicks were successfully reintroduced in a cross-fostering nest program, some had to be kept in captivity for later release. We hand-reared 14* A. barbadensis *and housed them for a year in a large outdoor aviary. Before release the birds were screened to determine their general health. Four parrots were fitted with radio transmitters and monitored for a minimum of 11 months. All 4 birds with radio transmitters survived and adapted successfully to their natural environment, 10 of the 12 released parrots survived at least 1 year, and 1 was seen alive 34 months after release. Integration into wild groups varied from 5 days to 9 months, with the two youngest parrots showing a slower integration process. None of the parrots reproduced the first year after release. Later three were seen scouting nesting holes with their partners, and one of the parrots was confirmed attending a nest with three eggs 28 months after release. Two chicks fledged from this nest. A substantial portion of the success of this program rests on 5 years of previous work on environmental education, public awareness, and studies on the parrot's biology. To provide some guidance on the costs of reintroduction projects, we estimated an overall expenditure of about U.S. $2800 per parrot. Previous attempts to reintroduce captive-raised parrots have had limited success, and our study indicates that reintroduction is feasible when captive-raised parrots are introduced to an area with a resident population. Although reintroduction can significantly reduce the chances of extinction, it also involves some risks. The long-term solution against extinction of* A. barbadensis *will be a combination of scientific understanding of their biology and habitat, awareness by local human communities, reduction in the wild bird trade, and continued commitment by conservation enforcement agencies.*

Reintroducción Exitosa del Loro Espalda Amarilla del Amazonas Criados en Cautiverio en la Isla Margarita, Venezuela

Resumen: *La cotorra cabeziamarilla (*Amazona barbadensis*) es uno de los loros más amenazados de Venezuela. Un programa integrado de conservación se enfocó a revertir las causas de la declinación poblacional de cotorras en la Península de Macanao, en la Isla de Margarita. Como resultado, la población total de cotorras en la isla se incrementó hasta los 1900 individuos en 1996, a partir de una población estimada de 750 individuos cuando comenzó el proyecto en 1989. La cooperación de las autoridades nacionales y locales y las actividades educativas, han conducido a varios decomisos de polluelos. Aun cuando la mayoría de los polluelos fueron reintroducidos en un exitoso programa de nidos nodriza, algunos se tuvieron que mantener en cautiverio para soltarlos después. Para este estudio, un total de 14* A. barbadensis *fueron criadas a mano y albergadas en un gran aviario durante un año. Antes de soltarlas, las aves fueron sometidas a análisis de salud*

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general. Se le pusieron radio transmisores a cuatro cotorras, y se monitorearon por 11 meses. Todas las cuatro cotorras con radio transmisores sobrevivieron y se adaptaron exitosamente a su ambiente natural. 10 de las 12 cotorras sobrevivieron al menos durante un año, y una cotorra estaba viva al menos 34 meses después de soltarlas. La integración a grupos silvestres varió entre 5 días y 9 meses, y las dos cotorras mas jóvenes mostraron un proceso de integración más lento. Ninguna de las cotorras se reprodujo el primer año después de soltarlas. Tres de las cotorras fueron vistas explorando oquedades con sus parejas durante el segundo año, y una cuarta fue vista atendiendo un nido con tres huevos, a los 28 meses después de soltarla. Dos polluelos volaron de este nido. Una parte significativa del éxito de este estudio se basa en 5 años de trabajo previo en educación ambiental, conocimiento del publico, y estudios de biología de las cotorras. Para guiar los costos de proyectos de reintroducción, estimamos que el costo total estuvo alrededor de U.S.$2800 por cotorra. Pruebas anteriores para reintroducir loros criados en cautiverio han tenido éxito limitado. Los resultados de nuestro estudio indican que la reintroducción es posible cuando los loros criados en cautiverio son introducidos en un área donde existe una población silvestre residente. Aún cuando la reintroducción puede contribuir a reducir las oportunidades de extinción de esta y otras especies de cotorras, también acarrea riesgos. La solución a largo plazo contra la extinción será una combinación de entendimiento científico de la biología y habitat, conocimiento por parte de las comunidades humanas locales, reducción de la demanda de aves silvestres para el tráfico de mascotas, y la dedicación y continuidad de agencias conservacionistas y de guardería.

Introduction

The Yellow-shouldered Amazon (*Amazona barbadensis*) is one of the most endangered species of parrots in Venezuela (Desenne & Strahl 1991). Its total population size is estimated at 5000 individuals, patchily distributed along the northern coast of Venezuela and the outer islands of Margarita, Blanquilla, and Bonaire (Netherlands Antilles) (Forshaw 1989; Desenne & Strahl 1994). The population of Margarita Island has suffered serious pressure from trapping for the illegal pet trade and from habitat destruction (Silvius 1989; Albornoz et al. 1994).

Since 1989, an integrated conservation program has focused on reversing the causes of population decline for the Margarita Island population. The program includes biological research, population management, environmental education, participation and awareness of local human communities, and strengthening of protected-area management and design. This collaborative effort was possible through a joint partnership of international and national conservation organizations, government agencies, and individuals. As a result, the total island population had grown to an estimated minimum of 1900 individuals in 1996 (A. Rodriguez, personal communication) from an estimated population of 750 in 1989, when the project started (Silvius 1989). Given the success of this program, a similar if less intensive program was started on Blanquilla Island, where the population was estimated at about 100 individuals in 1993.

The main reasons for the sustained population growth of this endangered parrot hinge upon an integrated conservation program. The main factors involved in the population's recovery are (in order of importance): (1) strengthening of enforcement measures by the project personnel at one of the main breeding areas, thus increasing yearly recruitment from 0 individuals in 1989 to about 53 individuals in subsequent years (M. F. Albornoz, J. P. Rodriguez, F. Rojas-Suárez, & V. Sanz, unpublished data); (2) a successful program of intraspecific cross-foster nests that moved 53 nestlings and eventually fledged 44 individuals between 1990 and 1994 (Sanz & Rojas-Suárez, in press); and (3) an environmental education project that focused on local people and on active community participation in the conservation project.

Thanks to these factors and the cooperation of enforcement authorities, several *A. barbadensis* chicks have been confiscated since the early stages of the project. Most of these chicks were returned to protected nests in the successful foster nest program (Sanz & Rojas-Suárez, in press). In some instances, however, foster nests were not a viable solution because the chicks were rejected by the foster parents or because chicks were confiscated after their wing feathers were clipped by poachers, which meant captive rearing was the only option.

Given the small size of the *A. barbadensis* population, reintroduction of captive-raised individuals could help reduce the chances of extinction. Moreover, the study of processes that foster successful reintroduction programs is also relevant to increase the conservation value of captive breeding initiatives. Reintroductions of captive-raised vertebrates are difficult, however, and the success rate has been relatively low (Beck et al. 1994). Previous efforts to reintroduce parrots have met with little success, although numerous feral parrot populations have been established through accidental introductions by humans, mainly in urban and agricultural landscapes (Bull 1973; Hardy 1973; Owre 1973; Ulloa & Fernandez-Badillo 1987; Wiley et al. 1992; Snyder et al. 1994). This seems to indicate that some parrot species have enough behavioral and ecological versatility to adapt to new conditions, particularly if they are wild-caught and if they are given enough food sources and reduced pressure from competition and predation, as is usually the case in human-modified environments.

The main objective of our study was to explore the technical and economic viability of reintroducing captive-raised *A. barbadensis* as a population management tool to reinforce critically endangered populations. We describe captive management techniques, adaptation processes, and the relevance of reintroduction of captive-raised individuals as a conservation technique for Neotropical parrots.

Study Area and Methods

The study took place in the 300-km² Macanao Peninsula, which is the western portion of Margarita Island (10°51′ - 11°10′N and 63°46′ - 64°24′W) off the northeast coast of Venezuela (Fig. 1). The topography of Macanao changes from sea level to a central mountain range that reaches a maximum of 760 m above sea level. Average yearly temperature is 27° C, ranging from 24° to 31° C, and mean rainfall is 500 mm, with a distinct dry season from November to May. This dry semiarid tropical climate results in an open cactus-chaparral plant community with columnar cacti and legumes (*Prosopis juliflora, Caesalpinia coriaria*) as the predominant vegetation feature, although seasonal riverbeds can support permanent deciduous forests (Hoyos 1985). These gallery forests are rapidly disappearing because of open-pit mining for construction sand, resulting in the disappearance of this rare but important nesting and roosting habitat. Other native Psittacine species on Margarita Island include the common Brown-throated Parakeet (*Aratinga pertinax margaritae*) and the now extremely endangered Margarita subspecies of the Blue-crowned Parakeet (*Aratinga acuticaudata neoxena*) (total population size ≤80; Rodriguez & Rojas-Suárez 1994). Individuals of other parrot species escaped from captivity can be seen occasionally on the island, but none has become established (personal observation). Blanquilla is a nearly flat island of 64 km² off the northeast coast of Venezuela (11°48′ - 11°54′N and 64°33′ - 64°38′W) with an arid tropical climate. The vegetation is mostly scruby desert with only few trees.

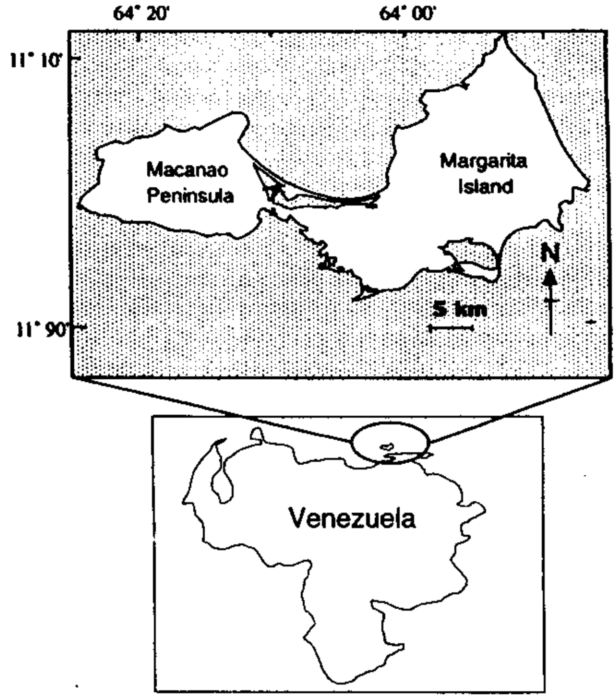

Figure 1. Macanao Peninsula, Margarita Island, and Venezuela.

We reared 14 *A. barbadensis*; 7 were confiscated in Margarita and 7 in Blanquilla but reared in Margarita. The Margarita parrots were of different ages and origins: four were hatched in 1990, of which one was from a nest attacked by predators; another one was donated by a local person; and the other two birds were siblings that were confiscated from poachers. The remaining 3 parrots hatched in 1991, all from the same nest, and were confiscated from poachers. The Blanquilla chicks were hatched in 1991 from unknown origins and moved to Margarita for captive rearing. The chicks were from 20 to 50 days of age when we received them. Their eyes were open, and they were partially or completely feathered, according to their age. Birds were not sexed because that would have required a surgical procedure and was deemed unnecessary for this study.

For the first 3 weeks, the captive maintenance protocol, designed by K. Silvius and F. Rojas, consisted of hand-feeding the chicks three times a day with a syringe. Their diet was a commercial, concentrated parrot food (Pikitos™, Purina Co.) and natural fruits such as guava, mango, papaya, and fruit compotes in a concentration of the right fluid consistency. At about 55 days of age (near the beginning of the fledging period) the chicks were offered chunks of naturally occurring fruits; larger chunks were introduced gradually until the parrots were feeding on whole fruits. Simultaneously, hand-feeding was phased out and the birds were transferred to a small wire cage of 1 × 1 × 1 m. Three weeks later, when the birds had a full plumage and could feed by themselves, they were transferred to two large outdoor aviaries of 5 × 5 × 5 m, away from casual human presence, partially shaded, and surrounded by natural habitat. The Margarita and Blanquilla parrots were housed in separate aviaries placed about 50 m from each other. The aviary allowed enough room to fly and for the birds to see and hear wild parrots and other creatures, as well as to experience the climate, insects, and other components of their natural environment. The aviaries were fitted with branches and twigs from natural vegetation, and the perches were changed frequently. The parrots were not in direct contact with other captive birds or domestic animals during the captive period. As part of the community outreach program, two assistants with good knowledge of the parrots' natural history and habitat were recruited from the local community and further trained in captive-rearing methods and field telemetry protocols. Both assistants were in charge of the direct captive-rearing of the parrots and later assisted in the telemetry portion of the study. Food and supplies were bought from local providers whenever possible.

The birds were offered wild foods, based on previous studies of the natural diet of *A. barbadensis* in the area (Silvius 1992). Their diet was complemented with some cultivated fruits and seeds, such as banana, plantain, mango, and sunflower seed, to complete the parrot's nutritional requirements. Foods were presented as they occurred in the wild, without any manipulation or preparation by the caretakers. For example, spines were not removed from cactus fruits and flowers, fruits, or leaf buds were offered on the branch. The diet changed as

Table 1. List of food items offered to Yellow-shouldered Amazon (*A. barbadensis*) during the captive period.

Family and species	*Common name*	*Part eaten*
Anarcardiaceae		
Mangifera indica[a]	mango	fruit
Asclepidaceae		
Matelea maritima	curichagua	fruit
Bignonaceae		
Tabebuia serratifolia	puy	seeds
Bromeliacea		
Bromelia chrysantha	chigüi-chigüi	fruit
Cactaceae		
Stenocereus griseus	cardón	stems,[b] flowers,[b] fruit[b]
Subpilocereus repandus	yaurero	stems,[b] flowers,[b] fruit[b]
Acanthocereus tetragonus	pitajaia	fruit
Pereskia guamacho	guamache	fruit
Capparaceae		
Capparis odoratissima	olivo	leaves, flowers, seeds[b]
Capparis hastata	paniagua	flowers, fruit[b]
Capparis flexuosa	ajito	flowers, fruit[b]
Compositae		
Helianthus annus	sunflower	seeds
Cucurbitaceaae		
Cucumis sp[a]	melon	seeds
Cucumis sp[a]	water melon	seeds
Flacurtaceae		
Casearia sp	manzanita	fruit[b]
Leguminoae		
Cercidium praecox	cuica	seeds
Prosopis juliflora	yaque	flowers, fruit[b]
Pithecelobium unguis-cacti	guichere	leaves, seeds[b]
Caesalpinia coriaria	guatapanare	seeds[b]
Caesalpinia granadillo	quebrahacho	seeds[b]
Caesalpinia mollis	durote	seeds
Calliandra sp	clavellina	seeds
Platymiscium sp	roble	flowers, seeds
Lonchocarpus violaceus	aco	seeds
Musaceae		
Musa sp[a]	plantain	fruit[b]
Musa sp[a]	banana	fruit
Rhamnacceae		
Ziziphus mauritania[a]	ponsingué	fruit
Sapindaceae		
Talisia oliviformis	coperí	fruit
Theophrastaceae		
Jacquinia revoluta	barbasco	fruit
Zygophyllaceae		
Bulnesia arborea	palosano	leaves, flowers, seeds[b]
Guaiacum officinale	guayacán	flowers, fruit[b]

[a] *Cultivated plants.*

[b] *Most selected items.*

food availability changed through the seasons, but at least three different types of foods were offered every day. Through the captive period, a variety of wild food items were offered according to their phenology. Cultivated food items were offered ad libitum (Table 1).

Three weeks before release, the birds were examined by veterinarians to determine their general health, including blood chemistry and blood parasites (hematocrit, plasma total solids, complete white blood cell count, white blood cell differential, and chemistry and enzyme panel including uric acid). Serological studies were conducted to detect infectious laryngotracheitis virus (Herpes), avian influenza, psittacosis, salmonellosis, avian polyoma virus, and paramyxovirus-1 (New Castle disease). Feces were analyzed to detect gastrointestinal parasites.

These veterinary analyses ensured that the birds were not carriers of some of the most common parrot diseases and reduced the risk of disease transmission to wild parrots. To enhance their health by release time, the birds were deparasited with Panacur™ (fendendazol). The potential exposure to other parrots and disease was considered minimal because none of the birds had entered the international pet trade and, even under the poor hygienic conditions of rural trappers, the birds had had little chance of exposure to exotic diseases.

Four parrots were provided with radio transmitters (Wildlife Materials Co.) attached to a brass neck collar. The transmitters were fitted to the birds 2 days before the scheduled release; the radios' function and the parrots' behavior were monitored inside the aviary. The radio and battery combination were covered with a hard epoxy resin, and only the 20-cm antenna protruded out from the system. The whole transmitter—collar, antenna, and batteries—weighed about 14.5 g, in all cases below 5% of body mass.

Two of the radio-collared parrots were 30 months old (hereafter identified as C2 and C6), whereas the other two were 18 months old (identified as C4 and C8). Before the release, all parrots were weighed, measured, and fitted with numbered stainless steel rings around the tarsus.

On the morning of 31 October 1992, one of the upper front panels (2 × 2 m) of the Margarita parrot aviary was removed to let parrots leave spontaneously. Most of the parrots were reluctant to fly out of the aviary, so branches of their favorite foods were placed just outside the hole in the aviary. For 15 days after release, food was offered twice daily in the vicinity of the aviary. Afterwards, supplemental food was offered once daily (in the afternoon); and after a month supplemental food was eliminated.

The parrots were radio-tracked upon release until 18 August 1993 for one parrot (C6) in which the radio battery ceased to work and until 10 October 1993 for the remaining three parrots. The parrots were located four to six times a week, twice each day, from 0600 to 1100 hours and then from 1530 to 1900 hours. The birds were tracked by means of a portable receiver (Telonics, Mesa, Arizona) and a manual three-element Yagui directional antenna. During the first 4 months the parrots were located by triangulation; afterwards they were located with the help of the radio signal until the parrots were within sight through use of a spotting scope or binoculars. Their position was later determined to the nearest 100 m with a global positioning system unit (Trimbell Navigation). In each visual encounter, the position of the parrot was recorded, as was the time of day, group size, and activity. If the parrots were feeding, food items were recorded for the released parrot and for the wild parrots in the vicinity.

During triangulation, the location polygons were plotted on a 1:5000 map of the area to determine the coordinates of the parrot's position. We followed the method of White and Garrott (1990) to measure the reception error by the equipment in the area, using 32 reception samples in 10 different locations. Measurement errors ranged between 0° and 20°, with an average of 0.63°, which was considered negligible and thus not taken into consideration in the calculations.

The adaptation period was quantitatively monitored by measuring (1) cumulative home range size, defined by the minimum convex polygon system (Mohr 1947), using the computer software package Wildtrack 1.1 (Todd 1992) for the 11 months of the study; (2) temporal variation of habitat use, measured as weekly variation up to 45 days after the parrots were released; and (3) the period of integration into wild groups and period to form permanent pairs, estimated from the first day that the parrots were seen together with wild parrots. Subsequent observations included information on the number of parrots in the group, social interactions with members of the group, vocalizations, joint flights, common use of feeding sites, allopreening, copulation attempts, nest exploration, and reproduction.

Following the existing reintroduction and captivity guidelines from the Margarita parrots, the Blanquilla parrots were successfully reared in captivity, and the surviving five individuals were reintroduced in 1993 in Blanquilla Island. All of these parrots were fitted with numbered stainless steel rings around the tarsus. They were transported by ship from Margarita; given the remoteness of the Blanquilla island, the monitoring was limited to one census in 1994. Therefore, most of the monitoring described below refers to the Margarita parrots.

Given the parameters to measure the adaptation period, reintroduction was considered successful by the following criteria: survival for at least a year after release, use of feeding area and food items similar to those of wild parrots, integration to social groups, use of communal roosting areas, and pair formation and reproduction attempts. Integration to social groups, pair formation, and the production of fertile eggs or fledglings were considered the best indicators of successful adaptation to wild conditions.

Results

Survival

The large outdoor aviaries were helpful in teaching predator avoidance. Not only were the young parrots able to see and hear wild parrot behavior during encounters with predators, but they experienced predator pressures themselves. During captivity, one of the young Blanquilla parrots was killed and eaten by a *Boa constrictor* at night. On another occasion, the same Blanquilla group aviary was attacked by a pair of hawks (*Parabuteo unicinctus*), who reached through the wire mesh, killing one parrot and injuring another. These accidents, even with the resulting deaths, were a learning experience for the surviving parrots, who learned predator avoidance and alarm behaviors—including fleeing the site with loud vocalizations—similar to behaviors reported for White-fronted Amazons (*A. albifrons*; Levinson 1980).

All four birds with radio transmitters survived during the 1-year monitoring period. Parrot C8 was seen alive at least until November 1995, 37 months after release (Table 2), whereas C4 was seen alive in April 1994, 18 months after release. One of the Margarita parrots without a radio transmitter was seen in June 1993, 8 months after release, although it could not be individually identified from the distance observed. All five Blanquilla birds were seen feeding with a social group of 16 individuals 1 year after release.

At a minimum, 10 out of 12 parrots survived the first year after reintroduction. Two of the Margarita birds without radios could not be located after the release. It is possible that the missing parrots survived through the study period but were not detected. Bands are difficult to observe on *Amazona* parrots because these birds have short tarsi that are usually covered by feathers.

Dispersal Patterns

One of the parrots without a radio transmitter flew out of the aviary the first few minutes after the release. All other parrots remained around the aviary during the first day, after the second day the two other parrots without radio transmitters abandoned the area around the aviary.

Even though the birds were of similar size and shared captive conditions for more than a year in the aviary, the group did not stay together after the release, except for the two siblings born in 1991 (C4 and C8). In 21 instances during the monitoring period, up to three radio-collared parrots were simultaneously using common feeding areas, including the same tree, but once integrated to wild groups the reintroduced parrots never abandoned their group to accompany their former captive companions.

The process of dispersal from the release site was slower for the two youngest parrots (C4 and C8). One of them (C4) dispersed more than 1 km from the release point during the first week, but finally returned to the immediate release area (Fig. 2). These two parrots were received with their wings clipped very short, and two or three wing primaries grew back almost white or clear, indicating feathers growing under stress. Early flights after release were clumsy, with awkward landings, which might be the reason why these parrots were so late in joining wild groups to distant roosting sites. Wallace and Temple (1987) observed that the youngest captive-bred, reintroduced Andean Condors (*Vultur gryphus*) were the ones that showed the longest readaptation period. Parrots, like condors, have a long period of parental care that seems to go from 3 months to several years, depending on the species (Cruz & Gruber 1980; Saunders 1982; Snyder et al. 1987; Enkerlin 1995, personal observation).

During the monitoring period, all parrots remained in the eastern portion of the Macanao peninsula, with great home range overlap (Fig. 3). One of the parrots (C6) had the largest home range and used three different communal roosting areas, whereas all other parrots used only one or sometimes two roosting areas.

Table 2. Parameters measured during the adaptation period of reintroduced Yellow-shouldered Amazon (*A. barbadensis*) in days (or months for confirmed survival) after the release date.

	Individual						
Adaptive process	*C2*	*C6*	*C4*	*C8*	*CJ30*[a]	*CT30*[a]	*CP18*[a]
Confirmed survival (months)	11	10	18	37	8	?	?
Abandonment of aviary area[b]	5	9	98	37	1	>1	1
Join social groups	6	14	288	288	>125	?	?
Communal roosting	10	20	306	306	>125	?	?
Pair formation[c]	95	91	?	870	?	?	?
Reproduction[d]	?	?	?	870	?	?	?

[a] *Parrots without radio transmitters; these parrots were not actively monitored, and information represents occasional sightings.*

[b] *Aviary area is the immediate area (100 m diameter) around the aviary.*

[c] *Confirmed and repeated sightings of the released parrots with another wild parrot during morning and afternoon flights.*

[d] *Confirmed and successful egg production.*

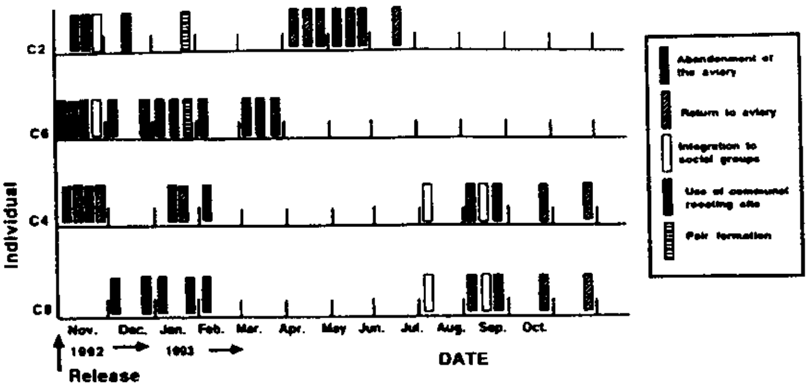

Figure 2. Chronological representation of the adaptation process for four reintroduced Yellow-shouldered Amazon (A. barbadensis) *fitted with radio collars from November 1992 to October 1993 on Margarita Island, Venezuela.*

Site Fidelity and Foraging Behavior

Although the parrots stayed around the release area, they spent most of the first few days directly on top of the aviary that held another group of captive *A. barbadensis* or feeding on plants in the immediate vicinity or on bits of food that fell through the floor of the aviary. The youngest parrots (C4 and C8) demonstrated the highest fidelity to the aviary and its surroundings, during the post-release period of adaptation and during the first 8 months of the monitoring period (Table 3).

Often groups of wild parrots came to the immediate release area early in the morning, feeding on wild plants and landing on the aviary that held the other group of *A. barbadensis*. During these visits, the radio-collared parrots vocalized and interacted with the wild parrots and even fed on the same branch. On other occasions, however, the radio-collared parrots were indifferent to the wild group. Beginning at day 20 after release, the parrots started to foray farther and farther from the release point, until they joined wild groups permanently. Even then, frequent visits to the release site were common (Fig. 2).

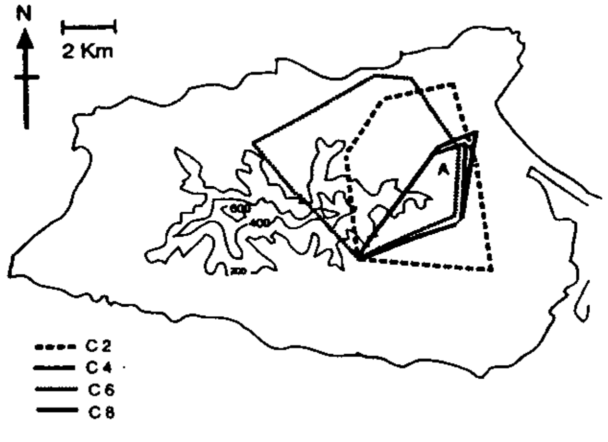

Figure 3. Macanao Peninsula, with the cumulative home range for each of the four radio-tracked parrots (C2, C4, C6, and C8) during the 11-month monitoring period from November 1992 to October 1993. A indicates the aviary position.

Recognition of food items by the released parrots was facilitated by the exposure to wild food items during the captive period. From the first day of release the parrots were eating wild foods and were able to manipulate different food items. All released parrots were seen feeding on the same food items as wild parrots (n = 121 sightings). During the 11 months of radio tracking, the released parrots consumed all 24 wild species of plants that were offered while in captivity plus three plants species that were unknown to them. In fact, C6 fed for 6 weeks mostly on the seeds of a plant, *Piptademia flava*, from higher mountain areas that was not previously offered in captivity.

Social Integration and Pair Formation

The process of social integration to wild groups varied among the reintroduced parrots (Fig. 2). Wild group size varied from 2 to 62 birds—and possibly larger during the afternoon flights to the communal roosting sites. Both young parrots (C4 and C8) presented some aberrant tame behavior for the first 8 months, allowing close proximity of humans (<15 m), but they eventually began to fly away to a safe distance (>50 m) when approached by humans.

Although pair formation is difficult to determine with precision, our observations indicated that the two older parrots (C2 and C6) formed stable pairs with wild birds beginning at 3 months after release (Fig. 2). Thereafter it was common to see them with another parrot, particularly during the morning feeding flight and the afternoon flight to the roosting area. Other observed behaviors suggest pair formation. For example, 6 months after release C2 performed the typical mating behavior of *A. barbadensis*, vocalizing like a young fledging and begging for food, while its presumed partner was feeding on the fruits of the columnar Cardón cactus (*Stenocereus griseus*). Later that month, C2 and C6 were seen inspecting potential nesting holes near the aviary area, each accompanied by a wild parrot.

Both older parrots (C2 and C6) were seen on at least two occasions in allopreening behavior with their wild partner. None of the released parrots reproduced the first year of field monitoring. In April 1995 a nest attended by C8 was found with three eggs within 200 m from the aviary. Parrot C8 was one of the younger birds with the longest adaptation period. By the time this nest was found C8 was 4 years old and our observations indicated that it was a male. Two eggs hatched and both chicks fledged from this nest.

The released parrots without radio transmitters were almost impossible to identify individually. One of them, however, was seen with a group of four wild parrots within 5 days after release, another was seen near the aviary flying with its wild partner 8 months after release, and a third was seen feeding with a wild group 5 months after release.

Discussion

Previous attempts to reintroduce captive-raised parrots with wild populations (Hispaniolan Amazon [*A. ventralis*] and Puerto Rican Amazon [*A. vittata*]) or without wild populations (Thick-bill Parrots in Arizona [*Rynchopsitta pachyrhyncha*]) have had limited success (Wiley et al. 1992; Snyder et al. 1994; Meyers & Lindsey 1996). For example, in reintroduction efforts with Thick-bill Parrots in Arizona, high predation by raptors, poor food-processing ability, and aberrant behavior reduced survival to nearly zero (Derrickson & Snyder 1992; Wiley et al. 1992; Snyder et al. 1994). Our study indicates that reintroduction is feasible when captive-raised parrots are introduced in an area with a resident population (Wiley et al. 1992; Association for Parrot Conservation 1994*b*). The presence of a wild population increases the probability of success because wild parrots have well-developed capacities for finding food and roosting sites and for avoiding predators.

The reintroduced parrots adapted successfully to their natural environment. The confirmed reproduction by at least one of the parrots indicates that some reintroductions can be successful. Their survival during the monitoring period indicates that the parrots were able to find food, develop a social life, and avoid predators. In fact, predator avoidance is a crucial behavior for the survival of reintroduced parrots (Snyder et al. 1994). For example, the most important cause of death in fledglings of the Puerto Rican Parrot (*A. vittata*) seems to be attacks by raptors (Lindsey et al. 1994). Potential parrot predators in the Macanao Peninsula include several species of large snakes (*Boa constrictor*, *Epicrates cenchria*, *Spillotes pullatus*, and *Corallus enidrys*; the last two are egg and chick specialists) and two species of hawks (*Buteo albicaudatus* and *Parabuteo unicinctus*). Potential mammalian predators include ocelots (*Felis pardalis*) and skunks (*Conepatus semiestriatus*). Our observations during the last 5 years, however, seem to indicate that adult parrots experience little predation, except occasional snake predation on incubating females.

The released parrots showed high site fidelity. Of 300 km^2 of available habitat, the released parrots used only the eastern half of the Macanao Peninsula; eventually, one of them nested very near the release site. It is probable that the released parrots will eventually use all the available habitat as they follow spatial variations in food resources. Our observations of other parrots that were tagged as chicks however, seem to indicate that these parrots nest in areas very near the site where they were born, which has been reported for other parrot species (Saunders 1982; Snyder et al. 1987).

The fast integration to social groups of at least three of the seven released animals reveals that these parrots did not display many aberrant behaviors common in other reintroductions of parrots or birds (Wiley et al. 1992). For example, from the beginning of the release period, the parrots showed typical behaviors, such as allopreening and a wide range of vocalizations, including more specialized social or sexual behaviors (e.g., food requests by females). These behaviors have been reported for other birds as a way to strengthen the links between the pair and as part of the repertoire of reproductive behaviors (Lack 1940; Cruz and Gruber 1980; Jeggo 1980; Levinson 1980; Saunders 1982; Snyder et al. 1987; Waltman & Beissinger 1992). Another indication of the development of reproductive behaviors is that three of the reintroduced parrots were seen scouting tree cavities with their wild partners. This is a typical pair behavior among parrots and an indication of interest in reproduction (Cruz & Gruber 1980; Saunders 1982; Lanning & Shiflett 1983; Snyder et al. 1987; Waltman & Beissinger 1992; Martuscelli 1995). The two parrots that scouted tree cavities did not reproduce in the first year after the release, even though they were of reproductive age (Rodriguez & Rojas-Suárez 1994). It is possible that the pairs were still not ready or experienced enough to reproduce. Indeed, Puerto Rico Amazons that form new pairs do not reproduce during the first year of pair formation (Snyder et al. 1987).

No aggressive interactions were seen between captive and wild parrots. On one occasion, however, we saw a group of parrots (including three with radio transmitters) chasing a lone Orange-winged Amazon (*A. amazonica*), which had probably escaped from captivity, not being a natural resident of the Macanao Peninsula.

Viability and Conservation Value of Reintroductions

Reintroductions are usually mentioned as an integral part of ex situ conservation programs and as an alternative to population management of endangered species. Few of these programs, however, include direct implementation of reintroductions, nor do they discuss the economic, social, or political issues affecting the viability of a reintroduction program.

It is common to underestimate the cost of a well-designed reintroduction project; considerable time and money are required for a long-term program. This reintroduction project was a portion of a larger program for the conservation of *A. barbadensis* and its natural habitat on Margarita Island. A significant portion of the success of this program rests on 5 years of previous work on environmental education, public awareness, and ecological studies of the parrots' behavior, habitat use, and diet. For example, *A. barbadensis* was officially declared the state bird by the governor of the island, and in most years there is a parrot float during the annual carnival parade. Similarly, the larger project provided transportation and training funds for field assistants and volunteers.

Excluding funds allocated to biological research, environmental education, or community outreach, we estimated an overall expenditure of about U.S. $2827 per reintroduced parrot. Economies of scale would reduce the costs per animal if the number of released animals were greater. Although it is difficult to compare this study to others, because costs and opportunities are different in each case, it is important to show these expenditures to provide a reference point for other reintroduction studies (Kleiman et al. 1991). Expenditures for this project were modest because we provided entry-level salaries, recruited assistants from the local community, and avoided paying large sums in consultancy fees. Other factors that helped reduce costs were the low costs of fuel and energy, in general, in Venezuela.

Given the economic costs of every reintroduction conservation project, it is important to decide the size of the maximum installed capacity and how many animals can be received and maintained at the captive-rearing facilities. This decision is difficult to make because such projects are confronted by the fact that enforcement regulations can provide more animals than recommended for the holding facilities. Similarly, reintroductions are vaguely referred to in conservation plans, but seldom if ever are the actual costs and long-term commitment specifically addressed from the beginning (Snyder et al. 1996).

It is also relevant to mention that not all confiscated parrots can be returned to their wild environment. Releases of confiscated parrots usually have been driven more by humanitarian or public relations goals than by conservation biology criteria, resulting in releases under conditions that do not assure the parrots' survival and that in some instances result in stressful deaths by predators or even a slow death from hunger. Several conservation organizations and specialists groups have issued recommendations for the treatment and destiny of confiscated animals (World Conservation Union 1987; Lambert et al. 1993; Association for Parrot Conservation 1994*a*, Ginsberg & Brautigan 1995). Given the potentially serious consequences of an irresponsible reintroduction program, it is important to follow these recommendations. Otherwise, the damage can easily be greater than the conservation value of the reintroductions.

Although the primary objective of our reintroduction experience was to study the economic and technical viability of reintroductions of captive-bred *A. barbadensis* in Margarita Island, our results and protocols are relevant to conservation programs for small populations of critically endangered parrots for which the pet trade, extraction of young, and low or negligible population recruitment preclude the application of cheaper and safer management techniques. Reintroductions of critically endangered species can also be important because the return of confiscated animals provides a direct contribution to the gene pool of the species, where each individual has a high value to the overall population genetic viability. For example, the *A. barbadensis* population in La Blanquilla Island has an estimated population size of 80–100 individuals, suffers low recruitment from nest poaching by fishermen and predation by feral cats, and has a low dispersal area in a small island (Rojas-Suárez 1994). Preliminary population viability analysis of this population indicates a probability of extinction of about 99.2% in 44 years if new individuals are not incorporated into the population (Rodriguez & Rojas-Suárez 1994). Given the results of this study and other recommendations on this subject (Wiley et al. 1992; Association for Parrot Conservation 1994*b*; Snyder et al. 1996), we suggest the following criteria to increase the chances of success in a parrot reintroduction program:

(1) The reintroduction program should be part of a research and conservation program that provides basic natural history information on the ecological requirements of the species, public awareness, and habitat protection.

(2) The origin of the confiscated animals should be known, so that the animals can be reintroduced in their natural range. This is especially important to avoid hybridization with different species or subspecies. When the genetic validity of a subspecies category is in doubt, genetic analysis should be performed (Amato 1995).

(3) Reintroductions of birds originating from the international pet trade should be carefully evaluated (and usually avoided) because these birds probably have been in direct contact with lethal diseases carried by exotic birds or domestic animals. If reintroduction is seen as a viable alternative, then quarantines should be strictly maintained and birds should be monitored for a long period of up to 2 years before their release. In this study the birds were confiscated before they reached the international trade and were housed only temporarily by

rural trappers, so they had less chance to be exposed to exotic diseases. The importance of monitoring diseases in confiscated birds cannot be underestimated because the risks of disease transmission may outweigh the conservation benefits of reintroductions (Derrickson & Snyder 1992; Beck et al. 1994).

(4) Reintroductions should be made in areas with some degree of protection, or at least the initial causes for the population decline should be addressed in the release area (Caughley 1994). In the Macanao Peninsula, awareness of the endangered status of the parrot among land owners, local villagers, and decision makers has increased greatly. In an ongoing process, local land owners and local and national authorities are now exploring new ways to increase habitat protection, decrease the pressure on the population, and ultimately create or expand protected areas.

(5) Reintroductions have the side benefit of contributing to environmental education goals and increasing the general awareness of the conservation needs of a species. It is important to take advantage of these opportunities with public media and awareness programs because of the emotional value to the general public. Media campaigns can also be used to draw public attention to the problems involving the illegal pet trade and maintaining wild animals as pets. For example, during the study, several talks and field demonstrations were offered to primary school children, high schools students, and volunteer youth conservation brigades as part of a larger environmental education program sponsored by Margarita Island environmental organizations, the Ministry of the Environment, and Provita (a national environmental nongovernmental organization). Local television, radio, and newspapers reported on the reintroduction project.

(6) Under critical situations (e.g., extremely small population sizes), reintroductions can be used to increase subadult recruitment rates and therefore the genetic variability of a wild population (Franklin 1980; Saunders 1982; Lindsey et al. 1994; Kuehler et al. 1995).

Our study provides a precedent for the successful readaptation of confiscated or captive-raised parrots to wild conditions, and it represents one of the first times that a successful reintroduction has been recorded in such detail. Given that nearly 20% of the world's 330 species of psittacines are globally endangered (Collar & Andrew 1988; Collar & Juniper 1992), we consider it important to try a variety of population recovery techniques that can increase conservation options and that can be differentially applied under different circumstances. Our study validates a captive raising and monitoring protocol that can be used for the reintroduction of parrots of the genus Amazona. To apply our results to other psittacines, these techniques should be tried in other species and the importance of various factors to reintroduction techniques should be analyzed. Previous experiences have shown that some of the most critical issues are predation by raptors, existence of a wild population within the reintroduction range, and diseases transmitted to confiscated animals from the international pet trade (Wiley et al. 1992; Snyder et al. 1994). If these factors can be controlled—by carrying out reintroductions in areas with low predation pressure or by locally confiscating animals before they get in contact with the international trade—then the probability of success seems to be high. We hope that more studies with other species of psittacines and under different ecological situations will provide further experiences upon which to base the management of endangered parrots and other birds.

Even with the restriction of imports of wild birds to the United States, the demand by national and international markets is still a significant pressure on wild populations. For example, from 1994 to 1996 a total of 119 chicks of *A. barbadensis* were confiscated from Aruba, Curaçao, and Caracas, presumably destined for European markets. All these confiscated parrots came from the less-protected western population of Falcon and Lara states of mainland Venezuela. Similarly, in July 1992 Venezuelan authorities confiscated a group of 10 *A. barbadensis* from Blanquilla Island, which has a total population of less than 100 individuals (Rojas-Suárez 1994). With larger confiscations, however, health issues and logistical and financial factors can limit the applicability of reintroduction as a viable alternative.

Whereas reintroduction can reduce the chances of extinction of this and other parrot species, this methodology still carries substantial risks. No instant conservation results can be achieved, so long-term protection from extinction will be a combination of scientific understanding of the biological and ecological requirements of the species, conservation awareness by local human communities, a termination of the demand for wild bird trade, and the continued commitment of enforcement and conservation agencies (Snyder et al. 1996).

Table 3. Weekly changes in home range size (ha) of reintroduced Yellow-shouldered Amazon (*A. barbadensis*) during the adaptation period.

Week after release	*Individual**			
	C2	*C6*	*C4*	*C8*
1	129.5	1.4	7.0	0
2	801.3	926.2	0	0
3	713.6	251.5	0	0
4	648.3	315.6	8.1	0
5–6	2932.0	1370.5	0.6	8.4
7–8	52.4	2326.2	0	3.0

**Home range increased abruptly when C2 and C6 joined two wild groups and followed the groups to communal roosting areas and new feeding areas. During week 6 the parrots changed feeding groups, which in turn increased the C2 home range to nearly 3000 ha, representing 10% of the total land surface of the Macanao peninsula. Meanwhile C4 and C8 remained in home ranges smaller than 10 ha for the first 9 months until they joined wild groups, which resulted in an increase in their home ranges. Zeros represent no measurable change in home range.*

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Translocation as a Species Conservation Tool: Status and Strategy

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Surveys of recent (1973 to 1986) intentional releases of native birds and mammals to the wild in Australia, Canada, Hawaii, New Zealand, and the United States were conducted to document current activities, identify factors associated with success, and suggest guidelines for enhancing future work. Nearly 700 translocations were conducted each year. Native game species constituted 90 percent of translocations and were more successful (86 percent) than were translocations of threatened, endangered, or sensitive species (46 percent). Knowledge of habitat quality, location of release area within the species range, number of animals released, program length, and reproductive traits allowed correct classification of 81 percent of observed translocations as successful or not.

A TRANSLOCATION IS THE INTENTIONAL RELEASE OF ANImals to the wild in an attempt to establish, reestablish, or augment a population (*1*) and may consist of more than one release. To date, translocations have been used to establish populations of nonnative species and restore native species extirpated by hunting. An increasing perception of the value of biological diversity has focused attention on translocations of rare native species. These latter translocations are expensive (*2, 3*) and are subject to intense public scrutiny (*4*). They have varied goals (*3*) that include bolstering genetic heterogeneity of small populations (*5–7*), establishing satellite populations to reduce the risk of species loss due to catastrophes (*8, 9*), and speeding recovery of species after their habitats have been restored or recovered from the negative effects of environmental toxicants (*2*) or other limiting factors.

In the face of increasing species extinction rates (*10–12*) and impending reduction in overall biological diversity (*12*), translocation of rare species may become an increasingly important conservation technique. If current patterns of habitat loss continue, natural communities may become restricted to disjunct habitat fragments and intervening development may disrupt dispersal and interchange mechanisms (*2*). Increased rates of extinction may be expected in small fragmented habitats (*13*) and translocation may be required to maintain community composition, especially for species with limited dispersal abilities.

The immediacy of reduction in biodiversity (*14*) demands a rigorous analysis of translocation methodology, results, and strategy. We need to know how well it works, what factors are associated with success, and what strategies suggest greatest potential success.

We conducted three surveys of contemporary (1973 to 1986) translocations of native birds and mammals in Australia, Canada, Hawaii, New Zealand, and the United States (*15*). In the first survey, we obtained general information on the number of programs completed by various organizations. In the later surveys, we sought detailed information on translocations of (i) threatened, endangered, or sensitive species and (ii) native game birds and mammals.

Current Status

At least 93 species of native birds and mammals were translocated between 1973, the year the Endangered Species Act became law, and 1986. Most (90%) translocations were of game species; threatened, endangered, or sensitive species accounted for 7%. Ungulates (39%), gallinaceous birds (43%), and waterfowl (12%) dominated translocations of game species; raptors (28%) and marsupials (22%) dominated threatened, endangered, or sensitive species translocations.

A typical translocation consisted of six releases over the course of 3 years. Many (46%) released 30 or fewer animals and most (72%) released 75 or fewer animals.

The average number of translocations per reporting organization doubled from 1974 (5.5) to 1981 (10.6) suggesting contemporary totals of 700 translocations per year. Most (98%) of these were conducted in the United States and Canada. Effort was not uniformly distributed; 21% of North American agencies conducted 71% of North American translocations. Only 27% of reporting organizations had protocols that specified the types of information to be recorded during translocation programs.

Theoretical Considerations

A translocation is a success if it results in a self-sustaining population; conversely, the founder group may become extinct. Theoretical considerations predict that population persistence is more likely when the number of founders is large, the rate of population increase is high, and the effect of competition is low (*13*). Low variance in rate of increase (*16*), presence of refugia (*9*), reduced environmental variation (*16*), herbivorous food habits (*17*), and high genetic diversity among founders (*18*) may also enhance persistence. Suitable, protected, and maintained habitat, control of limiting factors, and proper care and training of captive reared

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animals (*3, 19*) are also considered prerequisites of a successful translocation.

We found that several factors were associated with success of translocations (Table 1). Native game species were more likely to be successfully translocated than were threatened, endangered, or sensitive species. Increased habitat quality was associated with greater success. Translocations into the core of species historical ranges were more successful than were those on the periphery of or outside historical ranges. Herbivores were more likely to be successfully translocated than either carnivores or omnivores. Translocations into areas with potential competitors of similar life form were less successful than translocations into areas without competitors or areas with a congeneric potential competitor. Early breeders with large clutches were slightly more likely to be successfully translocated than were species that bred late and had small clutches.

Translocations of exclusively wild-caught animals were more likely to succeed than were those of exclusively captive-reared animals (Table 1). Among translocations of exclusively wild-caught animals, success depended ($P \leq 0.10$) on whether the source population density was high (77% success, $n = 109$), medium (78%, $n = 37$), or low (37%, $n = 8$). Success of translocations of wild-caught animals was also associated ($P \leq 0.10$) with whether the source population was increasing (83% success, $n = 93$), stable (63%, $n = 49$), or declining (44%, $n = 9$). Successful translocations released more animals than unsuccessful translocations (160 compared to 54, respectively; $P = 0.024$).

Our results are consistent with analyses of naturally invading or colonizing species that show (i) larger founder populations are more successful (*20, 21*), (ii) that habitat suitability is important (*21*), and (iii) increased number and size of clutches enhances successful invasion (*22*). Our data also support the hypothesis that herbivores are more successful invaders than carnivores (*17*) and the conclusion that, for birds, morphologically similar species have a greater depressing effect on successful invasion than do congeneric species (*23*).

Table 1. Percentage success of intentional introductions or reintroductions (translocations) of native birds and mammals to the wild in Australia, Canada, Hawaii, New Zealand, and the United States between 1973 and 1986. Data were obtained from a survey conducted in 1987 (*15*). The data include 134 translocations of birds and 64 translocations of mammals. For all variables listed, χ^2 was statistically significant ($P \leq 0.10$), implying true differences in the percentages of successful translocations among the categories. Animals that first give birth at age 2 or less with average clutch size of three or more are considered early breeders with large clutches; all others are late breeders with small clutches.

Variable	Translocations (n)	Success (%)
Threatened, endangered, or sensitive species	80	44
Native game	118	86
Release area habitat		
Excellent	63	84
Good	98	69
Fair or poor	32	38
Location of release		
Core of historic range	133	76
Periphery or outside	54	48
Wild-caught	163	75
Captive-reared	34	38
Adult food habit		
Carnivore	40	48
Herbivore	145	77
Omnivore	13	38
Early breeder, large clutch	102	75
Late breeder, small clutch	96	62
Potential competitors		
Congeneric	39	72
Similar	48	52
Neither	105	75

We found no consistent association of translocation success with number of releases, habitat improvement, whether the release was hard (no food and shelter provided on site) or soft, immediate or delayed release on site, or average physical condition of animals at release. We were unable to directly evaluate genetic heterogeneity, sex and age composition, or specific rearing and handling procedures for released animals because of inadequate response to survey questions.

Evaluating Alternative Strategies

Analyses of individual factors associated with translocation success do not adequately reflect the multivariate nature of actual translocations. To overcome this problem, we used stepwise logistic regression (*24, 25*) to develop preliminary predictive equations for estimating the success of translocations (Table 2). An expanded data set or independent sample would probably yield different regression coefficients and estimates of success than we report. As a result, extrapolation to conditions much different than those represented by our data and applications to individual species are discouraged.

The coefficients from Table 2 can be used to plot predicted success of different kinds of translocations as a function of continuous variables such as the number released. We present an example for a threatened, endangered, or sensitive bird (Fig. 1).

This exercise (Fig. 1) illustrates that the increase in success associated with releasing larger numbers of organisms quickly becomes asymptotic. Releases larger than 80 to 120 birds do little to increase the chances that a translocation will be successful for this particular set of conditions. The asymptotic property is consistent across other classifications of the data but the inflection point varies. For large native game mammals the asymptote is reached at releases of 20 to 40 animals with a concurrently higher predicted success.

The asymptotic property of the association of translocation success and number released (Fig. 1) is consistent with theoretical predictions (*13*) and analytical treatments (*26*) that suggest a threshold population size below which extinction is likely, primarily due to chance events affecting birth and death of individuals. The existence of the inflection (Fig. 1) is also consistent with the prediction of a threshold density below which population social interactions and mating success are disrupted (*27*), again leading to diminished population viability.

The coefficients from Table 2 and relationships presented in Fig. 1 can be used to assess alternative strategies. Suppose 300 threatened and endangered birds are available for a translocation program and they must be released during a 3-year time frame. Further suppose that two potential translocation areas are available within the core of the species historical range. If the goal of the translocation is to establish at least one geographically disjunct population to reduce the risk of catastrophic loss of the species, how should the birds be distributed between the two potential translocation areas to minimize the probability that both translocations will fail?

If both release areas have excellent habitat quality, and the areas are independent, the answer is obvious. The birds should be divided between the areas. The coefficients from Table 2 allow us to estimate the probability that a single release of 300 birds will fail (1.0 minus probability of success) is 0.257. Two releases of 150 birds each have individual probabilities of failure of 0.312. The probability that both will fail is $0.312 \times 0.312 = 0.097$; substantial gain is achieved by splitting the birds between areas.

If we complicate the picture and say that one potential area has excellent habitat quality and the other has only good habitat quality, we see that it remains slightly advantageous to split the birds between areas. Predicted probabilities of failure are 0.312 for excellent and 0.698 for good habitat, respectively. The probability that both translocations will fail is 0.312 × 0.698 = 0.218 compared to 0.257 for putting all birds in a single excellent habitat quality area. In this example, slight advantage to splitting the translocated birds between areas is maintained down to a total release of 40 birds. However, with so few birds released the probability that both translocations will fail is increased to about 0.42.

The model coefficients in Table 2 may be used to evaluate other scenarios. For example, given two alternatives, should a given number of birds be released in good habitat quality in the core of the historical species range or in excellent habitat quality on the periphery or outside the historical range? Good habitat quality in the core of the range is the better choice regardless of the number of birds released. This suggests that the physiological amplitude of a species may influence local population viability.

Enhancing the Chances of Success

Without high habitat quality, translocations have low chances of success regardless of how many organisms are released or how well they are prepared for the release. Active management is required. Limiting factors must be identified and controlled and assurances of maintenance of habitat quality obtained prior to translocation.

Identification and retention of adequate habitat will require a combined species and ecosystem approach. Ecological information will be necessary to identify critical life history traits, factors determining habitat quality, species interactions, and minimum habitat fragment size (*28*). Regional approaches to maintaining diversity (*29*) will be essential to ensure that existing species and habitat assemblages are identified, their interactions are understood, and remnant habitats are protected. The latter approach may ultimately reduce the number of species that require translocation if it enhances understanding of the effects of habitat fragmentation on persistence of multiple disjunct populations.

Table 2. Stepwise logistic regression (*24*) model coefficients for predicting probability $[P = 1/(1 + e^{-x})]$ of success of intentional introductions or reintroductions (translocations) of native birds and mammals in Australia, Canada, Hawaii, New Zealand, and the United States between 1973 and 1986; x is the sum of applicable coefficients for categorical variables plus the applicable coefficient times the value of continuous variables. The model is based on 155 translocations; 100 were of birds and 55 were of mammals. Data were obtained from a survey conducted in 1987 (*15*). The stepwise procedure was run at the $\alpha = 0.10$ level for entry of terms and the $\alpha = 0.15$ level for removal of terms. Probability of larger test statistics for the model were χ^2, $P = 0.90$ (*24*); Hosmer-Lemeshow χ^2, $P = 0.121$ (*24*); Brown's χ^2, $P = 0.537$ (*24*). The model correctly classified 81.3% of observed translocations based on a cutpoint of 0.50 in predicted probability of success.

Variable	Coefficient (SE)
	−1.418 (0.738)
Threatened, endangered, or sensitive species	−0.972 (0.253)[1]*
Native game	0.972 (0.253)[1]
Birds	−0.919 (0.374)[6]
Mammals	0.919 (0.374)[6]
Release area habitat	
Excellent	1.681 (0.438)[2]
Good	0.053 (0.314)[2]
Fair or poor	−1.734 (0.450)[2]
Release area	
Core of historic range	1.028 (0.267)[3]
Periphery or outside	−1.028 (0.267)[3]
Early breeder, large clutch	1.080 (0.355)[5]
Late breeder, large clutch	−1.080 (0.355)[5]
Log(number released)	0.887 (0.405)[7]
Program length (years)	0.181 (0.074)[4]

*Numbers in brackets represent order of entry.

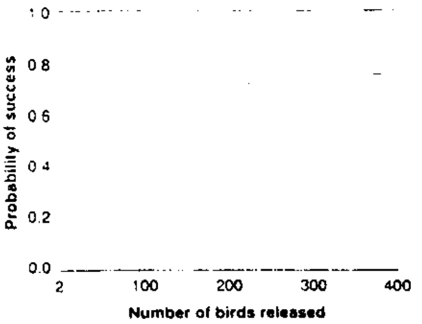

Fig. 1. Predicted probability of successful translocation as a function of the number of animals released during a 3-year period in the core of the historic species range in either excellent (solid line) or good (dashed line) habitat quality for a threatened, endangered, or sensitive bird species that first breeds at 2 years of age or more with average clutch size of three or less. Probabilities are based on stepwise logistic regression model coefficients (Table 2).

We may reduce the need for and increase the success of translocations if we can improve our ability to identify potentially tenuous situations and act before we are faced with a rescue. Simulation modeling (*28*, *32*) of the behavior of small populations of species or of groups of species with similar reproductive strategies can provide guidance for establishing minimum population and vital rate goals. Simulations will be most productive if set in a regional context that addresses the interaction among metapopulations and the spatial relation among reserves or potential release sites (*28*).

The asymptotic nature of the relation between translocation success and number of animals released emphasizes the point that releasing large numbers of animals does little to increase the success of translocations. Lack of demonstrated success after translocating large numbers of animals is cause for reevaluating other variables associated with success.

The asymptotic levels do suggest that there is a minimum number of animals that should be released. Because longer translocation programs are more successful (Table 2), the minimum number may be released over several years if insufficient animals are available for a single release. Captive rearing programs that are focused on translocation should have the goal of establishing multiple self-sustaining populations so they can provide sufficient animals over a number of years and increase the success of these expensive (*2*, *3*) programs.

Those planning translocations should adopt rigorous data recording procedures (*19*, *30*). Details of translocation attempts should be assembled in a database. It is critical that both failures and successes be adequately documented. Permit-granting agencies may need to assume the role of ensuring that adequate records are kept so the database can be increased and predictability of success enhanced.

Because of the low success of translocations of small numbers of endangered, threatened, or sensitive species, even in excellent habitat quality, it is clear that translocation must be considered long before it becomes a last resort for these species—before density has become low and populations are in decline. Both these traits are associated with low chances of successful translocation. In addition, obtaining sufficient numbers of animals to achieve reasonable chances of success may be impossible. The greatest potential for establishing satellite populations may occur when a candidate population is expanding and numbers are moderate to high. These conditions are the ones that tend to make endangered species biologists relax; our analysis suggests that these conditions may point out the time for action.

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Annex 6

Glossary

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accession	a sample of a crop variety collected at a specific location and time; may be of any size.
actual evaporation	estimate of how much of the existing precipitation could be evaporated or transpired from a standard 'sward' of grass on a standard soil.
adaptation	a genetically determined characteristic that enhances the ability of an organism to cope with its environment.
adaptive landscape	a graph of the average fitness of a population in relation to the frequencies of genotypes in it: peaks on the landscape correspond to genotypic frequencies at which the average fitness is low.
adaptive radiation	evolutionary diversification of species derived from a common ancestor into a variety of ecological roles.
adaptive zone	a particular type of environment requiring unique adaptations then allowing adaptive radiation to occur.
agroecology	the use of ecological concepts and principles to study, design, and manage agricultural systems. Agroecology seeks to evaluate the full effect of system inputs and outputs by integrating cultural and environmental factors into the analysis of food production systems and to use this knowledge to improve these systems, taking into account the needs of both the ecosystem as a whole and the people within it.
agroforestry	a collective name for land-use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are deliberately used on the same land management unit as agricultural crops and /or animals, either in some form of spatial arrangement or temporal sequence.
alien species	*see* introduced species.
Allee effect	phenomenon in which survival of individuals is increased by aggregation.
allele	one of several alternatives of a gene.

allopatric	occupying different geographical ranges.
allopatric speciation	speciation via geographically separated populations.
apoendemic	polyploid endemics that are derived from widespread species of a lower ploidy level.
aquaculture	breeding and rearing fish, shellfish, etc., or growing plants for food in special ponds.
artificial insemination	a breeding technique, most commonly used in domestic animals and sometimes in captive breeding of wild animals, in which semen is introduced into the female reproductive tract by artificial means.
artificial selection	selective breeding, carried out by humans, to produce a desired evolutionary response.
assets	goods that provide a flow of services over time.
baseline data	fundamental units of basic inventory information that are crucial for biodiversity conservation planning and management. These are both biotic and abiotic and usually include: (1) the presence and/or abundance of species and other units; (2) other dependent biotic data (e.g. plant cover for macroarthropods); (3) the appropriate influential abiotic variables, and (4) human variables.
benthos	living at the bottom of the sea or a lake.
bequest value	value, defined by willingness to pay, to ensure that peoples' offspring or future generations inherit a particular environmental asset.
biocoenosis	varied community of organisms living in the same small area, e.g. in the bark of a tree.
biogeography	the scientific study of the geographic distribution of organisms.
biological control	control of pests by using predators to eat them.
biological resources	those components of biodiversity of direct, indirect, or potential use to humanity.
biome	a major portion of the living environment of a particular region (such as a coniferous forest or grassland), characterized by its distinctive vegetation and maintained by local climatic conditions.
biopesticide	pesticide made from biological sources, that is from toxins which occur naturally.
bioregion	a territory defined by a combination of biological, social, and geographic criteria, rather than geopolitical considerations; generally, a system of related, interconnected ecosystems.
biosphere reserve	established under UNESCO's Man and the Biosphere (MAB) Programme, biosphere reserves are a series of protected areas linked through a global network, intended to demonstrate the relationship between conservation and development.
biotope	small area with uniform biological conditions (climate, soil, altitude, etc.).

biotype	group of genetically identical individuals.
buffer zone	the region near the border of a protected area; a transition zone between areas managed for different objectives.
breed	a group of animals or plants related by descent from common ancestors and visibly similar in most characteristics. Taxonomically, a species can have numerous breeds.
Cambrian	the earliest period of the Palaeozoic era, extending from 500 to 550 million years ago.
captive breeding	the propagation or preservation of animals outside their natural habitat (see *ex situ* conservation), involving control by humans of the animals chosen to constitute a population and of mating choices within that population.
centre of diversity	an area with a high number of species, which might be recognized on a global, regional or local scale.
character	any recognizable trait, feature, or property of an organism.
chemicalization	accumulation of unnatural concentrations of certain chemical compounds.
clade	set of species from a common ancestral species.
clear-cutting	the removal of the entire standing crop of trees. In practice, may refer to exploitation that leaves much unsaleable material standing (e.g. a commercial clear-cutting).
clone	a set of genetically identical organisms asexually reproduced from one ancestral organism.
co-adaptation	evolution of characteristics of two or more species to their mutual advantage.
co-evolution	evolution in two or more interacting species in which the evolutionary changes of each species influence the evolution of the other species.
co-management	the sharing of authority, responsibility, and benefits between government and local communities in the management of natural resources.
common property resource management	the management of a specific resource (such as a forest or pasture) by a well-defined group of resource users with the authority to regulate its use by members and outsiders.
community	all the organisms that live in a given habitat and affect one another as part of the food web or through their various influences on the physical environment.
compensating variation	the change in income necessary to restore the consumer to its original level of utility after a price change.
competition	use or defence of a resource by one individual that reduces the availability of the resource to other individuals.

competitive exclusion	the extinction of one species by another species in the same area through competition.
conservation	judicious use and management of nature and natural resources for the benefit of human society and for ethical reasons.
conservation values	the value to society of conserving environmental resources.
cost–benefit analysis (CBA)	the appraisal of an investment project which includes all social and financial costs and benefits accruing to the project.
counterurbanization	selling your apartment and buying a tent.
crossing over	the process in which the chromosomes of a diploid pair exchange genetic material. It produces genetic recombination.
cryogenic storage	the preservation of seeds, semen, embryos, or microorganisms at extremely low temperatures, below –130 °C. At these temperatures, water is absent, molecular kinetic energy is low, diffusion is virtually nil, and storage potential is expected to be extremely long.
cultivar	a cultivated variety (genetic strain) of a domesticated crop plant.
debt-for-nature swaps	a conservation agency buys up some of a developing country's international debt ('secondary' debt) on the world's money market. The agency then promises to dispose of the debt in return for a promise from the indebted country that it will look after a conservation area.
demography	the study of birth rates, death rates, age distributions, and size of populations. It is a fundamental discipline within the larger field of population biology and ecology.
development values	the value to society of converting environmental resources to development uses.
derived demand approach	*see* Revealed Preference Approach.
diploid	having two sets of genes and two sets of chromosomes – one from the female parent, one from the male parent.
direct use value	economic values derived from direct use or interaction with a biological resource or resource system.
direct valuation approach	*see* Stated Preference Methods.
directional selection	selection leading to a consistent directional change in any character of a population through time, for example selection for larger eggs.
discounting	lowering the importance that is attached to gains and losses in the future.
dispersal	movement of organisms away from place of birth.
disruptive selection	selection favouring individuals that deviate in either direction from the population average. Selection favours individuals that are larger or smaller than average.
domestication	the process by which plants, animals or microbes selected from the wild adapt to a special habitat created for them by humans.

domesticates	organisms that have undergone domestication.
domestic biodiversity	the genetic variation existing among the species, breeds, cultivars and individuals of animal, plant and microbial species that have been domesticated, often including their immediate wild relatives.
DNA	deoxyribonucleic acid, the molecule that controls inheritance.
drift	*see* genetic drift.
ecosystem	a dynamic complex of plant, animal, fungal, and micro-organism communities and their associated non-living environment interacting as an ecological unit; the organisms living in a given environment, such as a tropical forest or a lake, and the physical part of the environment that impinges on them.
ecosystem rehabilitation	the recovery of specific ecosystem services in a degraded ecosystem or habitat.
ecosystem/ecological resilience	ecological resilience can be defined in two ways. The first is as a measure of the magnitude of disturbance that can be absorbed before the (eco)system changes its structure by changing the variables and processes that control behaviour. The second, a more traditional meaning, is as a measure of resistance to disturbance and the speed of return to the equilibrium state of an ecosystem.
ecosystem restoration	the return of an ecosystem or habitat to its original community structure, natural complement of species, and natural functions.
ecosystem services/ ecological services	ecological processes or functions which have value to individuals or society.
ecotourism	travel undertaken to witness sites or regions of unique natural or ecological quality, or the provision of services to facilitate such travel.
edge effect	processes that characterize habitat fragmentation and the concomitant creation of edges.
endemic	restricted to a specified region or locality.
equilibrium theory	theory that suggests that under natural circumstances, species addition and loss are balanced, and furthermore, that displacement from the equilibrium value results in changes in speciation or extinction rate that tend to restore the system to its equilibrium state.
equity	the opposite of inequity.
equivalent variation	an income change that is equivalent which has the same effect on utility or welfare as a price.
ethical values	statements of ethical principle that inform the private and social valuation of biological resources.
ethnobiology	study of the way plants, animals and micro-organisms are used by humans.
eukaryote	an organism whose DNA is enclosed in nuclear membranes. The vast majority of species are eukaryotic.

eutrophication	process by which a lake becomes full of phosphates and other nutrients which encourage the growth of algae and kill other organisms.
existence value	the value of knowing that a particular species, habitat or ecosystem does and will continue to exist. It is independent of any use that the valuer may make of the resource.
***ex situ* conservation**	keeping components of biodiversity alive away from their original habitat or natural environment.
external costs/externalities	external costs/benefits exist when an activity by one person causes a gain/loss of welfare to another person that is uncompensated within the market
extinction	the death of any lineages of organisms. Extinction can be local, (when it is known as extirpation) in which one population of a given species vanishes while others survive elsewhere, or total, in which all its populations vanish.
extractive reserve	forest area for which use rights are granted by governments to residents whose livelihoods customarily depend on extracting forest products from the specified area.
fallow	the period during which land is left to recover its productivity (reduced by cropping) mainly through accumulation of water, nutrients, attrition of pathogens, or a combination of all three. During this period, the land may be bare or covered by natural or planted vegetation. The term may be applied to the land itself or to the crop growing on it.
fauna	all of the animals found in a given area.
fecundity	rate at which females produce offspring.
fitness	the expected contribution of an allele, genotype, or phenotype to future generations. the fitness of genes and organisms is always relative to the other genes and organisms that are present in the same population. Usually it is measured as the average number of offspring produced by individuals with a certain genotype, relative to the number produced by other genotypes.
flagship species	popular, charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action.
flora	all of the plants found in a given area.
Flora	a book listing, with descriptions, all plants that grow in a particular area.
food web	an abstract representation of the various paths of energy flow through populations in the community.
founder effect	the loss of genetic diversity when a new colony is formed by a very small number of individuals from a larger population.
fragmentation	the breaking up of extensive landscape features into disjunct, isolated, or semi-isolated patches as a result of land-use changes.
free-rider problem of public goods	because the use of public goods by one person does not exclude others, each user has an incentive to allow others to pay the cost of the public good.

functional diversity	this can refer to two rather different concepts: the diversity of the ecological functions performed by different species, and the diversity of species performing a given ecological function.
gene	the functional unit of heredity. It is part of the DNA molecule that encodes a particular protein.
gene bank	a storage facility where germplasm is stored in the form of seeds, pollen, embryos, semen, pollen, or *in vitro* culture, or in cryogenic storage, or, in the case of a field gene bank, as plants growing in the field.
gene flow	exchange of genetic traits between populations by movement of individuals, gametes or spores.
genetic diversity	variation in the genetic composition of individuals within or among species; the heritable genetic variation within and among populations.
genetic drift	random gene frequency changes in a small population due to chance alone.
genetic erosion	loss of genetic diversity between and within populations of the same species over time; or reduction of the genetic basis of a species due to human intervention, environmental changes, etc.
genetic resources	genetic material of plants, animals or micro-organisms, including modern cultivars and breeds, primitive varieties and breeds, landraces and wild/weedy relatives of crop plants or domesticated animals, of value as a resource for future generations of humanity.
genome	all the genes of a particular organism or species.
genotype	the entire genetic constitution of an organism, or the genetic composition at a specific gene locus or set of loci.
germplasm	a set of different genotypes that may be conserved and used; the genetic material, especially its specific molecular and chemical constitution, that comprises the physical basis of the inherited qualities of an organism.
guild	a group of species found in the same place that share the same food resource. Example: the lizard species of a sand dune that feed on insects.
habitat	the space used by an organism, together with the other organisms with which it coexists, and the landscape and climate elements that affect it; the place where an animal or a plant normally lives and reproduces.
haploid	cell or organism that contains one set of chromosomes.
heterosis	situation in which the heterozygote has a higher fitness than either homozygote.
heterozygosity	genetic variability among individuals within populations and variability among populations.
homozygote	individual having two copies of the same allele at a genetic locus.
hybridization	crossing of individuals from genetically different strains, populations or species.

hybrid zone	region of reproduction among individuals of different species.
inbreeding	mating among related individuals.
inbreeding depression	a reduction in fitness and vigour of individuals as a result of increased homozygosity through inbreeding in a normally outbreeding population.
***in situ* conservation**	the conservation of biodiversity within the evolutionary dynamic ecosystems of the original habitat or natural environment.
***in situ* gene banks**	protected areas designated specifically to protect genetic variability of particular species.
income	a flow of money, goods or services deriving from the productive use of assets.
indicator species	a species whose status provides information on the overall condition of the ecosystem and of other species in that ecosystem. Species which flag changes in biotic or abiotic conditions. They reflect the quality and changes in environmental conditions as well as aspects of community composition.
indigenous peoples	people whose ancestors inhabited a place or country when persons from another culture or ethnic background arrived on the scene and dominated them through conquest, settlement, or other means and who today live more in conformity with their own social, economic, and cultural customs and traditions than with those of the country of which they now form a part. (Also: 'native peoples' or 'tribal peoples'.)
indirect use or derived value	economic value derived from the role of resources and systems in supporting or protecting activities whose outputs have direct value in production or consumption.
indirect valuation methods	*see* Revealed Preference Approach.
inefficiency	an allocation of resources is said to be inefficient if there is another allocation such that one person can be made better off without making anyone worse off.
infochemical	information in the form of chemical substances.
instrumental values	*see* Use Values.
insurance value	the value of biodiversity in maintaining ecosystem functions over a range of environmental conditions.
integrated pest management	an ecologically based strategy that relies on natural mortality factors, such as natural enemies, weather, and crop management, and seeks to control tactics that disrupt these factors as little as possible while enhancing their effectiveness.
intellectual property right	a right enabling an inventor to exclude imitators from the market for a limited time.
intergenerational equity	a core proposition is that future generations have a right to an inheritance (capital bequest) sufficient to allow them to generate a level of well-being no less than that of the current generation. Fairness in the treatment of different members of the same generation.

introduced species	a species occurring in an area outside its historically known natural range as a result of intentional or accidental dispersal by human activities. (Also known as an exotic or alien species.)
introgression	incorporation of genes of one species into a gene pool of another species.
invasive species	an introduced species which invades natural habitats.
inventorying	the surveying, sorting, cataloguing, quantifying and mapping of entities such as genes, individuals, populations, species, habitats, ecosystems and landscapes or their components, and the synthesis of the resulting information for the analysis of process.
iron law of the discount rate	species with a growth rate less than the rate of discount will be optimally driven to extinction unless extraction is regulated or the growth in the value of the species compensates for the difference.
joint products	commodities which are produced in such a way that a change in the output of one of them necessarily involves a change in the output of the other.
karyotype	characteristic chromosomes of a species.
keystone species	a species whose loss from an ecosystem would cause a greater than average change in other species populations or ecosystems processes; species that have a disproportionately large effect on other species in a community.
landrace	a crop cultivar or animal breed that evolved with and has been genetically improved by traditional agriculturalists, but has not been influenced by modern breeding practices.
land tenure	the right to exclusively occupy and use a specified area of land. Tenure may also be limited to certain resources ('resource tenure') such as timber but not to all resources in a given area. Tenure may be held by individuals, communities, government, or corporations.
large marine ecosystems	regions of ocean space encompassing coastal areas from river basins to estuaries to the seaward boundary of continental shelves and seaward margins of coastal current systems. They are relatively large regions, characterized by distinct bathymetry, hydrography, productivity and trophically linked populations.
locus	the site on a chromosome occupied by a specific gene.
macroevolution	large-scale evolution, entailing major changes in biological traits.
managed forest	productive forest where harvesting regulations are enforced, silvicultural treatments are carried out, and trees are protected from fires and diseases.
marginal values	the change in the value of a resource that is due to an incremental change in its quantity.
market failure	this occurs when market prices are not equal to the social opportunity cost of resources. External effects or externalities are evidence of market failure.

market prices	prices generated through a market mechanism. When all costs and benefits (societal) have not been taken into account, this may be less than the social cost.
maximum sustainable yield	the largest yield that can be obtained which does not deplete or damage natural resources irreparably and which leaves the environment in good order for future generations.
Mesozoic	era extending from 245 to 66 million years ago.
metapopulation	a set of partially isolated populations belonging to the same species. The different populations are able to exchange individuals and recolonize sites in which the species has recently become extinct.
microevolution	evolutionary changes on the small scale, such as changes in gene frequencies within a population.
minimum viable population	the smallest isolated population having a good chance of surviving for a given number of years despite the foreseeable effects of demographic, environmental, and genetic events and natural catastrophes. (The probability of persistence and the time of persistence are often taken to be 99% and 1000 years, respectively.)
monitoring	the intermittent (regular or irregular) surveillance to ascertain the extent of compliance with a predetermined standard or degree of deviation from an expected norm (Hellawell 1991).
monophyletic group	set of species containing a common ancestor and all its decendants.
mutation	any change in the genotype of an organism occurring at the gene, chromosome or genome level.
mutualism	interspecific relationship in which both organisms benefit. Example: flower pollination by insects.
native species	plants, animals, fungi, and micro-organisms that occur naturally in a given area or region.
natural forest management system	controlled and regulated harvesting of forest trees, combined with silvicultural and protective measures, to sustain and increase the commercial value of subsequent stands; relies on natural regeneration of native species.
natural selection	process by which the genotypes in a population that are best adapted to the environment increase in frequency relative to less well-adapted genotypes over a number of generations.
neoendemics	clusters of closely related species and subspecies that have evolved relatively recently.
net present value	the discounted value of the net benefits of use of a resource.
niche	the place occupied by a species in its ecosystem and its role: where it lives, what it feeds on and when it performs all its activities.
nitrogen fixation	biological assimilation of atmospheric nitrogen to form organic nitrogen-containing compounds.

non-consumptive value **non-use or passive use value**	the value of resources which are not diminished by their use. Values that do not require access to or active use of a biological resource by the valuer. Passive use value may imply that the resource is used by other humans whose welfare matters to the valuer. It therefore includes vicarious use value, bequest value and existence value.
non-equilibrium theory	suggests that the number of species increases or decreases depending on how the environment influences species production, exchange and extinction at any particular time.
non-exclusive goods	public goods to which it is impossible, or excessively costly, to operate any exclusion mechanism.
non-rival goods (in consumption)	public goods whose consumption by one individual does not preclude consumption by others.
normalizing selection	selection favouring individuals in the middle of the distribution of phenotypes in a population and disfavouring the extremes (also called: stabilizing selection).
nucleotide	unit building block of DNA. It consists of a sugar and phosphate backbone with a base attached.
null model	the model of no effect.
opportunity cost	the value of the best alternative use of a resource. This consists of the maximum value of other outputs we could and would have produced had we not used the resource to produce the item in question.
option value	the potential value of the resource for future (direct or indirect) use.
parapatric speciation	speciation in which the new species forms from a population contiguous with the ancestral species' geographic range.
parasite	an organism that consumes part of the tissues of its host, usually without killing the host.
parasitoid	kind of insect whose larvae develop within and kill their host.
parataxonomists	explicitly trained lay professionals who collect specimens and other information for Costa Rica's national Biodiversity Institute (INBio) from their biodiversity offices in or near the Conservation Areas.
patroendemics	restricted diploid species that have spawned younger, widespread polyploid species.
palaeoendemics	phylogenetically high-ranking taxa that might be regarded as evolutionary relicts; also ancient isolated taxa with high ploidy levels, whose diploid ancestors are extinct or unknown.
perfect complements	resources which are always used in fixed proportions to each other. Left shoes and right shoes are said to be perfect complements.
perfect substitutes	resources which are always used as replacements for each other.

Permian	last period of the Palaeozoic era, extending from 290 to 245 million years ago.
Phanerozoic	the major division of geological time during which most biodiversity has evolved and existed, 550 million years ago to the present.
phenotype	the observed traits of an organism, resulting from an interaction of its genotype and its environment.
phyletic evolution	genetic changes that occur within an evolutionary line.
phylogenetic	pertaining to the evolutionary history of a particular group of organisms.
phylum	the highest level of classification below the kingdom. For instance, Mollusca (slugs, snails, clams, etc.) constitute a phylum.
plant functional attributes	readily observable features of vegetation that are considered significant for growth, physiology and survival (for example pollination mechanisms, seed dispersal mechanisms, rooting systems).
plasmid	a genetic element that exists independently of the main DNA in the cell. In bacteria, plasmids appear as small loops of DNA, able to pass between cells independently.
Pleistocene	the span of geological time preceeding the Recent epochs, during which the human species evolved. It began 2.5 million years ago and ceased with the end of the last Ice Age 10 000 years ago.
ploidy	number of chromosome sets contained by a cell: 1 = haploid, 2 = diploid and so on.
policy failure	occurs when government policies do not correct for market failures.
polyploid	organism containing two or more sets of genes or chromosomes.
population	a group of individuals with common ancestry that are much more likely to mate with one another than with individuals from another such group.
population viability analysis (PVA)	a comphrehensive analysis of the many environmental and demographic factors that affect survival of a population, usually small.
potential evapotranspiration	measure of total heat flux.
precautionary principle (PP)	if the costs of current activities are uncertain, but are potentially both high and irreversible, the precautionary principle holds that society should take action before the uncertainty is resolved.
predator	an animal that kills and eats animals.
preferences	these are the orderings of different bundles of goods according to the wants of the consumer in question. Preferences may be influenced by ethical values, culture, age, gender and other political, social and demographic variables.
primary forest	relatively intact forest that has been essentially unmodified by human activity.
primary value	the value of the system characteristics upon which all ecosystem functions depend.

private opportunity cost	the opportunity cost faced by an individual agent of using a resource (not including any externalities).
private value	the value to the private agent of using or refraining from using a resource.
production function	this describes the outputs that may be obtained from combining different quantities of inputs.
prokaryote	cell without a distinct nucleus. Bacteria are prokaryotic.
proportional sampling	the alternative to saturation; when the local richness increases proportionately with the size of the regional species pool when the sample area is held constant.
protected area	a legally established land or water area under either public or private ownership that is regulated and managed to achieve specific conservation objectives.
public good	a good which, once provided to one user, must be provided in the same amount to all users due to its non-rival and non-excludable nature.
quasi-option value	the value of the future information made available through the preservation of a resource.
Quaternary period	the second and last period of the Cenozoic era extending from 2.5 million years ago to the present.
rational expectations	the hypothesis that decision-makers base their decisions on predictions which contain no systematic errors.
recalcitrant seed	seed that does not survive drying and freezing.
reciprocal externality	these are externalities where all parties using some resource impose external costs on all others.
resource	a substance or place required by an organism for its growth, maintenance and reproduction.
revealed preference approach	these approaches, which include derived demand approaches and indirect valuation methods, infer values from data on behavioural changes in actual markets related in some way to the missing market(s).
rights	entitlements assured by custom, law or property.
risk	the outcome of an action is said to involve risk where: the set of all possible outcomes of that action is known, and where the probability distribution of all possible outcomes is also known.
safe minimum standard	a restriction (taboo, prohibition, harvesting season) which limits the use of resources to levels that are thought to be safe, e.g. conservation of a sufficient area of habitat to ensure the continued provision of ecological functions and services, at the ecosystem level.
schizoendemics	vicariant species of equal ploidy level, resulting from either gradual or rapid divergence.

scramble competition	exploitation of a resource by one individual that reduces the availability of that resource to others. Usually also called 'indirect competition', because there is no direct interaction between competing individuals (see direct competition).
secondary forest	natural forest growth after some major disturbance (eg. logging, serious fire, or insect attack).
secondary value	the value of ecosystem functions.
seed bank	a facility designed for the *ex situ* conservation of individual plant samples through seed preservation and storage.
sibling species	species so similar to each other as to be difficult to distinguish by human observers.
silviculture	the science of cultivating forest crops (usually timber), based on a knowledge of forest tree characteristics.
social value	*see* Social Opportunity Cost.
social opportunity cost	the opportunities forgone by society, including externalities, in using a resource in some way. For biological resources this may be different than the market price of that resource.
speciation	separation of one population into two or more reproductively isolated, independent evolutionary units.
species diversity	the number and variety of species found in a given area in a region.
species richness	the number of species within a region. (A term commonly used as a measure of species diversity, but technically only one aspect of diversity.)
species selection	the differential multiplication and extinction of species as a result of differences in certain traits possessed by the organisms belonging to the various species, and causing a spread of the favouring traits through the fauna or flora as a whole.
stabilizing selection	selection favouring individuals in the middle of the distribution of phenotypes in a population and disfavouring the extremes. Also called normalizing selection.
stated preference methods	a survey instrument is designed in which a market-like situation is constructed. These include direct valuation approaches, like contingent valuation method.
stochastic	referring to patterns or processes resulting from random factors.
strong sustainable development principle	the opportunity set for future generations can only be assured if the level of biodiversity they inherit is no less than that available to present generations.
subsidies	government grants to suppliers of goods or services.
subspecies	groupings or populations within a species that are distinguishable by morphogical characteristics or, sometimes, by physiological or behavioural traits.
surrogate markets	markets used in place of the missing markets for environmental resources. Surrogate markets are at least existing markets for resources with some of the properties of the non-marketed resource being valued.

sustainable development	development that meets the needs and aspirations of the current generation without compromising the ability to meet those of future generations.
sympatric	occurring in the same place.
sympatric speciation	speciation via populations with overlapping geographic ranges.
taxon (pl. **taxa**)	the named classification unit (e.g. *Mus musculus*, Muridae, or Mammalia) to which individuals, or set of species, are assigned. Higher taxa are those above the species level.
Tertiary period	the first period of the Cenozoic era, beginning 66 million years ago and closing with the start of the Pleistocene, 2.5 million years ago.
tetraploid	referring to a cell or organism containing four sets of chromosomes (*see* ploidy).
theory of local existence	suggests that the number of species increases or decreases depending on how the environment influences species production, exchange and extinction at any particular time.
threatened species	species that are, often genetically impoverished, of low fecundity, dependent on patchy or unpredictable resources, extremely variable in population density, persecuted or otherwise prone to extinction in human-dominated landscapes.
tissue culture	a technique in which portions of a plant or animal are grown on an artificial culture medium (also '*in vitro* culture').
total economic value	the sum of use and non-use values with due consideration of any trade-offs or mutually exclusive uses or functions of the resource/habitat in question.
total environmental value	it is a function of primary value and total economic value.
tracheophyte	a plant with tracheae or vessels such as flowering plants and ferns.
translocation	switching of a segment of a chromosome to another chromosome.
triploid	referring to a cell or organism containing three sets of chromosomes (*see* ploidy).
trophic	pertaining to food or nutrition.
umbrella species	species whose occupancy area (plants) or home range (animals) are large enough and whose habitat requirements are wide enough that, if they are given a sufficently large area for their protection, will bring other species under that protection.
uncertainty	the outcome of an action is said to involve uncertainty where the set of all possible outcomes of that action is unknown, and where the probability distribution of all possible outcomes is also unknown.
unidirectional externality	these are externalities in which the external costs or benefits of the resource use are 'one way.'
use value	values obtained through the use of a resource. This includes direct and indirect use values and instrumental values. Preservation in this sense is as much a use as development

utility function	a description of the way in which the well-being of individuals depends on different combinations of goods and services consumed.
valuation	this is a method for determining the importance of environmental consequences of economic activity that are not taken into account in market transactions.
variance	a statistical measure of the dispersion of a set of values about its mean.
variety	*see* cultivar.
vicariant patterns	when several taxa are subdivided by the same tectonically and climatically produced barriers to dispersal.
vicarious use value	altruistic value of benefits received by friends, relatives or others who are users of a resource. This is a passive use value.
voucher specimens	collections of organisms that are maintained to provide permanent, physical documentation of species identifications and associated data resulting from inventories.
weak complementarity	this describes a relation between a marketed/produced good and a non-marketed environmental good. If consumption expenditure is zero on the marketed/produced good, then the marginal utility of the public good is also zero.
welfare	an index of well-being.
wild relative	plant or animal species that are taxonomically related to crop or livestock species and serve as potential sources for genes in breeding of new varieties of those crops or livestock.
willingness to pay (WTP)	WTP is the amount an individual is willing to pay to acquire some good or service. This may be elicited from stated or revealed preference approaches.
willingness to accept (WTA)	WTA is the amount of compensation an individual is willing to take in exchange for giving up some good or service. This may be elicited from stated or revealed preference approaches.